Tácticas comportamentales de forrajeo y apareamiento y dinámica poblacional de dos especies de otáridos simpátricas con tendencias poblacionales contrastantes

Valentina Franco Trecu

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ÍNDICE GENERAL

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Resumen

Comprender las causas que determinan la dinámica en poblaciones salvajes es fundamental para conservarlas y diseñar prácticas de gestión eficaces. El estudio del comportamiento ayuda a entender los mecanismos implícitos en los patrones observados, por lo que su incorporación en los modelos poblacionales permite obtener predicciones más fiables. En este contexto, conocer las diferentes tácticas o estrategias individuales, ya sea en la adquisición de recursos como en la reproducción, dentro de una población adquiere gran relevancia. En Uruguay se reproducen dos especies de otáridos, el león marino (*Otaria flavescens*-LM) y el lobo fino (*Arctocephalus australis*-LF). Estas especies de ecología similar, poseen tasas de crecimiento poblacional contrastantes, desconociéndose los mecanismos que las determinan. Dado que para comprenderlos es importante investigar la presencia y diversidad de tácticas en sus poblaciones el objetivo de esta tesis fue evaluar la existencia de tácticas alimenticias y reproductivas a nivel individual en el LM y en el LF, estimando además sus abundancias y tendencias poblacionales en los últimos 60 años. La composición de la dieta fue estudiada complementando métodos tradicionales con la técnica de isótopos estables por medio de modelos de mezcla (*Mixing models*). Además, el patrón de uso del hábitat fue estudiado utilizando transmisores satelitales (GPS) y su comportamiento de buceo por medio de sensores de presión. Se evaluó el grado de especialización alimenticia individual en ambas especies utilizando un tejido de crecimiento continuo (bigotes) que integra una ventana temporal de aproximadamente 2-3 años. Por otro lado, las estrategias reproductivas de los machos en ambas especies fueron estudiadas combinando observaciones comportamentales sobre individuos marcados con su éxito reproductivo, a través de análisis de paternidad (microsatélites). En relación a la demografía se realizaron censos aéreos para estimar la abundancia actual, lo que sumado a datos históricos permitió obtener la tendencia poblacional en cada colonia reproductiva para cada especie. Finalmente, debido a que el LM tuvo diferentes tendencias en las dos colonias de cría, se compararon diversos parámetros para intentar explicarlas. En relación a los hábitos alimenticios se encontró que el LF utilizó áreas de alimentación alejadas de la costa (~500km de las colonias), consumiendo presas y realizando buceos principalmente pelágicos, siendo una población compuesta de individuos generalistas. Por otro lado, el LM utilizó áreas de alimentación costeras, consumiendo principalmente recursos demersales, generando un importante solapamiento con las pesquerías costeras, siendo una población compuesta por individuos con un alto grado de especialización. En relación al comportamiento reproductivo, categorizamos el sistema de apareamiento del LF en un sistema de Lek, a diferencia de lo previamente descrito. El LM presentó la coexistencia de dos tipos de poliginia (defensa de hembras y defensa de recursos), siendo la primer colonia donde se reportó simultáneamente más de un sistema de apareamiento. En ambas especies se detectaron tácticas reproductivas alternativas que se tradujeron en elevadas varianzas en el éxito reproductivo de los machos. Finalmente, durante los últimos 60 años la tendencia poblacional total del LF fue positiva (tasa ~1.5 anual), mientras la del LM fue negativa (-2 anual). Sin embargo, el LM presentó una tendencia estable en Cabo Polonio y una decreciente en Isla de Lobos (-5 anual). Si bien las crías crecieron más rápido en Isla de Lobos, tuvieron una supervivencia menor, lo que podría ser explicado por una mayor proporción de machos en esta colonia. En esta especie los machos satélites realizan comportamientos de infanticidio, donde el secuestro de crías generalmente determina su muerte, ya sea por agresiones o por inanición. Los efectos acumulados de las extracciones realizadas únicamente en Isla de Lobos probablemente hayan generado una desestructuración social en esta colonia hasta el punto donde un efecto del tipo Allee podría estar obstaculizando la recuperación del LM en Uruguay. Por medio de diversos enfoques, los resultados de esta tesis pretenden aportar de forma significativa a la conservación de ambas poblaciones en Uruguay, brindando herramientas para el manejo y gestión de las mismas.

Estructura de la tesis

La primera parte de la tesis contiene la *Introducción general*, donde se expone el marco teórico relacionado con los objetivos ya sea generales como específicos. Posteriormente se presentan 4 capítulos, siendo cada uno de ellos las investigaciones realizadas en relación a cada objetivo específico. En el ***Capítulo 1*** se estudió el comportamiento alimenticio de hembras lactantes de ambas especies por medio de métodos tradicionales (análisis de fecas) y análisis de isótopos estables para estimar la composición de la dieta por medio de modelos de mezcla. Para cumplir con este objetivo se realizó una colaboración e intercambio con el Dr. Andrew Parnell de School of Mathematical Science, University College Dublín, Irlanda. Además se estudiaron los patrones de uso del hábitat mediante seguimiento telemétrico (GPS) y el comportamiento de buceo para estimar las áreas de forrajeo generándose una colaboración con el Laboratorio ECOTONO, Universidad Nacional del Comahue, Argentina donde participaron el Dr. Juan Manuel Morales y uno de sus estudiantes Pablo Alarcon. En el ***Capítulo 2*** se evaluó el grado de especialización trófica a nivel individual en ambos sexos de cada especie. Este objetivo se llevó a cabo por medio del análisis de isótopos estables de C y N en vibrisas, que por ser un tejido de crecimiento continuo integra información de los hábitos tróficos de 2 a 3 años. Para cumplir con el mismo realicé una pasantía de trabajo en el laboratorio de Ecología trófica de pinnípedos del Centro Interdisciplinario de Ciencias Marinas, Instituto Politécnico Nacional (CICIMAR - IPN), La Paz, México. Por otro lado, en el ***Capítulo 3*** se evaluó la presencia de tácticas reproductivas de los machos y su efecto en el éxito reproductivo, por medio de la combinación de observaciones comportamentales sobre individuos marcados de cada especie y técnicas moleculares como el análisis de paternidad (microsatélites). Los resultados conllevaron a re-clasificar los sistemas de apareamiento para ambas especies. Para cumplir con estos objetivos realice una pasantía de trabajo en el Laboratorio de Ecología Molecular de la Universidad Autónoma de Baja California, México bajo la supervisión de la Dra. Yolanda Schramm y la colaboración de la Dra. Paula Costa como parte de una cooperación. Finalmente, el ***Capítulo 4*** se investigaron diversos aspectos de la demografía de ambas poblaciones de otáridos (lobos y leones marinos). Se realizaron censos aéreos para tomar fotografías de las colonias reproductivas y estimar la abundancia y estructura poblacional de cada especie. Dado que es necesario que los conteos sean realizados por observadores independientes se contó con la participación y colaboración del Dr. Enrique Crespo del Laboratorio de

Mamiferos Marinos del CENPAT - Argentina y de la Dra. Florencia Grandi de su mismo laboratorio y del Dr. Massimiliano Drago (Centro Universitario Regional Este). Se recopilaron datos de abundancia históricos para estimar la tendencia poblacional en cada colonia, así como las tasas intrínsecas de incremento. Para el león marino particularmente se evaluaron diferentes hipótesis para explicar las tendencias opuestas entre ambas colonias de cría en Uruguay. Dado que uno de los objetivos de la tesis era estimar los parámetros poblacionales para generar matrices y modelar la dinámica de la población de cada especie a futuro, se marcaron más de 1.200 individuos entre el año 2004 y el 2012. Sin embargo, no fue posible cumplir con este objetivo debido a que los modelos de captura-marcaje-recaptura de ambas especies realizaron estimados de sobrevivencia adulta muy bajos (Ver Anexo). A pesar de que se intentó, durante el 2013 y 2014, obtener mayor número de recapturas visuales para mejorar los modelos con mayor cantidad de años de muestreo, no fue posible debido a que la DINARA (Dirección Nacional de Recursos Acuáticos), organismo estatal encargado de la gestión del recurso no otorgó los permisos de investigación en ambas temporadas. Los resultados de los modelos de captura-recaptura (sobrevivencia) y de la proyección poblacional futura representan un aporte significativo para un correcto manejo de las poblaciones de pinnípedos en Uruguay como base sólida para su gestión. A pesar del interés que representa esta información para la DINARA, la respuesta de los expedientes donde se solicitan los permisos fue demorada más de 7 meses por motivos desconocidos impidiendo efectuar los muestreos de campo necesarios (censos aéreos 2014, marcaje de crías y recapturas visuales de individuos marcados en las colonias reproductivas). La tesis concluye con una *Discusión general* donde se exponen los aportes realizados en diferentes aspectos de la ecología del comportamiento, así como en relación a la biología de ambas especies de otáridos. De esta forma se pretende realizar un aporte significativo al conocimiento científico de ambas especies, recursos importantes de nuestro país, para contribuir a su conservación.

INTRODUCCIÓN GENERAL

Comprender los mecanísmos que determinan la dinámica espacial y temporal de las poblaciones naturales es el objetivo central de la ecología de poblaciones y es información imprescindible para realizar un correcto manejo de los recursos naturales. Es ampliamente aceptado que la interacción de tres grandes procesos incide en dicha dinámica: la variabilidad intrínseca de los hábitats naturales, las interacciones bióticas y el efecto de los impactos antrópicos (ej. destrucción y transformación de hábitats) (Bulleri and Chapman 2010; Millenium-Ecosystem-Assessment 2005). Estos tres grandes procesos co-determinan los cambios en las abundancias de los recursos a diversas escalas espacio-temporales, afectando la dinámica de las poblaciones naturales, desencadenando en algunos casos la extinción de especies (Millenium-Ecosystem-Assessment 2005). En los ecosistemas marinos y costeros, donde habita un alto porcentaje de la población humana, la degradación de los hábitats está principalmente asociada a la sobreexplotación de recursos pesqueros así como a las actividades comerciales y turísticas (Bulleri and Chapman 2010; Dobson et al. 2006; Sala and Knowlton 2006). Además, se reconoce el impacto creciente del cambio climático sobre estos ambientes en relación al aumento de la temperatura del agua, del nivel del mar y a la disminución de las cubiertas de hielo (Learmonth et al. 2006). La multiplicidad y la complejidad de los efectos de las actividades humanas sobre las comunidades frecuentemente limita la posibilidad de realizar predicciones fiables sobre la dinámica espacio-temporal de las poblacionales animales (Halpern et al. 2008), sobre todo cuando las mismas estuvieron bajo el efecto de la explotación. La magnitud de los cambios generados como consecuencia de la explotación es tal, que incluso sus efectos podrían resultar irreversibles aunque la misma haya cesado (Petraitis and Dudgeon 2004). En este contexto, comprender las causas que provocan cambios en la dinámica poblacional es fundamental para la conservación y el diseño de prácticas de gestión eficaces (Fig. 1).

En este proceso de degradación y modificación de hábitats marino-costeros, los depredadores tope son uno de los grupos más afectados, pues los mismos generalmente poseen poblaciones locales relativamente pequeñas con bajas tasas de crecimiento demográfico. Entre ellos destacan los pinnípedos que representan uno de los taxones animales que más ha sufrido y sufre el efecto de las actividades humanas (explotación comercial) y que se enfrenta a un elevado riesgo de extinción (Bonner 1982; Estes et al. 2006; IUCN 2013; Perrin et al. 2009). Diversos modelos sugieren que la disminución de los servicios ecosistémicos se acelera a medida que se ven afectadas las poblaciones de niveles tróficos superiores (Dobson et al. 2006; Loreau et al. 2001; Naeem 2002; Naeem and Hawkins 1994), ya que en general, los servicios ecosistémicos provistos por las mismas se perderán antes de los proporcionados por las poblaciones de especies a niveles tróficos inferiores (Dobson et al. 2006).

Si bien existen diversos enfoques para estudiar la dinámica de las poblaciones, se ha observado que la incorporación explícita de información comportamental en los modelos de dinámica de poblaciones animales cambió notoriamente la dinámica y la distribución esperada (Gerber and VanBlaricom 2001; Gonzalez-Suarez and Gerber 2008). De esta forma, se sugiere que los datos de comportamiento en la modelación poblacional mejora la comprensión de los patrones observados o los mecanismos implícitos en ellos, y permite obtener predicciones más fiables. Sin embargo, la posibilidad de incorporar esta información depende de la existencia de datos detallados a nivel individual que raramente están disponibles para la mayor parte de las poblaciones de vertebrados (Clutton-Brock and Sheldon 2010). En este contexto, conocer las diferentes tácticas o estrategias individuales, ya sea en la adquisición de recursos como en la reproducción, dentro de una población adquiere gran relevancia.

Las estrategias y tácticas alternativas refieren a la presencia de dos o más variantes discretas de cierto comportamiento, entre un grupo de individuos dentro de una población, que tienen un mismo objetivo, como puede ser la obtención de alimento o de parejas reproductivas (Brockmann 2001; Taborsky et al. 2008; Wolff 2008). Si bien la existencia de variantes conductuales discretas están frecuentemente asociadas a características morfológicas y fisiológicas de los individuos, existe una clara distinción entre lo que se denomina estrategia y táctica. Cuando los fenotipos alternativos son producto de variantes genéticas nos referimos a estrategias, mientras que cuando las variantes se relacionan con las condiciones ambientales - individuales (condición-dependiente), nos referimos a tácticas (Brockmann 2001; Gross 1996). En cualquier caso, estas variantes discretas permanecen en las poblaciones en frecuencias que no se pueden explicar por mutación o simples errores (Ford 1940).

Las tácticas (o estrategias) comportamentales denotan el conjunto organizado de acciones que en un contexto dado permiten a los individuos adquirir la energía necesaria para satisfacer sus necesidades metabólicas y maximizar su fitness (Krebs and Davies

1991). Las tácticas desarrolladas para adquirir la energía y reproducirse son los mecanismos proximales a través de los cuales las fluctuaciones ambientales, de origen natural o antrópico, se traducen en cambios en las tasas demográficas y afectan la dinámica espacio-temporal de las poblaciones animales (Fig. 1). Éstas tácticas de comportamiento tienen consecuencias directas sobre el fitness estando sujetas a la acción (y reflejando el resultado) de la selección natural (Krebs and Davies 1991).

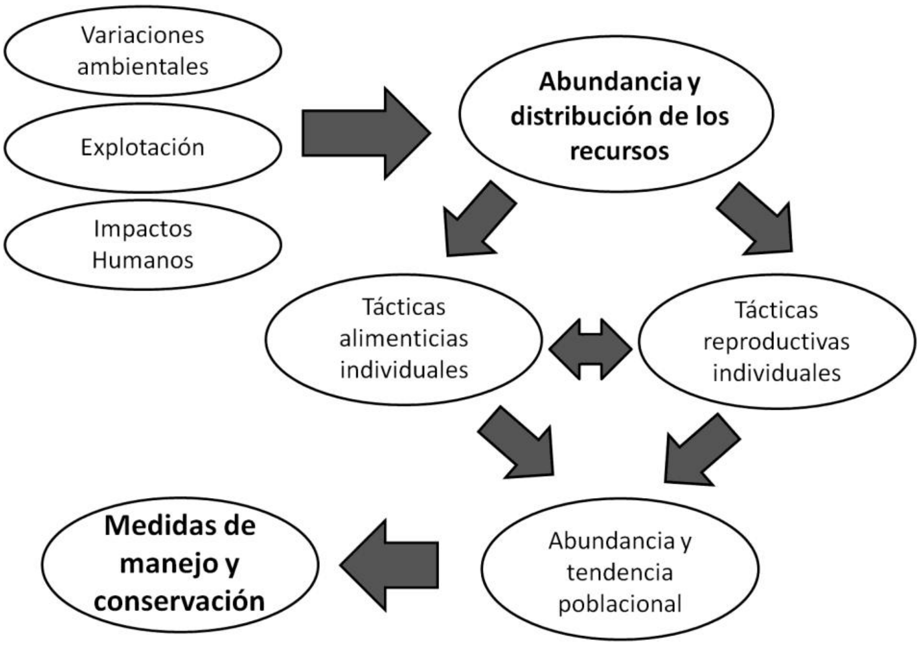

Figura 1. Relaciones entre los factores que generan variación en la abundancia y distribución espacial de recursos y en la calidad de hábitats, y afectan las tácticas de adquisición de recursos y de apareamiento, mecanismos a través de los cuales, dichos cambios inducen variaciones en los parámetros demográficos que se traducen en tendencias poblacionales a largo plazo y éstas condicionan las medidas de manejo para su conservación.

Tácticas de forrajeo

Numerosos trabajos muestran que la abundancia global y la heterogeneidad espacial de los recursos tróficos condicionan la potencial distribución espacial de los consumidores (Coll and Libralato 2012; Coll et al. 2009; Estes et al. 2003; Ferger et al. 2014). Sin embargo, más allá de los patrones generales, es importante considerar la presencia de tácticas de forrajeo a nivel individual ya que pueden afectar el patrón de uso de hábitats y de recursos tróficos a nivel poblacional (Stephens and Krebs 1986). El grado de especialización trófica (o tácticas de forrajeo) de los individuos de una poblaciones refiere a el grado de selectividad o a la preferencia por una fracción limitada de los recursos tróficos disponibles (Bolnick et al. 2003).

En los últimos años, se ha puesto de manifiesto en muchas especies de vertebrados que la amplitud del nicho trófico poblacional no tiene por qué reflejar la amplitud individual, ya que no puede suponerse que los individuos realicen un uso homogéneo de dichos recursos (Bolnick et al. 2011; Bolnick et al. 2003). Muchas poblaciones son consideradas generalistas porque utilizan una amplia diversidad de recursos, pero dichas poblaciones en muchos casos son la sumatoria de individuos especialistas segregados en el espacio de nicho (Bolnick et al. 2007; Bolnick et al. 2003; Bolnick et al. 2002). Aunque la especialización individual tradicionalmente era considerada rara y de poca influencia en los procesos ecológicos a nivel poblacional, recientemente se han demostrado que es más frecuente de lo esperado (Estes et al. 2003; Tinker et al. 2007; Villegas-Amtmann et al. 2008; Villegas-Amtmann et al. 2013) y ha sido reportada en especies de teleósteos (Brodersen et al. 2012), tiburones (Matich et al. 2011), aves (Woo et al. 2008), tortugas marinas (Vander Zanden et al. 2010) y carnívoros (Newsome et al. 2010). De hecho, es cada vez más reconocida como un proceso ecológico y evolutivo que posee importantes influencias en la dinámica poblacional y en la estructura de las comunidades (Araujo et al. 2011; Bolnick et al. 2011; Bolnick et al. 2003). La diferenciación trófica intra-poblacional resultante de la coexistencia de tácticas individuales de forrajeo que determinan un uso diferencial del hábitat, podría constituir una respuesta adaptativa frente a la variación espacio-temporal de los recursos alimenticios (Bolnick et al. 2003; Schindler et al. 1997).

Tácticas reproductivas

El sistema de apareamiento integra las interacciones entre los individuos de una población sexual y conforma el contexto en que tiene lugar la unión de los gametos, considerando la cantidad y la forma de adquisición de las parejas y los patrones de cuidado parental de cada sexo (Emlen and Oring 1977). El sistema de apareamiento más común en los mamíferos es la poliginia (Clutton-Brock 1989). El grado de agregación espacial y de la sincronía en la receptividad de las hembras son factores clave que determinan el grado de poliginia en una población, ya que dichos factores determinan el grado en que los machos pueden monopolizar el acceso a las cópulas (Emlen and Oring 1977; Ims 1990; Shuster and Wade 2003). El acceso a las parejas puede ocurrir directamente por medio de la defensa de las hembras (poliginia de defensa de hembra) o indirectamente por medio de la defensa de los recursos (poliginia de defensa de recurso) (Emlen and Oring 1977). Por otro lado, en los sistemas de lek, los machos se agrupan y defienden territorios muy pequeños que raramente contienen recursos, pero que son comúnmente utilizados por las hembras (Clutton-Brock 1989; Fiske et al. 1998; Shuster and Wade 2003).

A pesar del tipo de sistema de apareamiento poligínico observado en una población, los machos pueden adoptar diferentes tácticas individuales de comportamiento (Gross 1996; Oliveira et al. 2008) asociadas a rasgos fenotípicos como la experiencia reproductiva previa o la condición corporal (Harcourt et al. 2007), o con diferencias en el rango social dentro de la población (Rodriguez-Llanes et al. 2009; Wiszniewski et al. 2011). Estas tácticas reproductivas individuales comúnmente se describen como comportamientos contrastantes, tales como dominante *vs.* subordinado o territorial *vs.* satélite (McGuire and Getz 2010; Young et al. 2007). Las tácticas reproductivas se definen de acuerdo al éxito reproductivo alcanzado por los individuos que la componen. Los machos más competitivos y en mejor condición corporal adoptarán la táctica comportamental dominante, alcanzando un éxito reproductivo mayor, mientras las tácticas alternativas con un éxito reproductivo inferior, son generalmente adoptadas por aquellos individuos que no satisfacen los costos que impone la táctica dominante (Wolff 2008). Si bien algunos estudios han evaluado el éxito que alcanza cada táctica reproductiva por medio de observaciones de comportamiento (McGuire and Getz 2010), estas evaluaciones deberían complementarse con herramientas moleculares, debido al sesgo de los datos comportamentales en la estimación del éxito reproductivo (Pörschmann et al. 2010; Westneat 2000). Según mi conocimiento, el aporte de evidencia utilizando métodos moleculares para cuantificar el éxito reproductivo alcanzado por machos de mamíferos con distintas tácticas reproductivas es escaso (Young et al. 2007).

Recientemente, se ha demostrado en varias especies de mamíferos que los machos pueden cambiar la táctica reproductiva en función de la densidad poblacional o de la variación de los recursos tróficos (Schradin et al. 2012). Ciertas condiciones pueden generar que adoptar una táctica determinada sea más ventajoso para algunos individuos; por ejemplo en función de su propia condición corporal, los machos de una población podrían defender un territorio o desarrollar una táctica alternativa de acceso a las hembras. Así, si la distribución espacial o temporal de los recursos críticos cambiase entre años o áreas, el potencial poligámico del medio también se modificaría, y de la misma forma cambios en la densidad poblacional o en la sincronía reproductiva de las hembras modificarían la posibilidad de monopolizar recursos o parejas (Carranza 2000). Esta flexibilidad de las tácticas reproductivas permitiría atenuar los impactos de la variabilidad demográfica y ambiental en poblaciones pequeñas.

¿Cómo se traducen las decisiones individuales en las tácticas alimenticias y reproductivas y qué consecuencias tienen a nivel poblacional? El fitness individual depende del desempeño y/o condición de los organismos en un contexto ambiente-específico, ya que es el resultado de confrontar un fenotipo con el ambiente donde vive el organismo. Si bien es un concepto central en ecología evolutiva, el fitness ha sido medido con una diversidad de métricos o índices, siendo los más frecuentemente utilizados la tasa de crecimiento poblacional (λ o R_0) y el éxito reproductivo individual (Dugdale et al. 2010). Cuando la eficacia o el fitness individual se estima a través del número total de descendientes, se evidencia una gran disparidad en el éxito reproductivo entre los individuos de una población, ya que una pequeña fracción de los mismos es responsable de gran parte de la progenie (Fig. 2) (Dugdale et al. 2010). Esta heterogeneidad en la contribución a la descendencia revela diferentes estrategias o tácticas comportamentales en la obtención de los recursos (alimentos, territorios, parejas) y la variación entre individuos adquiere un importante valor ecológico y evolutivo que puede reflejarse en la dinámica de la población. Dicha heterogeneidad en el éxito individual es frecuente en especies de zooplancton, insectos, peces, reptiles y mamíferos (Clutton-Brock and Parker 1992; Miller et al. 2010; Rios-Cardenas et al. 2007; Tinker et al. 2008) aunque hasta el momento no se han encontrado explicaciones mecanicistas generales a estos patrones basadas en estrategias o tácticas comportamentales.

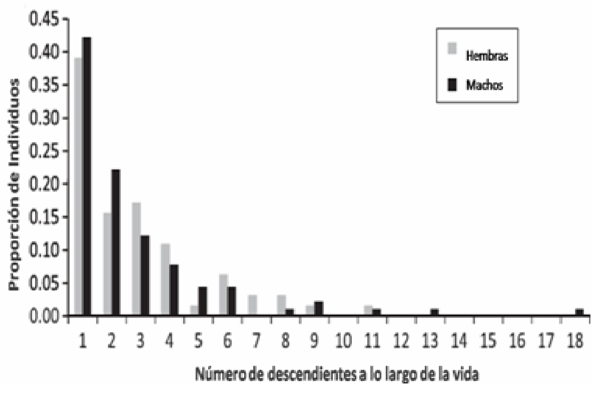

Figura 2. Disparidad en el fitness individual, medido como éxito reproductivo entre los individuos de una población de tejones europeos (*Meles meles*), diferenciado por el sexo de la progenie. Obtenido de Dugdale et al. 2010

Antecedentes específicos a los modelos de estudio

En las últimas décadas, varias poblaciones de pinnípedos (focas, lobos y leones marinos) ha experimentado severas reducciones de sus abundancias locales o globales y la mayor parte de las que aún son abundantes muestran evidencias de impactos negativos que a la larga podrían resultar insostenibles (IUCN 2013). A parte de la explotación comercial, que en un intervalo de tiempo relativamente corto ha causado la extinción de algunas especies y la drástica reducción de otras, una de las principales causas de la no recuperación de las poblaciones de pinnípedos tras el cese de la explotación es la reducción de la disponibilidad de alimento causada por la sobreexplotación pesquera (Davidson et al. 2012; Kovacs et al. 2012; Perrin et al. 2009). Además, al impacto pesquero se le debe añadir el cambio climático y otros fenómenos ambientales de tipo estacional o periódico susceptibles de actuar de modo aditivo a la pesca produciendo alteraciones, ya sean periódicas o a largo plazo, en la productividad primaria y la consecuente disponibilidad de alimento (Chavez et al. 2003; Davidson et al. 2012; Evans and Raga 2002; Trillmich and Ono 1991; Trites et al. 2007). El efecto de estos procesos sobre la supervivencia de los individuos y sus repercusiones sobre la dinámica poblacional es bien conocido. La fertilidad, la calidad de la leche, así como la resistencia a las enfermedades y la supervivencia de los neonatos, entre otras variables, inciden en las tasa de crecimiento poblacional de los pinnípedos y se ven severamente afectadas por la disponibilidad de alimento (Guinet et al. 1998; Lunn and Boyd 1993; Lunn et al. 1994; Soto et al. 2004; Trillmich and Ono 1991; Trites and Donnelly 2003). Las relaciones entre las tácticas alimenticias y el éxito reproductivo han sido estudiadas en varias especies de otáridos - lobos y leones marinos (e.g. Beauplet et al. 2004; Soto et al. 2006). Se ha reportado que diversos componentes de la estrategia alimenticia, tales como la duración de los viajes de forrajeo, el patrón de buceo y el tipo de presas consumidas afectan la calidad de la leche producida por las hembras, la masa de la cría al momento del destete y la sobrevivencia juvenil en varias especies de otáridos (Arnould and Boyd 1995; Luque et al. 2007; Soto et al. 2006). También se han encontrado relaciones entre parámetros demográficos, como la sobrevivencia juvenil - adulta y el éxito reproductivo, con variables ambientales correlacionadas con la abundancia de recursos tróficos consumidos por los otáridos tales como las anomalías térmicas y la clorofila (Beauplet et al. 2005).

Dentro de los pinnípedos, se ha reportado la existencia de especialización individual en relación al uso de recursos tróficos y a las tácticas de reproducción. Las hembras de los otáridos amamantan a su cría a lo largo de varios meses, generalmente alcanzando un año de lactancia, lo que determina que las hembras de estas especies se alimenten en zonas relativamente cercanas a las islas ocupadas por sus cachorros (Berta et al. 2006). Esta asociación ha facilitado el estudio de los hábitos alimenticios de este sexo por medio de telemetría satelital y registros de buceo, motivo por el que de forma más frecuente la especialización individual en este grupo ha sido reportada en hembras. En varias especies de otáridos, se ha evidenciado diversificación de los hábitos alimenticios en las hembras reproductivas, ya sea en relación a la fidelidad a las áreas de forrajeo, incluso entre años consecutivos (Bonadonna et al. 2001; Chilvers et al. 2005, 2006), selección de especies presas particulares (Bowen et al. 2002) y uso del hábitat reflejado en patrones individuales de buceo (Villegas-Amtmann et al. 2008; Villegas-Amtmann et al. 2013). Sin embargo, el uso de otras técnicas, como el análisis de isótopos estables, ha permitido ampliar dicha evaluación a ambos sexos, como ha sido el caso del lobo fino Antártico y subantártico (*Arctochepalus gazella* y *A. tropicalis*) (Kernaléguen et al. 2012). En el caso de especies simpátricas, la especialización trófica podría surgir de la segregación en las áreas de alimentación o en el uso de recursos entre especies, generándose así una diferenciación a nivel individual (Franco-Trecu et al. 2012; Jeglinski et al. 2013; Páez-Rosas et al. 2012; Páez-Rosas et al. 2014). De esta forma, es posible evaluar la diversificación en las área de forrajeo y nivel trófico de las presa consumidas a nivel individual en cada población simpátrica, utilizando los isótopos estables de carbono y nitrógeno ($\delta^{13}C$ y $\delta^{15}N$) respectivamente. Esto se debe a que la composición isotópica del tejido del consumidor es una función de $\delta^{13}C$ y $\delta^{15}N$ de las especies presa consumidas y de la proporción que es asimilada (Gannes et al. 1997). Al pasar de un nivel trófico al siguiente, la materia orgánica asimilada se ve enriquecida de una manera predecible en la señal isotópica del nitrógeno, debido a la excreción preferencial de los isótopos ligeros (DeNiro and Epstein 1981). Por lo tanto, la señal isotópica de carbono proporciona información sobre la fuente de carbono que sustenta la red trófica a la que pertenece la especie de interés (DeNiro and Epstein 1978), y permite distinguir entre hábitos alimenticios bentónico-costero o pelágico-oceánico. Además, ya que la composición isotópica de cada tejido cambia en el tiempo de acuerdo con su tasa de renovación, tejidos con diferente tasa de renovación integraran la señal isotópica de la dieta ingerida en un plazo de tiempo distinto (Bearhop et al. 2004; Dalerum and Angerbjörn 2005).

Dentro de los pinnípedos existe una amplia variedad de sistemas de apareamiento que van desde la monogamia serial hasta la poliginia extrema (Atkinson 1997), donde los otáridos presentan una amplia gama en el grado de poliginia (Cassini 1999). Los otáridos crían en colonias de alta densidad donde existe el potencial para una fuerte competencia entre los machos por la monopolización de los territorios que les permita el acceso a las hembras reproductivas (Boness 1991; Cassini 1999). En estas especies, la temporada de cría se inicia con la monopolización por parte de los machos de los territorios utilizados por las hembras. Cuando las hembras dan a luz un cachorro engendrado en la temporada reproductiva anterior, las mismas permanecen en tierra por varios días hasta el primer viaje de alimentación, periodo en el que entran en estro (Berta et al. 2006). Debido a que las hembras de los otáridos son altamente sincrónicas en los partos y por lo tanto en la receptividad sexual (Boness 1991; Cassini 1999), los machos de estas especies que sean capaces de defender los territorios durante el período de sincronía, deberían tener un elevado éxito reproductivo. Esto diferencia principalmente dos tácticas reproductivas entre los machos de los pinnípedos poligínicos. Como patrón general se ha observado que una pequeña proporción de la población monopoliza los territorios con hembras, mientras otros se ubican en zonas marginales no ocupadas por éstas (Berta et al. 2006). Debido a la sincronía de las hembras (Boness 1991; Cassini 1999), los machos más exitosos serán aquellos que logren mantener un territorio durante el pico de cópulas maximizando así su éxito reproductivo. Bajo estas condiciones, el tamaño corporal de los machos aparece como un rasgo que estaría bajo una intensa selección sexual, ya que permite la conquista y la exclusión territorial (Le Boeuf 1986). Sin embargo, en un contexto de alta competencia reproductiva intrasexual, la maximización del éxito reproductivo individual puede conducir a la aparición de comportamiento reproductivos flexibles y / o de otros rasgos de comportamiento involucrados en tácticas reproductivas alternativas (Taborsky and Brockmann 2010; Taborsky et al. 2008). Estos motivos hacen que los otáridos sean un buen modelo de estudio para evaluar la presencia de tácticas reproductivas entre los machos y su relación con el éxito reproductivo individual.

En los últimos años, la aplicación de técnicas genético-moleculares ha generado un cambio en la visión clásica sobre los sistemas de apareamiento, mostrando en muchos casos inconsistencias con el sistema propuesto a partir de observaciones comportamentales directas (Fabiani et al. 2004). En la foca gris (*Halichoerus grypus*), las medidas comportamentales sobrestimaron el éxito reproductivo de los machos territoriales, y por consiguiente el nivel de poliginia de la población (Wilmer et al. 1999). En el lobo marino antártico (*A. gazella*), las observaciones realizadas y el sistema de apareamiento propuesto para la población, no fueron respaldados por los análisis de paternidad (Gemmell et al. 2001). En el elefante marino del sur, los resultados genéticos concordaron con el éxito hallado a través de observaciones, pero indicando una varianza extrema en el éxito reproductivo de los machos no detectada previamente (Fabiani et al. 2004).

Área de estudio

Las dos especies de otáridos que se reproducen en aguas uruguayas, son el lobo fino (*Arctocephalus australis*) y el león marino sudamericano (*Otaria flavescens*). Ambas especies forman colonias reproductivas en grupos de islas de la costa Atlántica (Figura 3): Isla e Islote de Lobos (35°01'S, 54°50'W), en Maldonado, Islas de Torres (Isla Rasa, Isla Encantada e Islote), Isla de Marco frente a Cabo Polonio - Valizas (34º24'S, 53º45'W), Isla Verde e Islote de la Coronilla en Rocha (Vaz-Ferreira 1976a, b). Estas islas se dividen en dos principales colonias reproductivas ubicadas aproximadamente a 70 km de distancia. En Isla de Lobos se encuentra la mayor proporción de lobos finos, mientras en las islas de Cabo Polonio - Valizas se encuentra la mayor proporción de leones marinos. Es importante destacar que Cabo Polonio y 5 millas náuticas costeras a su alrededor fueron recientemente declaradas como la segunda Área Marina Protegida del Uruguay (según Decreto 337/09), ya que es una zona que presenta una importante diversidad de especies y hábitats. En nuestro país ocurre una situación única en América ya que dos especies simpátricas de otáridos con una ecología similar, tienen abundancias y tasas de crecimiento poblacional contrastantes.

Especies objeto de estudio

El **lobo fino** es una especie sexualmente dimórfica, siendo los machos entre 4 y 5 veces más pesados que las hembras (200 vs 40 Kg). Sus sitios reproductivos tienen una distribución fragmentada a lo largo las costas del sur de Argentina, norte y sur de

Chile, Perú y Uruguay (Vaz-Ferreira 1976a). En Uruguay, la estación reproductiva se inicia a fines de noviembre cuando los machos conquistan y defienden los territorios donde las hembras entran en estro pocos días después de parir a sus cachorros. La sincronía reproductiva en la población uruguaya dura aproximadamente 35 días, con partos y cópulas concentrados en el mes de diciembre (Franco-Trecu et al. 2010). El lobo fino tiene un sistema de apareamiento poligínico, tradicionalmente fue definido como de harén (Vaz-Ferreira 1976a), pero recientemente reclasificado (ver capitulo 3). Las hembras exhiben una baja fidelidad a los territorios defendidos durante el período del estro indicando que no establecen una relación estrecha con ningún territorio o macho, contrario a lo que se esperaría bajo un sistema de harenes (Vaz-Ferreira 1976a). En relación a su dieta, el lobo fino fue descrita como generalista y oportunista de acuerdo a la disponibilidad de presas (Naya et al. 2002) con áreas de forrajeo ubicadas entre 41 y 185 Km de las zonas de cría (Vaz-Ferreira 1976a). Esta especie fue comercialmente explotada en Uruguay donde al menos 273.000 individuos fueron sacrificados entre 1950 y 1991 (Ponce de León 2000). Quince años después del cese de la explotación, la población uruguaya del lobo fino posee una abundancia estimada en 300.000 individuos (la mayor colonia reproductiva de la especie) y una tasa de incremento positiva (Páez 2000). En Argentina, el lobo fino era una especie abundante durante el siglo XVIII, pero los niveles de explotación la llevaron al borde de la extinción (Clark 1885), siendo hoy una especie rara. La explotación de esta especie fue mínima en Chile durante la década de los ’70, con una población que no presenta problemas actuales de conservación (Sielfeld 1999). El lobo fino está globalmente categorizado como una especie de “Preocupación Menor” por la UICN. Sin embargo, esta listada en el Apéndice II de CITES, organismo que regula el comercio internacional de especies amenazadas.

El **león marino** también presenta un marcado dimorfismo sexual, siendo los machos de mayor tamaño que las hembras (350 vs 150 Kg). La temporada de cría en Uruguay comienza con la llegada de los machos a los territorios a mediados de noviembre, tras lo cual las hembras dan a luz a sus crías entre principios de enero y de febrero (Trimble and Insley 2010) y aproximadamente una semana después entran en estro. Luego de las cópulas, las hembras comienzan a intercalar viajes de alimentación en el mar con asistencias en tierra durante casi un año (Campagna and Le Boeuf 1988). El león marino presenta diferentes sistemas de apareamiento a lo largo de su área de distribución geográfica yendo desde la poliginia de defensa de hembra, defensa de recursos - territorios (Campagna and Le Boeuf 1988) hasta un sistema de lek (Soto and Trites 2011).

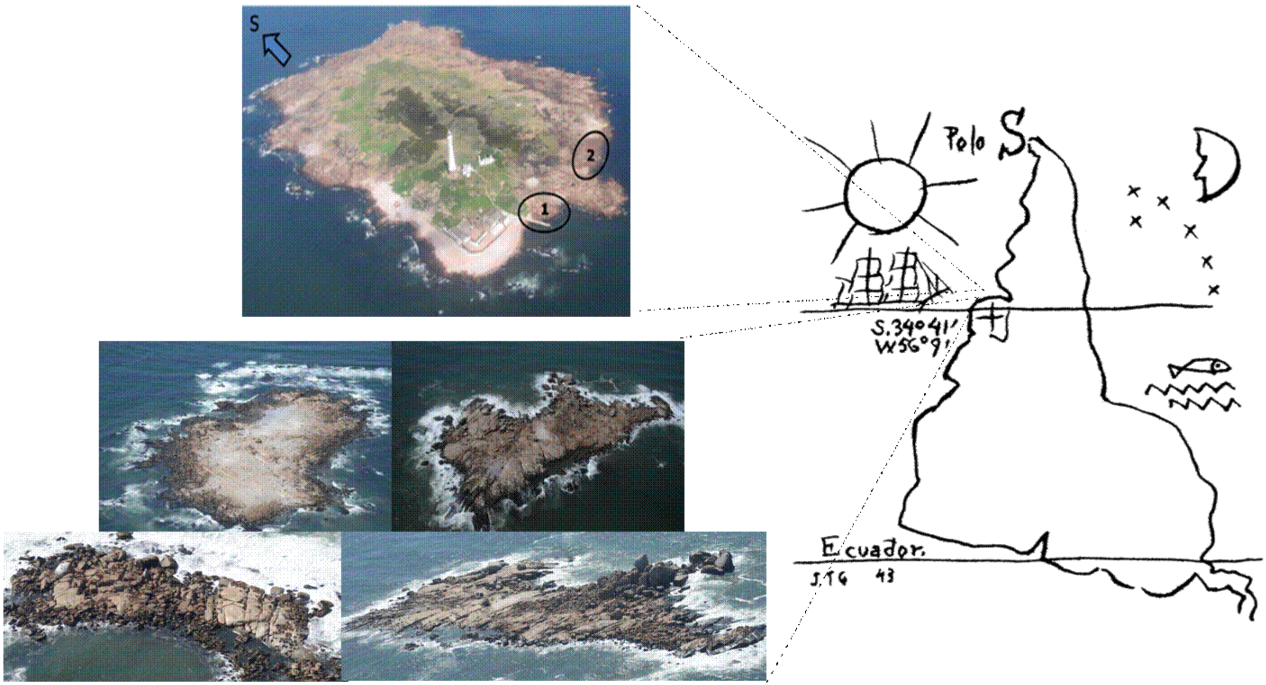

Figura 3. Área de estudio. Arriba Isla de Lobos ubicada frente a la costa de Punta del Este, Maldonado. 1- Zona reproductiva "El Muelle" exclusivamente utilizada por el lobo fino sudamericano, 2- Zona "La Cachimba", principal área reproductiva del león marino sudamericano en la Isla de Lobos. Abajo Islas de Torres (Rasa, Encantada e Islote) ubicadas frente a Cabo Polonio, e Isla del Marco, Rocha.

La variación de los sistemas de apareamiento se relaciona con el tipo de sustrato de la colonia de cría y su abundancia local. La información sobre la composición de la dieta del león marino en nuestro país proviene de una investigación menos detallada que en el lobo fino (Naya et al. 2000), pero se conoce información sobre sus hábitos tróficos por medio del uso de isótopos estables (Franco-Trecu et al. 2012). La distribución geográfica del león marino es similar a la del lobo fino pero sin presentar hiatos a lo largo de Chile (Vaz-Ferreira 1976b). En Argentina, el león marino fue intensamente explotado a comienzos del siglo XX y su abundancia poblacional sólo comenzó a recuperarse a partir de 1990 (Dans et al. 2004); una situación análoga ocurrió en Chile (Sielfeld 1999). Contrariamente, la población de Uruguay no ha logrado recuperarse y de hecho representa la única población en el área de distribución de esta especie que actualmente tiene tasas de crecimiento negativas, generando tendencias poblacionales decrecientes (Páez 2006; Pedraza et al. 2009). Esta especie ha sido fuertemente explotada en Uruguay (47 mil cachorros entre 1963-1986), y su tamaño poblacional estimado en el año 2005 fue de 12 mil individuos (Páez 2006). La interacción entre la población uruguaya de león marino y las pesquerías artesanales (Szteren and Páez 2002) e industriales costeras (Szephegyi et al. 2010) podrían llegar constituir un problema ecológico y social. Sin embargo, el león marino está catalogado como una especie de Preocupación Menor por la UICN debido a que presenta una tendencia poblacional global relativamente estable.

El objetivo general de esta tesis fue: **Evaluar la existencia de tácticas alimenticias y reproductivas a nivel individual, así como estimar las abundancias y tendencias poblacionales en dos especies de otáridos simpátricas con tendencias poblaciones contrastantes.**

Estrategia de investigación

Para llevar adelante esta tesis se contó con información recopilada a lo largo de un programa de investigación desarrollado desde el año 2004 cuando inicié mi investigación durante mis estudios de Licenciatura en Biología. A partir de ese momento, realicé investigaciones en las colonias reproductivas de lobos marinos de Uruguay en cada estación de cría. Al momento de comenzar mi doctorado contaba con diversos datos colectados a lo largo de 7 años. La información faltante fue recabada durante intensos muestreos de campo en las siguientes 3 temporadas reproductivas (2011, 2012, 2013) continuando algunas actividades previamente realizadas (marcaje de crías) y realizando otras nuevas (equipado de hembras). Por otro lado, durante el verano de 2011 y 2013 se realizaron censos aéreos de las colonias reproductivas de Isla de Lobos y Cabo Polonio – Valizas para realizar las estimaciones de abundancia poblacionales.

COMPORTAMIENTO ALIMENTICIO EN HEMBRAS LACTANTES DEL LOBO FINO (Arctocephalus australis) Y DEL LEÓN MARINO SUDAMERICANO (Otaria flavescens)

Objetivo específico:

1. Estudiar el comportamiento alimenticio en hembras reproductivas del lobo fino y león marino (*A. australis y O. flavescens*) en relación a la composición de su dieta, los patrones de buceo y las áreas de forrajeo durante la lactancia temprana.

Hipótesis

El análisis de isótopos estables realizado en un estudio previo indicó la existencia de una segregación trófica entre hembras adultas del lobo fino y león marino sudamericano de Isla de Lobos tanto en el período preparto como postparto (Franco-Trecu et al. 2012). Por otro lado, en Uruguay es frecuente la interacción entre el león marino y las pesquerías costeras (Szteren and Páez 2002), mientras que para el lobo fino dichas interacciones son ocasionales (Franco-Trecu et al. 2009; Szephegyi et al. 2010). En base a estos antecedentes, la hipótesis propuesta plantea mientras el león marino utilizará presas y áreas de alimentación costeras con un comportamiento de buceo bentónico, el lobo fino utilizará principalmente áreas de alimentación alejadas de las colonias de cría, con un comportamiento de buceo y consumo de presas pelágicas.

RESUMEN

Conocer los hábitos alimenticios de las especies que integran una comunidad nos ayuda a comprender las interacciones entre las poblaciones que la componen, y determinar el grado de solapamiento entre especies y sus roles en el ecosistema (Arim et al. 2010; Pauly et al. 1998; Pauly et al. 2000). Tradicionalmente la composición de la dieta a nivel poblacional ha sido investigada por medio de métodos clásicos como el análisis del contenido estomacal (Cortés 1997; Koen Alonso et al. 2000) o de fecas (Naya et al. 2002), entre otros. Si bien estos métodos brindan alta resolución respecto a las especies que componen la dieta, poseen sesgos intrínsecos relacionados con la digestión o retención diferencial de las partes duras (ej. Arim and Naya 2003). En consecuencia, estos sesgos pueden sub- o sobre-estimar la intensidad de las interacciones entre las especies, obteniéndose una visión distorsionada de la estructura comunitaria. En las últimas décadas se ha incrementado el uso de los isótopos estables de $\delta^{13}C$ y $\delta^{15}N$ para estudiar los hábitos tróficos de poblaciones silvestres (Crawford et al. 2008; Forero and Hobson 2003; Perga and Gerdeaux 2005). Adicionalmente, el desarrollo reciente de los modelos de mezcla ha permitido reconstruir la composición de la dieta de diversas especies a partir de valores isotópicos en tejidos de los depredadores y sus potenciales presas (Moore and Semmens 2008; Parnell et al. 2010). Estas reconstrucciones permiten detectar ítems alimenticios que no son posibles de reconocer a través de los métodos clásicos. Además, los modelos de mezcla basados en enfoques bayesianos permiten incorporar información previa (ej. proveniente de métodos tradicionales) para realizar estimaciones con mayor precisión (Parnell et al. 2010; Parnell et al. 2013; Phillips et al. 2014; Semmens et al. 2009). Por otro lado, para describir el uso del hábitat, durante los últimos 30 años, se ha incrementado el uso de tecnologías como la telemetría satelital para obtener de forma remota posiciones geográficas (ej. Costa et al. 2007; Costa et al. 2010). En especies marinas, esta tecnología sumada a los registradores del comportamiento de buceo han permitido delimitar áreas de alimentación utilizadas por los depredadores marinos, cuantificar la intensidad del uso de dichas áreas y determinar variables que afectan la selección de hábitat o preferencias (Costa et al. 2007; Jeglinski et al. 2013; Villegas-Amtmann et al. 2013). Además estos métodos permiten investigar los hábitos tróficos a nivel individual y así posibilitan evaluar el efecto de variables internas del individuo (ej. estado reproductivo, tamaño corporal) sobre ciertas características de las áreas utilizadas (ej. tamaño del *home range*, distancias de las zonas de cría). En este capítulo complementamos estas 4 herramientas (métodos tradicionales, análisis de isótopos estables, telemetría satelital y sensores de buceo) para estudiar los hábitos alimenticios del lobo fino y león marino sudamericanos.

Para estimar la composición de la dieta utilizamos de forma complementaria la información obtenida por medio de la identificación de partes duras (otolitos, picos, etc.) en fecas, junto con los análisis de isótopos estables en piel de hembras del lobo fino y león marino colectadas durante el mismo período. La conjunción de ambas fuentes de información fue

realizada por medio de modelos de mezcla bayesianos (*stable isotope mixing models* - SIMM) que permiten incorporar información previa (SIMM-IP). Estos modelos estiman la composición de la dieta en base a los contenidos isotópicos en los tejidos de los depredadores, de sus potenciales presas y del factor de discriminación isotópico del tejido en cuestión. En nuestro caso, la información previa que se incorporó en los modelos provino de la composición de la dieta del lobo fino y del león marino determinada por el análisis de fecas. Es importante destacar que en **el lobo fino** se encontraron restos duros sólo en el 37% de las fecas colectadas (94 otolitos y 77 picos cefalópodos), mientras que para **el león marino** esto ocurrió en el 73% de las fecas (39 otolitos y 40 picos cefalópodos). De acuerdo con el SIMM-UP (sin información previa), más del 60% de la dieta del lobo fino se compone de especies pelágicas como la merluza (*Merluccius hubbsi*), anchoita (*Engraulis anchoita*) y el calamar (*Illex argentinus*). Para el león marino la dieta fue más diversa sin el dominio claro de ninguna de las potenciales presas. Al incorporar la información proveniente del análisis de las fecas, los modelos de mezcla estimaron una dieta dominada por las mismas especies presa que fueron importante en el análisis de las fecas (Tabla 1 en Franco-Trecu et al. 2013). La inclusión de información previa en los SIMM mejoró la precisión en la estimación de la dieta (disminuyó el ancho de los intervalos de confianza para cada presa) y cambió de forma más notoria la composición de la dieta en el lobo fino. Esto último probablemente se deba al hecho de que esta especie se alimenta en zonas más alejadas de las áreas de cría, de manera que la información obtenida por medio de las fecas estaría muy sesgada, tal como se observó en la alta proporción de fecas sin restos duros.

Las áreas de alimentación de las hembras lactantes de **león marino** en Isla de Lobos, se ubicaron exclusivamente en la plataforma continental, presentando diferentes patrones de dispersión entre hembras (Fig. 4 en Riet-Saprisa et al. 2013). La mayoría de las hembras viajó al oeste / suroeste o sur / sureste de la Isla de Lobos, aunque dos viajaron al noroeste y a lo largo de la costa. El *home range* para todas las hembras de león marino tuvo un área total de 3.199,5 km^2 según el mínimo polígono convexo (95%) con una media individual de 2.224,3 km^2 (SD = 1.638,9). Los viajes de alimentación tuvieron una duración promedio de 1,5 días (SD = 0,9) y las asistencias en tierra de 1,1 día (SD = 0,8). Las distancias máximas que las hembras se alejaron desde la colonia reproductiva en sus viajes de alimentación variaron entre 38 y 135 Km, mientras que la distancia total recorrida (suma de todos los viajes de alimentación para cada individuo) varió entre 249 y 1.062 km. No encontramos correlación entre ninguna medida morfométrica (largo estándar y masa corporal) y las variables empleadas para describir el comportamiento de forrajeo de las hembras. En el caso de las hembras de **lobo fino**, las áreas de alimentación estuvieron claramente divididas en un área cercana a la colonia, sobre la plataforma continental, durante el primer viaje (después del parto), y otra área en aguas abiertas, a la altura del quiebre del talud continental al S-SW de la isla utilizadas durante los siguientes viajes de alimentación. El *home range* (95% MPC) de todas las hembras de lobo fino juntas fue de 78.752,06 km^2 (95% MPC) y se extendió principalmente en sentido latitudinal. Los *home range* individuales variaron entre 6.892,9 km^2 y 46.958,3 km^2. Debido a la diferenciación de áreas utilizadas entre el primer viaje y los siguientes, se estimó el *home range* de cada hembra de lobo fino durante su primer viaje de alimentación, el cual varió entre 2 y 3.203 km^2 (586 ± 1.063 km^2), mientras en los siguientes viajes de alimentación (segundo) varió entre 7.990 y 45.786 km^2 (30.193 ± 11.452 km^2). La duración del primer viaje de alimentación fue significativamente más corta (7,3 ± 4,9 días) que la del segundo (13,3 ± 4,3 días, t = -5.66, P << 0.01). La primer asistencia en tierra de las hembras de lobo fino tuvo una duración media de 3,3 días (SD = 1,5). La distancia máxima que las hembras se alejaron de la colonia reproductiva durante un viaje de alimentación osciló entre 451 y 736 km, mientras que la distancia total recorrida por cada hembra varió entre 512 y 1.622 km. El solapamiento espacial entre cada hembra y el resto de las hembras de lobo fino equipadas fueron altos con un promedio de 95,6% (SD = 9,4) y un rango que osciló entre 71% y 100%. Encontramos una correlación positiva entre la masa corporal individual y la distancia total viajada por cada hembra (r = 0.67, P = 0.02), la distancia máxima viajada (r = 0.77, P = 0.01) y el *home range* 95% MCP (r = 0.63, P = 0.04) durante el primer viaje de alimentación. Sin embargo durante el segundo viajes de alimentación se encontró una correlación negativa entre el índice de condición corporal y el *home range* al 95% MCP (r = 0.71, P = 0.005). De esta forma las hembras que usaron mayores áreas de actividad durante el primer viaje de alimentación, las acotaron durante el segundo. Además, para las hembras de lobo fino, la heterogeneidad, medida como el desvío estándar, del tiempo de buceo en el fondo (r = 0.79, P = 0.001), del tiempo de buceo (r = 0.77, P = 0.002), del tiempo de tránsito (r = 0.67, P = 0.01), del esfuerzo de buceo (r = 0.71, P = 0.006) y de la profundidad (r = 0.71, P = 0.005) también estuvieron correlacionados positivamente con la masa corporal durante todo el período de muestreo.

En relación al comportamiento de buceo, **el león marino** (n=7) realizó principalmente buceos someros, ya que el 70% de las inmersiones fueron entre 15 y 25 m, el 23% entre 5 y 10 m, y solo el 7% de los buceo se registraron a profundidades mayores a 30 m (profundidad máxima= 78 m). La distribución de la duración de buceo fue unimodal, mostrando que el 84% de las inmersiones realizadas tuvieron una duración entre 1,0 y 2,5 min. No se encontró un patrón distintivo a la escala diaria del comportamiento de buceo, ya que el león marino realizó buceos indistintamente a lo largo del día. El límite aeróbico de buceo de las hembras de león marino equipadas varió entre 4,3 y 4,8 minutos, y el porcentaje de buceos que excedieron dicho límite varió entre el 0 y 0.2%. El cociente entre el tiempo en el fondo y el tiempo total de buceo varía entre cero y uno. Cuanto más se aproxime a cero refleja buceo pelágicos, mientras al acercarse a 1 refiere a buceos bentónicos. El promedio de este cociente para el león marino fue de 0.57 (SD= 0.06). Por otro lado, **el lobo fino** (n=12) realizó el 64% de sus buceos a menos de

20 m, 31% entre 21 y 60 m, y sólo cerca del 5% a profundidades mayores de 61 m. El buceo más largo tuvo una duración de 5.25 minutos, mientras que el 45% de los buceos tuvieron una duración entre 0,08 y 0,5 min y otro 45% entre 0,51 y 1,75 min. En el 60% de los buceos el tiempo en el fondo fue inferior a 0.25min, en el 30% esta duración varió entre 0,26 y 1,0 min, y el 10% restante tuvieron una duración entre 1,01 y 4,75 min. La profundidad máxima, el esfuerzo de buceo, el tiempo en el fondo y el tiempo total del buceo así como su cociente, variaron entre el día y la noche, y entre el primer viaje de alimentación y los siguientes con interacciones significativas. Durante el primer viaje de alimentación, las hembras lactantes de lobo fino bucearon significativamente más profundo durante el día (media = 18,2 m) que durante la noche (12,6 m) (P << 0,001), con un patrón inverso durante los viajes sucesivos (día = 14,4 m; noche = 14,9 m), encontrándose un patrón similar para el esfuerzo de buceo a nivel individual. Sin embargo, el tiempo de fondo, el tiempo de buceo y su relación siempre fueron mayores durante la noche que durante el día. El límite aeróbico de buceo para las hembras del lobo fino osciló entre 3,4 y 3,8 minutos, y el porcentaje de buceos que excedieron dicho límite varió entre el 0,1 y 0,3%. El cociente entre tiempo en el fondo y tiempo total de buceo promedio fue 0.43 (0.06) siento significativamente menor que en el león marino (t= -4.9, p<<0.01).

Estos resultados confirman la hipótesis propuesta indicando que en Uruguay estas dos especies difieren en las áreas de alimentación utilizadas, en el comportamiento de buceo y principales presas consumidas. Esta aparente segregación, no implica necesariamente la ausencia de una potencial competencia entre ambas especies. A pesar de que el león marino posee una masa corporal cuatro veces mayor que la del lobo fino, las hembras de esta última especie realizan buceos hasta tres veces más profundos. Esto es posible gracias a que las hembras de lobo fino realizan prolongados viajes de alimentación (promedio 10 ± 6 días), durante los que recorren largas distancias y llegan a zonas más profundas en el quiebre de la plataforma continental. En otras partes del mundo, varios estudios evalúan el comportamiento trófico en poblaciones de pinnípedos simpátricas (ej. Waite et al. 2012) que generalmente ocurren entre una especie de león marino y una de lobo fino. Normalmente, los leones marinos que tienen un mayor tamaño corporal, poseen hábitos tróficos bentónicos y realizan buceos más profundos, mientras los lobos finos poseen hábitos pelágicos. Sin embargo, nuestros resultados constituyen el primer caso donde el lobo fino (de menor tamaño corporal) realiza buceos más profundos que el león marino. La plataforma continental uruguaya es extensa y somera, con una profundidad máxima alrededor de 50-70m únicamente en área puntuales. El quiebre del talud continental se encuentra aproximadamente a 200 km de la costa, donde la profundidad aumenta rápidamente, alcanzando los 200 a 1000 m. Al alimentarse exclusivamente en la plataforma continental, el león marino no explota sus capacidades aeróbicas para realizar buceos más profundos ya que usa recursos bentónicos principalmente entre 20 - 25 m.

A nivel mundial, las poblaciones de leones marinos son las especies de pinnípedos más amenazadas, ya que la mayoría poseen tendencias negativas aún luego del cese de su caza comercial (Gerber and Hilborn 2001). Uno de los probables motivos de estas tendencias poblacionales desfavorables es que las poblaciones locales de leones marinos se enfrentan a un baja disponibilidad de recursos tróficos, ya que los recursos costeros han sido y son ampliamente sobre explotados por las pesquerías (Alleway et al. 2014; Milessi et al. 2005; Pauly et al. 1998). Es importante considerar que los ambientes costeros se encuentran ampliamente afectados por distintas actividades humanas como las pesquerías, el patrón de uso de los suelos, el turismo, actividades náuticas y los puertos que generan sobreexplotación de recursos, fragmentación del hábitat y altos niveles de contaminación en estos ecosistemas (Bulleri and Chapman 2010; Clausen and York 2008; Davenport and Davenport 2006). De esta forma, mientras que el lobo fino utiliza áreas de alimentación alejadas de la costa, con recursos pelágicos energéticamente más ricos (Eder and Lewis 2005) y sujetas a un impacto antrópico potencialmente menor, el león marino utiliza recursos tróficos de menor calidad energética, en áreas de alimentación altamente degradadas por las actividades humanas. Esto, en conjunto con el solapamiento, directo (captura incidental ~50 individuos al año, (Szephegyi et al. 2010)) e indirecto (competencia por recursos) con las pesquerías costeras podría afectar los parámetros poblacionales, como la sobrevivencia y fertilidad, traduciéndose en la dinámica y tendencia poblacional observada para cada especie en Uruguay.

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Bias in Diet Determination: Incorporating Traditional Methods in Bayesian Mixing Models

Valentina Franco-Trecu[1], **Massimiliano Drago**[2], **Federico G. Riet-Sapriza**[1], **Andrew Parnell**[3], **Rosina Frau**[1], **Pablo Inchausti**[4*]

1 Proyecto Pinnípedos, Sección Etología, Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay, **2** Department of Animal Biology, Faculty of Biology, University of Barcelona, Barcelona, Spain, **3** School of Mathematical Sciences (Statistics), Complex Adaptive Systems Laboratory, University College Dublin, Dublin, Ireland, **4** Departamento de Ecología y Evolución, Centro Universitario Regional Este (CURE), Universidad de la República, Maldonado, Uruguay

Abstract

There are not "universal methods" to determine diet composition of predators. Most traditional methods are biased because of their reliance on differential digestibility and the recovery of hard items. By relying on assimilated food, stable isotope and Bayesian mixing models (SIMMs) resolve many biases of traditional methods. SIMMs can incorporate prior information (i.e. proportional diet composition) that may improve the precision in the estimated dietary composition. However few studies have assessed the performance of traditional methods and SIMMs with and without informative priors to study the predators' diets. Here we compare the diet compositions of the South American fur seal and sea lions obtained by scats analysis and by SIMMs-UP (uninformative priors) and assess whether informative priors (SIMMs-IP) from the scat analysis improved the estimated diet composition compared to SIMMs-UP. According to the SIMM-UP, while pelagic species dominated the fur seal's diet the sea lion's did not have a clear dominance of any prey. In contrast, SIMM-IP's diets compositions were dominated by the same preys as in scat analyses. When prior information influenced SIMMs' estimates, incorporating informative priors improved the precision in the estimated diet composition at the risk of inducing biases in the estimates. If preys isotopic data allow discriminating preys' contributions to diets, informative priors should lead to more precise but unbiased estimated diet composition. Just as estimates of diet composition obtained from traditional methods are critically interpreted because of their biases, care must be exercised when interpreting diet composition obtained by SIMMs-IP. The best approach to obtain a near-complete view of predators' diet composition should involve the simultaneous consideration of different sources of partial evidence (traditional methods, SIMM-UP and SIMM-IP) in the light of natural history of the predator species so as to reliably ascertain and weight the information yielded by each method.

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* E-mail: pablo.inchausti.f@gmail.com

Introduction

Trophic interactions determine the flow of energy among trophic levels that ultimately drives population dynamics, community and food web structure and most ecosystem processes. Determining the diet composition of predators in a community is essential to measure the potential niche overlap and the strength of their interspecific interactions [1]. There are no "universal methods" allowing the reliable determination of the diet composition of predators. In the case of vertebrate, diet composition can rarely be determined through the direct observation of prey consumption [2,3]. Ecologists must then employ several indirect methods to determine diet composition. These methods include the analyses of stomach contents [3,4], scats [5–7], regurgitations [8] and pellets [9,10]. Nevertheless, all these indirect methods rely on the recovery and identification of hard items (e.g. otholites, beaks, bones) of consumed preys, but yield high-resolution information on the species composition, body length and mass of the prey consumed [10]. However, all these traditional methods possess intrinsic biases mostly due to differential digestion, retention and recovery of preys' hard items that can severely biased estimates of diet composition when the latter contains preys that are either fully digested or lack such hard items [6,11,12]. Scat analysis is perhaps the least invasive of the traditional, indirect methods to determine diet composition and probably the one yielding the highest sample size for the lowest effort and cost [13].

Others indirect methods for diet determination in vertebrates do no depend on the recovery of hard items of the preys consumed. These alternative indirect methods include molecular identification [14], signature fatty acids analysis [15] and stable isotope analyses [16]. In the last decades, stable isotope (^{13}C and ^{15}N) analysis has become a standard tool in the study of the foraging ecology of vertebrate [17–20]. Stable isotope analysis can provide indirect but otherwise unobtainable information on habitat and resource use [21]. The use of stable isotopes to determine diet composition is based on three assumptions: (1) carbon and nitrogen contents come directly from the ingested food and hence they can be used to ascertain the relative importance of potential preys [22,23]; (2) the isotopic signal of each tissue depends on its metabolic rate and thus the time reference of dietary information is tissue-dependent [24]; and (3) the assimilated organic compounds are enriched in the heavy isotopes (^{13}C, ^{15}N) after transference between consecutive trophic levels [25]. This differential enrichment occurring in the conversion from proteins of preys to the consumer tissues is called fractionation or trophic discrimination factor and, by varying among taxa and tissues [26], it can substantially affect the estimates of diet composition.

The recent development of mixing models has allowed their use to obtain diet composition based on isotopic contents of predators' tissues and their potential preys [27,28]. Mixing models aim to obtain the relative contribution of all preys consumed to a predator's diet [28]. Recent developments of mixing models (MixSIR [29]:; SIAR [27]:) based on Bayesian methods allow considering many potential preys and can deal with the uncertainty inherent in isotopic measurements. Bayesian stable isotope mixing models (SIMM) can incorporate prior information (i.e. either the proportional prey consumption or the diet composition as determined by traditional methods) that often lead higher precision in the estimated dietary composition than when the latter is obtained using uninformative priors [27,29]. Therefore, both the diet composition and the precision of the estimated contribution of each prey species can be affected by the uncertainty of inputs to SIMMs [29]. To our knowledge, there have been few comparisons of the estimated diet compositions obtained using SIMMs with more traditional methods of diet determination [30–32]. We believe that both traditional methods such as stable isotope analysis have different biases associated with its interpretation to determining the diet composition of a species [33]. For this reason, the combination of both techniques through SIMMs seems a promising approach to estimate the diet composition because their use of prior information allows incorporating different sources of variability as input in the analysis [33]. The goal of this paper is to evaluate the biases and precision of three commonly used methods (scat analysis, SIMM with and without informative priors) to study predators' diet composition using the South American fur seal (SAFS, *Arctocephalus australis*) and sea lions (SASL, *Otaria flavescens*) as a study system

Materials and Methods

Study area and sample collection

The study was conducted at Isla de Lobos, one of the main breeding colony of SASL and SAFS in Uruguay (35° 01' S; 54° 52' W), located at five nautical miles from the mainland. Females of SAFS and SASL have colonial breeding while males fast while defending territories for mating. Therefore, scats collected in the rookery at this time can only reflect the feeding by breeding females. Two hundred twenty-seven SAFS scats and 52 SASL scats [34] were collected during the breeding season in December/2006 and January/2009, respectively. Scats samples were washed through a 0.5 mm mesh sieve at the laboratory; prey hard items recovered were compared with reference collection [35,36] and an otoliths reference collection (Franciscana Project, Facultad de Ciencias, University of República, Uruguay). Otoliths used to estimate diet composition were only those having minimal erosion that allowed prey identification to species level and cephalopod beaks were identified to the lowest possible taxon; hard items digested beyond recognition were not included in the analysis.

During the same breeding seasons when scats samples were collected, we gather skin samples from the caudal flippers from randomly selected lactating SAFS (n=35) and lactating SASL (n=10). Skin samples were stored in the field and were used for isotope analysis in the lab. We obtained skin samples from the caudal flippers for isotope analysis from randomly 35 lactating SAFS and 10 lactating SASL selected during same breeding seasons. Lactating females were captured with a hoop net and sedated using ~2ml of Midazolan 0.5% in the case of SAFS, while SASL were anaesthetized using isoflurane gas mixed with oxygen (0.5–2.5%) using a portable-field vaporizer [34]. The present research was conducted under the permits 603/2006 and 572/2008 approved by DINARA (National Administration of Aquatic Resources), Ministry of Livestock, Agriculture and Fisheries, Uruguay. All procedures of animal manipulation were submitted and approved as valid according to the national laws in animal welfare by the Ethics Committee in Animal Experimentation, Universidad de la República, Uruguay. Skin samples were dried in a stove at 60°C for 36 h, and lipids extraction was made as Bligh and Dyer [37]. Approximately 0.3 mg of skin without lipids were weighed into tin cups (3.3 x 5 mm), combusted at 900°C, and analysed in a continuous flow isotope ratio mass spectrometer and stable isotope abundances are expressed in delta (δ) notation. Samples were processed at Stable Isotope Laboratory of the University of República (Uruguay) with an analytical error estimated in 0.1‰ for nitrogen and 0.03‰ for carbon. Isotopic values of potential prey species in waters of the Río de la Plata and the Uruguayan continental shelf were obtained from Franco-Trecu et al. [20] and were used in the Bayesian mixing models based on stable isotopes.

Diet composition from scat analysis and using SIMMs on stable isotopes

We characterized the diet composition of each predator species by the relative abundance of each species of fish or cephalopod in the set of scat samples for each predator species. The number of individuals of each fish and cephalopods species found in each scat sample was calculated following [38]. Diet composition in the scat analysis was estimated by its relative numerical abundance of each prey species across all scats samples of each predator species. To have analogous estimates of the estimated diet composition and its variability for all method used, we calculated the average and the percentiles of the importance of each prey species in the diets by bootstrapping the matrices of results for each predator species using a sampling size equal to the number of scats observed with at least one hard and using 10,000 iterations [39].

We also estimated diet composition of each predator species using the SIMMs in the SIAR (Stable Isotope Analysis in R) library [27] of the R free software [40] with and without informative prior distributions based on the relative abundance of each prey species estimated from the scat analysis. The input of the SIMMs [27] comprised the δ^{13}C and δ^{15}N values from the all skin samples of SAFS and SASL females, the mean and standard deviation for their potential prey species (selected according to the results of the scat analysis) in the Uruguayan marine ecosystems, and the mean and standard deviation of prey elemental concentration (C and N) and we used skin trophic enrichment factor obtained from [41].

For both SIMMs with and without informative priors, we used the Dirichlet multinomial distribution to define these prior distributions. In the case of the SIMM with uninformative prior (SIMM-UP), the mean and variance defining the Dirichlet distribution were 1/k and $(k-1)/k^2*(k+1)$ with k being the number of potential preys of SASL and SAFS [27]. In the SIMM with uninformative prior (SIMM-IP), the mean and variance of the prior Dirichlet distribution were obtained from the relative numerical abundances of potential preys of SAFS and SASL and the standard deviation of the relative abundance of one of these potential prey species [27]. We chose the Striped weakfish (*Cynoscion guatucupa*) to SAFS and Lergehead hairtail (*Trichiurus lecturus*) to SASL. The SIMM output gives the diet composition as the posterior probability distribution having absorbed the prior information (or lack thereof) and the likelihood function containing a probability model and the isotopic data [27]. Each SIMM was based on 500,000 iterations, thinned by 15 and with an initial discard of 50,000 iterations, resulting in 30,000 posterior draws of the posterior distribution. Convergence to the posterior distribution in each model was assessed by the Geweke's criterion [42] and was shown to be acceptable for all models here considered. We compared the similarity in the diet compositions obtained by the scat analysis and the SIAR with and without informative priors using Bhattacharyya's Coefficient [43]. This coefficient of similarity between sampling distributions is analogous to other indices of diet or niche overlap (e.g. Horn-Morisita), taking values between 0 (completely different diets) and 1 (equal diets) [44].

Results

We found prey hard parts only in 37% of the SAFS (94 otoliths and 77 cephalopods beaks) and in 73% of the SASL scats samples (39 otoliths and 40 cephalopods beaks).The most abundant identified preys in the scats of SAFS was Striped weakfish (38%) and in SASL was the Argentine shortfin squid (36%) (Table 1, Figure 1a, b). According to the SIMM-UP, more than 60% of SAFS's diet was composed by pelagic species such as Argentine hake (*Merluccius hubbsi*), Argentine anchovy (*Engraulis anchoita*) and Argentine shortfin squid (Figure 1a), whereas that of SASL was more diverse and even without any clear dominance of the consumed preys (Table 1, Figure 1b). In contrast, the bulk of the diets of both predators estimated by SIMM-IP tended to be dominated by the same preys showed to be important in the scat analysis (Figure 1a, b, Table 1). Although including informative priors in the SIMM improved the precision (i.e. decreased the width of the 95% CI for each prey) of the estimated diet compositions of each predator compared with those obtained with uninformative priors (Figure 1a, b), the results maybe do not look more reasonable.

There were important differences in the estimated diet composition of SAFS when informative priors were included. Estimates of diet composition obtained scat analysis and SIMM-UP had a much smaller similarity (BC coefficient) for SAFS (68%) than for SASL (89%). The similarity of the diet compositions estimated by scat analysis and SIMM-IP was greater than 96% for both species, whereas those of the SIMMs had a similarity of 83% and 92% for SAFS and SASL, respectively. The differences in estimated SAFS diets between scat and SIMM-UP were mostly due to the marked decrease in relative importance of the Argentine anchovy and Argentine hake decreased, while the importance of Stripped weakfish and Sao Paulo squid (*Loligo sanpaulensis*) increased (Figure 1a). A similar comparison for SASL showed both the increase in the relative importance of Stripped weakfish, Whitemouth croaker (*Micropogonias furnieri*) and Argentine shortfin squid and the decline in the importance of Argentine and Marini's anchovy (*Anchoa marinii*) (Figure 1b).

Discussion

The development of SIMMs to determine the diet composition and the strengths of trophic interactions based on stable isotopes has led to stream of publications over the past years [33]. Recently, research on the SIMMs have addressed the effect of uncertainties in the discrimination factor of each tissue and species [32,45], the number of stable isotopes used [46] and on whether lipids need be extracted in samples [47]. Being based on Bayesian methods, SIMMs must incorporate priori knowledge on diet composition as informative priors that can be obtained by different means, including assessing the relative prey consumption from their relative abundance in the environment [48], expert opinion and on several indirect methods of estimating diet composition [27]. However, to our knowledge, there has been little research (see 29) comparing the diet compositions simultaneously estimated by traditional

Table 1. Scat and Bayesian mixing models diet composition.

Prey species	**SAFS**			**SASL**		
Common and scientific name	**Scats**	**SIMM-UP**	**SIMM-IP**	**Scats**	**SIMM-UP**	**SIMM-IP**
Brazilian codling (*Urophysis brasiliensis*)	-	0.02 (0-0.05)	0.01 (0-0.02)	0.04	0.04 (0.01-0.09)	0.05 (0-0.1)
Whitemouth croaker (*Micropogonias furnieri*)	-	0.01 (0-0.04)	0.01 (0-0.02)	0.09	0.04 (0.05-0.15)	0.1 (0.03-0.16)
Striped weakfish (*Cynoscion guatucupa*)	0.38	0.05 (0-0.14)	0.33 (0.24-0.4)	0.13	0.05 (0.08-0.21)	0.14 (0.07-0.22)
Argentine croaker (*Umbrina canosai*)	0.05	0.02 (0-0.07)	0.04 (0.01-0.07)	0.04	0.05 (0.01-0.09)	0.05 (0-0.1)
Banded croaker (*Paralonchurus brasiliensis*)	0.01	0.02 (0-0.06)	0.01 (0-0.02)	-	0.05 (0-0.04)	0.01 (0-0.05)
American harvestfish (*Peprilus paru*)	0.01	0.04 (0-0.11)	0.01 (0-0.03)	-	0.07 (0-0.04)	0.01 (0-0.05)
King weakfish (*Macrodon ancylodon*)	-	0.02 (0-0.05)	0.01 (0-0.02)	0.01	0.04 (0-0.04)	0.01 (0-0.04)
Red Shrimp (*Pleoticus muelleri*)	-	0.01 (0-0.04)	0.01 (0-0.02)	-	0.04 (0-0.03)	0.01 (0-0.04)
Narrownose smooth-hound (*Mustelus schmitti*)	-	0.01 (0-0.02)	0 (0-0.01)	-	0.02 (0-0.03)	0.01 (0-0.03)
Argentine hake (*Merluccius hubbsi*)	-	0.13 (0.01-0.23)	0.01 (0-0.03)	0.03	0.08 (0-0.08)	0.04 (0-0.09)
Marini's anchovy (*Anchoa marinii*)	-	0.05 (0-0.12)	0.01 (0-0.03)	-	0.07 (0-0.04)	0.01 (0-0.05)
Argentine anchovy (*Engraulis anchoita*)	0.02	0.25 (0.08-0.42)	0.04 (0-0.07)	0.04	0.13 (0.01-0.08)	0.05 (0-0.1)
Largehead hairtail (*Trichiurus lepturus*)	0.08	0.08 (0-0.18)	0.09 (0.04-0.14)	0.10	0.09 (0.05-0.17)	0.11 (0.04-0.18)
Argentine shortfin squid (*Illex argentinus*)	0.18	0.25 (0.08-0.41)	0.25 (0.18-0.32)	0.36	0.13 (0.23-0.35)	0.28 (0.2-0.35)
Sao Paulo squid (*Loligo sanpaulensis*)	0.27	0.05 (0-0.14)	0.18 (0.11-0.12)	0.11	0.09 (0.05-0.17)	0.11 (0.04-0.18)

Diet composition of the South American fur seal (SAFS, *Arctocephalus australis*) and South American sea lions (SASL, *Otaria flavescens*) in the summer of 2006 and 2009 respectively estimated by the scat analysis (expressed as the proportion of the prey individuals across all individuals in total scat samples) and by the Bayesian mixing models with (SIMM-IP) and without (SIMM-UP) informative priors (showing the mean and 95% CI for each prey).

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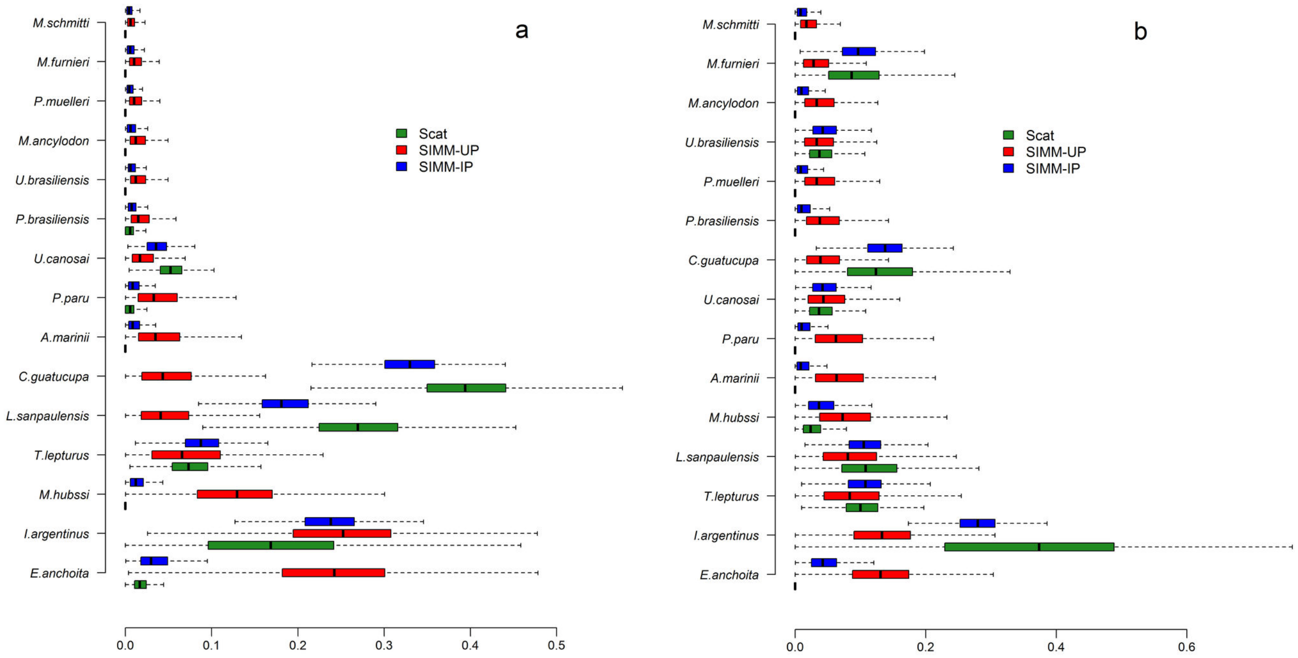

Figure 1. Diet composition comparison by scat and Bayesian mixing models with and without prior information. Diet composition of the South American fur seal (*Arctocephalus australis*) (a) and South American sea lion (*Otaria flavescens*) (b) in Isla de Lobos, Uruguay estimated by scat analysis (light grey bars), Bayesian mixing modes with uninformative (SIMM-UP; dark grey bars) and informative (SIMM-IP; black bars) priors. Mixing models were obtained with the library SIAR in the R software [27]. The error bars for the scat analysis were obtained by bootstrap.

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indirect methods and by SIMMs with and without informative priors.

One of well-known biases of traditional indirect methods of diet estimation comes from the non-detection of preys lacking hard remains. In our case, however, SIMMs did not show that soft-bodied species (e.g. Red shrimps, Narrownose smooth hounds) were at all important in the diet compositions of either predator species. Thus, while scat analysis and SIMMs agreed on which preys composed each predator's diet, they differed in the relative importance of each prey species, with the difference being very pronounced for the SAFS but not for SASL (see Figure 1). When compared with other mixing models, SIMMs do incorporate different sources of uncertainty occurring in the data, they should not be expected to estimate diet composition with reasonable precision when there is only a moderate information content in the data [29,48]. The increase in precision in diet composition may sometimes come at the price of obtaining biased estimation of diet composition. Including biased prior information into SIMMs may lead to biased posterior distribution depending on the nature of input data [33]. It is well known in Bayesian analysis that prior information may strongly affect the posterior distribution only when the data contain a modest amount of information allowing discriminate single prey contributions to the diet [29]. The latter would happen when prey isotopic contents have a large overlap in isotopic space [48–50], as it is the case of Argentine anchovy and Argentine shortfin squid (Figure 2). In such cases where overlapping isotopic data does not allow differentiating the relative contribution of each prey species, the SIMM-UP renders each of these preys have a similar importance in the predators' diets, with a relative large uncertainty shows as a wide CIs (Figure 1). The reduction of the widths of 95% IC after including informative prior (Figure 1) was probably due to the availability of other sources of information that allowed discriminating between preys having similar isotopic values. Therefore, one must pay particular attention to the potential biases associated with the prior information in SIMMs because the latter are bound to both reduce and increase the importance of certain prey species in a predator's diet (see Figure 1).

Ideally, prior information would convey the potential (or known) prey consumption, which involves knowing the actual prey abundances as perceived by predators and their selectivity or diet preferences. On a technical level, the elicitation of prior information for compositional data like that input to SIMM is an ongoing research problem. The Dirichlet prior used in SIMM requires the input of mean proportion estimates for each food source, and a standard deviation estimate for a single one of these. Clearly this is not necessarily using all of the information that may be available (e.g. standard deviations for other food sources). One option is to use the product of individual Beta distributions [29], though this has the unfortunate side effect that prior specifications for different food sources may conflict with each other. The most promising way forward appears to be the use of log-ratio transforms, for which all quantities can be specified without any conflict (Parnell et al. 2013), though this is yet to be incorporated in any of the widely software packages. Obtaining prior information based on empirical data with reasonable accuracy and precision is rather difficult (if not impossible) for most predator species and habitats. Scat analysis and other traditional methods estimating diet composition seem to be the only practical means by which ecologists may obtain data that can be used as informative priors in SIMMs [29]. The issue is then how to discern whether these informative priors actually lead to biased posterior estimates of diet composition.

We believe that the only answer to the potential biases induced by prior information in SIMMs can come from using extensive knowledge on the natural histories of studied species and of habitats so as to interpret potential differences in the posterior distributions arising from using different priors [50]. Our studied objects were two sympatric pinnipeds species breeding in rookeries along the Uruguayan coast. Summer breeding involves a long lactation period lasting approximately 11 months for both species during which mothers alternate their foraging trips at sea with suckling bouts on land [51]. Both species mostly forage in the Uruguayan continental shelf (an extended and shallow area of approximately 200 km wide) and the shelf break. The foraging trips of lactating SASL females last only a few days and they largely remain in nearshore areas [34]. In contrast, SAFS females mainly forage in offshore areas [20] carrying out long foraging trips often lasting around 15 days [52] and traveling up to 500km away from the rookery (Franco-Trecu unpublished data). These differences in foraging behaviour between SAFS and SASL could lead to other biases in the estimated diet composition when scat analysis is used as prior information in SIMMs.

Given that the gut transit time in pinnipeds is at most five days [53] and that SAFS females forage for many days and far away from the rookery, many scats collected upon their return were empty [5] as in this study. Therefore, preys consumed by SAFS farther away from the rookery may be represented with low frequency or be altogether absent in scats, which would result in a biased estimation of SAFS diet composition towards those prey species consumed near the rookery. The latter may explain why the similarity of SAFS diet composition obtained with SIMM-UP and scats was much smaller that for all other paired comparisons. The SIMM-UP showed that SAFS's main preys were pelagic species (see Figures 1, 2) that can mostly be found far away from the rookery [54,55], thus matching both the foraging areas used by SAFS and the long duration of its foraging trips [52]. However, incorporating informative priors in SIMM shifted the rankings of preys such that Stripped weakfish represents about one-third of SAFS diet, an importance very similar to that obtain from the scat analysis. The Stripped weakfish is a very abundant species [54,55] that is one of the main targets of commercial fisheries in the Uruguayan continental shelf. On these grounds, Stripped weakfish ought to be well represented in SAFS scats and its high importance in the diet estimated by SIMM-IP suggests that SAFS mostly consumes this prey while returning to the rookery. In contrast, by foraging in areas close to the rookery and having short foraging trips, SASL scats are likely to contain representative samples of the preys consumed by this species.

Traditional indirect methods of diet composition (i.e. scat, pellet and gut contents) typically require intensive effort over

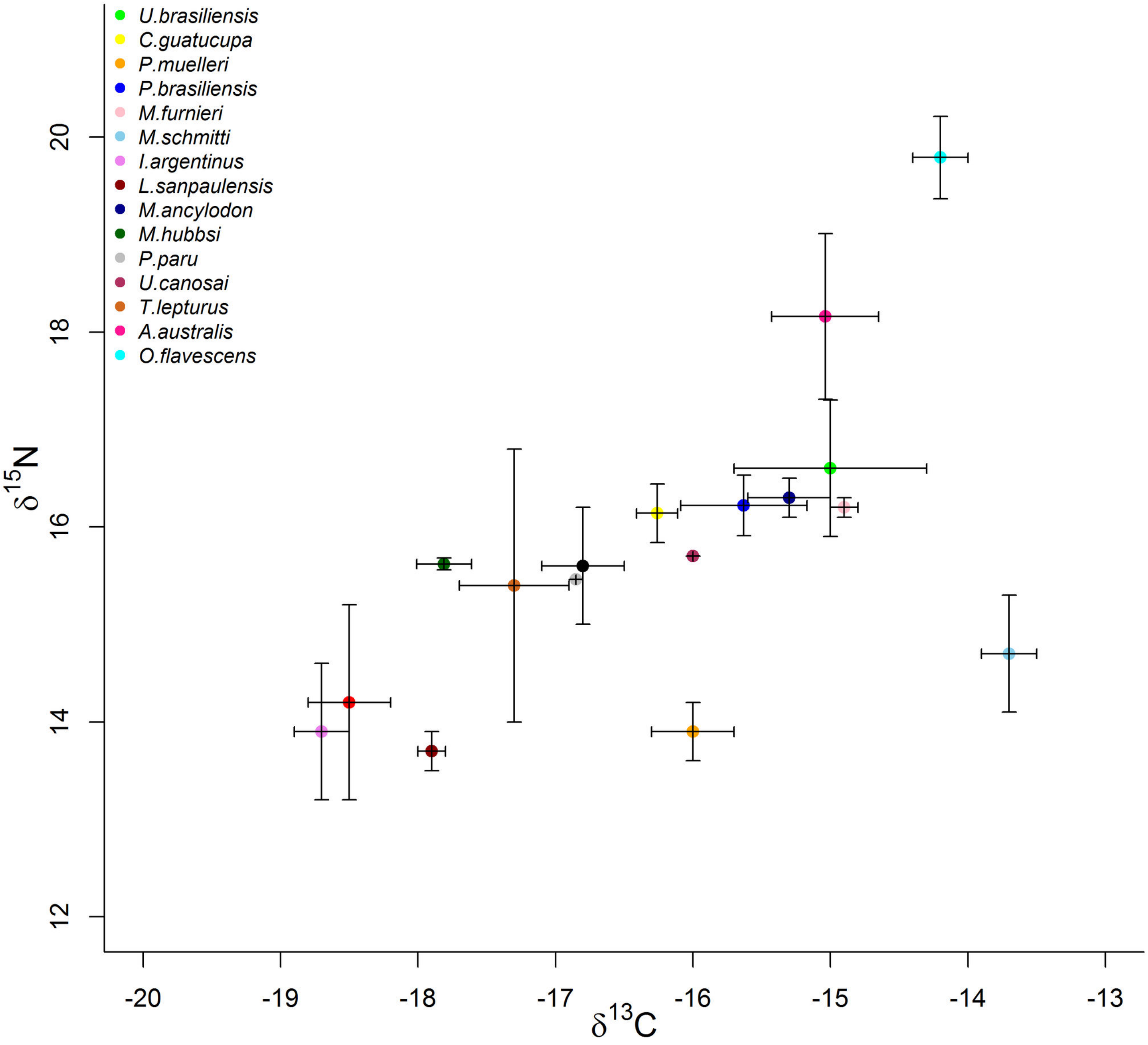

Figure 2. Predator and potential preys' stable isotope signal. Biplot of the isotopic contents of δ^{15}N and δ^{13}C of the South American sea lion (*Otaria flavescens*), the South American fur seal (*Arctocephalus australis*) and their main potential preys in Uruguay. Prey species were captured in the pelagic and neritic areas of the Uruguayan continental shelf and their names are fully indicated in Table 1. Error bars correspond to standard deviations. These averages and standard deviations were used as input for the mixing models.

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time to obtain representative samples of the preys consumed. Also, differential digestibility of preys and their reliance on recovering hard items make these methods prone to both under- and over-estimate the importance particular preys in the diet [6,12]. In contrast, stable isotope analysis require more easily obtained samples depending on the tissue analysed and the SIMMs can resolve many problems related to bias due to the different digestibility of preys [56] because they only consider assimilated food. However, SIMMs have other problems such as their sensitivity to have correct and accurate fractionation factors for the tissue and species analysed. Nevertheless, compared with other indirect methods, the information generated by stable isotopes seems at present the most reliable method to determine diet composition. While some studies have shown that diet composition obtained from traditional indirect methods coincide with SIMMs [30,57], this agreement is far from universal [31,58], leading to disparities in estimated length of trophic chains, trophic level and diet diversity [59]. For instance, the importance of trash in seagulls' diet and of fish discards in other seabirds is often found by traditional methods [30] but SIMMs can hardly ascertain its importance because of the near impossibility of assigning a unique isotopic content [46].

Both SIMMs and traditional indirect methods seem to have complementary strengths and limitations that almost always yield a partial understanding of diet composition. In cases when prior information influences the posterior distribution of SIMMs, incorporating informative priors should almost always lead to improvements in the estimates of diet composition at the risk of inducing biases in the contributions of prey species to the diet. Therefore, just as estimates of diet composition obtained using traditional indirect methods need be critically interpreted because of their known biases, care must be exercised when interpreting diet composition obtained by SIMMs with informative priors. However, as preys isotopic data allow a better discriminatory power of preys' contributions to the diet, using informative priors should lead to more precise but largely unbiased estimates of diet composition. This should be particularly important for species living in very productive habitats with a high diversity of potential preys having similar signals in the isotopic space [46]. We believe that the best approach to obtain a near-complete view of predators' diet composition should involve the simultaneous consideration of different sources of partial evidence (traditional methods and SIMM with and without informative priors) in the light of known natural history of the predator species under study so as to reliably ascertain and weight the information yielded by each method.

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Author Contributions

Conceived and designed the experiments: VFT. Performed the experiments: VFT RF FRS. Analyzed the data: VFT PI AP MD. Contributed reagents/materials/analysis tools: VFT PI AP. Wrote the manuscript: VFT PI AP MD FRS.

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Foraging behavior of lactating South American sea lions (*Otaria flavescens*) and spatial–temporal resource overlap with the Uruguayan fisheries

Federico G. Riet-Sapriza [a,*], Daniel P. Costa [b], Valentina Franco-Trecu [a], Yamandú Marín [c], Julio Chocca [c], Bernardo González [c], Gastón Beathyate [c], B. Louise Chilvers [d], Luis A. Hückstadt [e]

[a] *Proyecto Pinnípedos, Cetáceos Uruguay, Sección Etología, Facultad de Ciencias (UDELAR), Iguá 4225, CP 11400 Montevideo, Uruguay*
[b] *Department of Ecology and Evolutionary Biology, University of California, 100 Shaffer Road, Santa Cruz, CA 95060, USA*
[c] *Laboratorio de Tecnología Pesquera, Dirección Nacionalde Recurso Acuáticos, M.G.A.P., Constituyente 1497, P.O. Box 1612, CP 11200 Montevideo, Uruguay*
[d] *Aquatic & Threats Unit, Department of Conservation, P.O. Box 10-420, Wellington 6011, New Zealand*
[e] *Ocean Sciences Department, University of California, 100 Shaffer Road, Santa Cruz, CA 95060, USA*

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ABSTRACT

Resource competition between fisheries and marine mammal continue to raise concern worldwide. Understanding this complex conflict requires data on spatial and dietary overlap of marine mammal and fisheries. In Uruguay the South American sea lions population has been dramatically declining over the past decade. The reasons for this population decline are unknown but may include the following: (1) direct harvesting; (2) reduced prey availability and distribution as a consequence of environmental change; or (3) biological interaction with fisheries. This study aims to determine resource overlap and competition between South American sea lions (SASL, *Otaria flavescens*, $n=10$) and the artisanal fisheries (AF), and the coastal bottom trawl fisheries (CBTF). We integrated data on sea lions diet (scat analysis), spatial and annual consumption estimates; and foraging behavior-satellite-tracking data from lactating SASL with data on fishing effort areas and fisheries landings. We found that lactating SASL are benthic divers and forage in shallow water within the continental shelf. SASL's foraging areas overlapped with CBTF and AF fisheries operational areas. Dietary analysis indicated a high degree of overlap between the diet of SASL and the AF and CBTF fisheries catch. The results of our work show differing degrees of spatial resource overlap with AF and CBTF, highlighting that there are differences in potential impact from each fishery; and that different management/conservation approaches may need to be taken to solve the fisheries-SASL conflict.

1. Introduction

Marine mammals are abundant, large animals with high energetic demands, and consume prey over a wide range of trophic levels (Bowen, 1997; Trites, 2001) and as such they are thought to have a role in the structure and function of marine communities (Estes, 1979; Katona and Whitehead, 1988; Laws, 1984; Ray, 1981). These ecosystem interactions may lead to conflicts with commercial fisheries and may have detrimental effects for both parties (Alverson, 1992; Australian Government Department of Agriculture Fisheries and Forestry, 2006; Beddington et al., 1985; Bjorge et al., 2002; Harwood and Croxall, 1988; Kaschner and Pauly, 2004; Kovacs et al., 2012; Northridge, 1985; Northridge and Hofman, 1999; Plaganyi and Butterworth, 2002; Smith, 1994). However, in most cases the impact of fisheries on marine mammal populations is difficult to determine, especially considering that so little is known about the status and trends for most species (National Research Council, 2003).

Interaction between marine mammals and fisheries can be categorized as "operational or direct" and "ecological, biological, trophic or indirect" interactions (Beverton, 1985). The former, implies interacting directly with fisheries operations that results in bycatch of marine mammals, or consumption of catch by marine mammals (Dans et al., 2003; Gulland, 1986; Hamer et al., 2012; Read, 2005, 2008; Read et al., 2006; Shaughnessy et al., 2003; Wickens, 1994; Wickens, 1995; Wilkinson et al., 2003). Biological interactions between marine mammal and fisheries are complex, poorly understood, largely unmanaged (Cornick et al., 2006; Goldsworthy et al., 2003; Lowry and Frost, 1985; Planganyi and Butterworth, 2005; Trites et al., 1997) and imply competition for food resources, either directly or indirectly (Abrams et al., 1996). This interaction can go both ways; fisheries may be depriving marine mammals of food resources; and consequently limiting the growth and the recovery of their population (Butterworth, 1992; Butterworth et al., 1988; DeMaster et al., 2001; Gulland, 1987; Trites et al., 1997;

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* Corresponding author. Tel.: +598 22041835.
E-mail address: frietsapriza@gmail.com (F.G. Riet-Sapriza).

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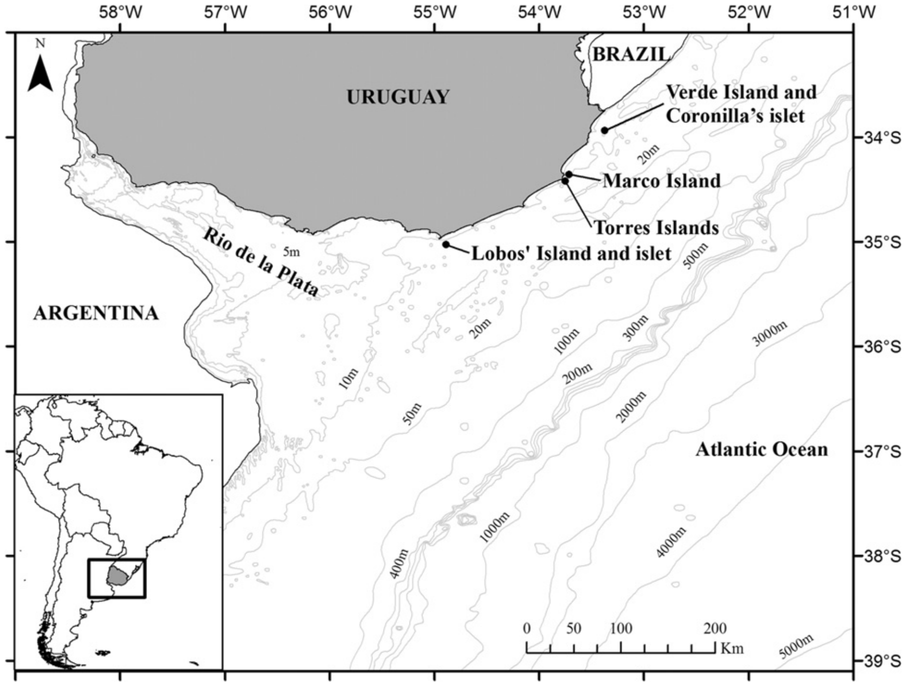

Fig. 1. Map of the locations of the main breeding rookeries of South American sea lions *Otaria flavescens*, in Uruguay. Isobath data layer obtained from FREPLATA-Proyecto de Protección Ambiental del Río de la Plata y su Frente Marítimo (www.freplata.org).

Wickens et al., 1992) or marine mammals may reduce prey population thereby reducing the catch available to commercial fisheries (Trites et al., 1997). At a large scale, the intensity of interaction will depend on the extent to which marine mammals and fisheries overlap in space and time. At the individual scale, the interaction will vary as function of individual preferences and its response to changes in the population composition and abundance (Matthiopoulos et al., 2008).

South American sea lions (SASL, *Otaria flavescens*) are widely distributed along the Atlantic and Pacific coast of South America, from northern Peru to southern Brazil (Vaz-Ferreira, 1981). In Uruguay, SASL breeds in coastal islands, namely Lobos' Island and islet (approximately 36% total annual pup production); Torres Islands (Rasa, Encantada and Islet, 37%), Marco's Island (27%); and Verde Island and Coronilla's islet (Fig. 1.) (Vaz-Ferreira, 1981). SASL have been extensively exploited in the past throughout their geographical range. Although, most populations are currently recovering (Reijnders et al., 1993) this not the case in Uruguay. In Uruguay the SASL population has declined dramatically over the past decade (Páez, 2006) and continues to do so at an annual rate of 1.7% (Dirección Nacional, de Recursos Acuáticos, 2012). The reason for this decline is unknown but may include the following: (1) direct harvesting; (2) reduced prey availability and distribution due to environmental change; or (3) biological interaction with fisheries or competition with the sympatric South American fur seal (*Arctocephallus australis*). However, the overlap in consumed prey species between SASLs and fur seals suggests that this interaction is limited (Franco-Trecu et al., 2012). Within the Atlantic SASL have a very broad diet that consists of a number of species in common with fisheries suggesting that a fisheries interaction is occurring (Crespo et al., 1997; George-Nascimento et al., 1985; Koen-Alonso et al., 2000; Naya et al., 2000; Thompson et al., 1998). The interaction between SASLs and artisanal and commercial fisheries has been examined across its entire geographic range (Aguayo and Maturana, 1973; Campagna et al., 2001; Hückstädt and Antezana, 2003, 2006; Hückstädt and Krautz, 2004; Koen-Alonso et al., 2000; Romero et al., 2011; Sepúlveda et al., 2007; Szteren, 2006; Szteren and Páez, 2002; Thompson et al., 1998).

Within Uruguay, interactions between fisheries and SASL have been reported (Szteren et al., 2004; Szteren and Páez, 2002) and two important prey items of SASL diet, stripped weakfish (*Cynoscion guatucupa*) and whitemouth croaker (*Micropogonias furnieri*) are targeted by both the AF and CBTF fisheries. Naya et al.'s (2000) and Szteren et al.'s (2004) results and the SASL bycatch (PROMACODA[1] unpublished data) in the coastal bottom trawl fisheries indicate an operational interaction and a potential biological interaction with SASL, although none of these studies addressed the spatial extent of these interactions by examining the overlap between the areas of fishery operation and SASL home range in Uruguayan waters.

Lactating SASL are central place-foragers (Orians and Pearson, 1977) that make foraging trips at sea and return to their rookeries or colony (central place) to nurse their young (Thompson et al., 1998). As a consequence, the latter behavior and foraging are separated in time and space (Bonner, 1984; Oftedal et al., 1987); therefore, it is crucial that foraging areas be close to the rookeries since travelling to these sites can incur high energy cost. This is particularly important for lactating pinniped females that must forage during lactation (Boness et al., 1994). The duration and distance of maternal foraging trips are constrained by the fasting ability of the offspring on land. Under conditions when local prey availability is scarce due to natural perturbations or anthropogenic factors, maternal foraging behavior may change, thereby creating sub-optimal foraging conditions (increase foraging energy cost, scarce food resources) (Boyd et al., 1994).

The magnitude of the competition between a predator (e.g. sea lion) and the fisheries will depend partly on the degree of spatial and temporal resource overlap, what prey species are preferred by the two competitors and how the abundance of those prey vary in time and space (Matthiopoulos et al., 2008). Given the overlap between Uruguayan CBTF and AF (Uruguay Dirección Nacional de Recursos Acuáticos, 2010) and the diet of SASL (Naya et al., 2000), there is potential for competition for resources. Understanding the extent of the potential resources competition between SASL and the fisheries is

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[1] Onboard Tagging and Data Collection. Program, NGO Karumbé, Uruguay.

necessary for effective sea lion conservation efforts and fisheries management. In this study we hypothesized that the biological interaction between SASL and fisheries may create sub-optimal foraging conditions for lactating females breeding in Isla de Lobos the second largest breeding colony. The objectives of the present study were as follows: (i) to examine the diving behavior of lactating SAS, (ii) to determine the spatial distribution of foraging effort of lactating SASL, (iii) to study the diet of lactating SASL, and (iv) to integrate these data with information of spatial distribution of fishing catch and effort to quantify the trophic and spatial overlap between SASL and the Uruguayan artisanal and coastal bottom trawl fisheries.

2. Materials and methods

2.1. Study site, animal handling and instruments

This study was conducted at Isla de Lobos breeding colony (Fig. 1, 35°01'S; 54°52'W) between mid-January and late February, 2009. We selected 10 adult lactating based on approachability and appearance, and captured with hoop nets to later anesthetize using isoflurane gas mixed with oxygen (0.5–2.5%) using a portable-field vaporizer (Gales and Mattlin, 1998). While anaesthetized we weighed sea lions with a 250 kg ($\pm$0.1 kg precision) capacity digital scale and we recorded morphometric measurements. Uniquely numbered plastic tags (Allflex® USA Inc.) were placed onto the trailing edge of both fore-flippers. To monitor at-sea movements, female sea lions were fitted with smart position and transmitting (SPOT) Argos tag (SPOT5 model, 32 g, Wildlife Computers, Redmond, WA, USA) or a Rechargeable Fastloc^{TM} GPS dataloggers (F1G 238A model, 217 g, Sirtrack, Havelock North, New Zealand). Time–depth recorders (TDR) (Mk9 model, 30 g, Wildlife Computers Inc.) were deployed to obtain diving behavior (resolution of 0.5 m for depth, and 0.05 °C for temperature with a 2 s sampling rate) and VHF radio transmitters (MM170B model, 31 g, Advanced Telemetry Systems, Inc. Isanti, MN, USA) were used to locate the sea lions for recovery when on land. Each instrument was attached with epoxy onto a neoprene patch, then mounted on mesh netting and secured with plastic cable ties before deployment. The instrument assemblage attached to the neoprene patch were glued either to the fur on the lower back or between the shoulders of the sea lions using 5 min quick set epoxy (Qm-50 Master Mend Epoxy, Loctite, Henkel Consumer Adhesives, Inc., OH, USA). To recover the instruments the animals were sedated with a dosage of 1 mg/kg Midazolam, concentration of 50 mg/ml administered with a Dan-Inject Rifle (Børkop, Denmark). After sedation, we restrained the animals with a hoop net. The instruments were removed by cutting through the neoprene mounting patch leaving behind the epoxy mount that would later fall off when the animals molt.

2.2. Diving behavior data analysis

Diving data were analyzed using custom-written software (IKNOS toolbox Y. Tremblay, *unpublished*) in Matlab® (The MathWorks^{TM}, Natick, MA, USA). Foraging dives were distinguished from travelling dives by assuming that these dives consisted of a sequence of shallow dives or “porpoising” (<5 m), a behavior characteristic to travelling sea lions (Blake, 1983; Williams, 2001). A frequency distribution of dive depth was used to determine the maximum depth at which shallow dives occur following Tremblay and Cherel (2003). Following this approach we defined porpoising dives as dives <5 m and these were excluded further analysis. Total vertical distance during foraging trips ($\sum$(dive depths from all dives) $\times$ 2) was calculated following the method of Horning and Trillmich (1997). We defined an index of dive effort calculated from the rate of vertical distance covered in the water column as a function of time (Arnould et al., 1996), which was modified to account for the distance covered at the bottom by benthic divers (Costa and Gales, 2000). The Intra-Depth-Zone index (IDZ) or the tendency to repeatedly dive to a given depth was calculated for all dives (Tremblay and Cherel, 2003). Transit time was calculated as the descent plus ascent time of the dive. To visually determine difference in dive depth between daylight and night (i.e., diel pattern) we plotted a frequency distribution of the number of dives against time of day and dive depth. In addition, we tested the significant effect of time of day (daylight vs. night) by using repeated-measures mixed models (PROC MIXED in SAS version 9.1.3, SAS Institute Inc.) for each response (mean dive depth, mean bottom time, mean dive duration). A spherical spatial autocorrelation model was used in the mixed model as described by Frost et al. (2001). Residuals were assessed using quantile–quantile plots and transformation was not necessary for subsets of randomly selected dive parameters. The best model selection was determined using Akaike's Information Criterion (AIC) with fixed effects (time of day, interaction) and sea lion as a random effect with repeated measured analysis. The duration of foraging trips (time at sea), was calculated by using the diving records, and when the TDR was not recovered we used the satellite records. The satellite tags (SPOT5 and Rechargeable Fastloc^{TM} GPS dataloggers) are equipped with wet/dry sensor set to turn off when dry. If the tag was dry (i.e. not submerged) for more than 2 h the sea lion was recorded as hauled-out; a haul-out period was determined to have ended when the tag became wet for 2 h; whilst a foraging trip ended when the wet/dry sensor reported the animal as hauled-out (dry for 2 h). To determine if SASLs were performing their dive within their physiological limits, we calculated Aerobic Dive Limit (cADL) using (Gentry et al., 1986) equation: ADL (min)= 1.57*mass (kg)$^{0.22}$.

2.3. Animal tracking data analysis

GPS tracking data were downloaded from Rechargeable Fastloc^{TM} GPS dataloggers and was filtered using Sirtrack FastLoc Admin Tool software (version 1.1.3.34, Sirtrack, Havelock North, New Zealand). A simple fast-forward speed filter was used to eliminate unrealistic locations from the data after resolving the GPS data (McConnell et al. 1992). Satellite location data were obtained from Service Argos (Service Argos, 1996), and filtered using a forward looking particle filter (Tremblay et al., 2009). The algorithm used several criteria to remove unlikely satellite locations: (1) realistic travel speeds of a subject between two fixes (>10 km h^{-1}); (2) change in azimuth between successive fixes; (3) Argos location class; and (4) time lapse between two consecutive fixes. Dive locations were interpolated from the filtered track data for each individual to produce a map of foraging area (dive locations) using ArcMap^{TM} 9.3 GIS (ESRI®, ESRI Inc., Redlands, CA, USA). To minimize autocorrelation in spatial analysis, we generated a mean hourly location for each sea lion from the filtered locations. Thereafter, we tested our data from departures from independence using the Schoener index (Schoener, 1981), and the Swihart and Slade index (Swihart and Slade, 1985). A Schoener index value <1.6 or >2.4 and a Swihart and Slade index value >0.6 indicate significant autocorrelation. The resulting coordinates were placed onto local UTM projection (zone 21S, WGS84) using ArcMap^{TM} 9.3.1 GIS. Home range sizes were estimated with the kernel (KR) method (Worton, 1989) and the peeled minimum convex polygon method (95% MCP) (Mohr, 1947), excluding 5% of observations most peripheral to the mean (Schoener, 1981). We used a fixed kernel least-square cross-validation smoothing factor for each KR (Seaman and Powell, 1996). KR density plot (with 25%, 50.75% and 99.99% isoline) and peeled MCP (95%) of home ranges for all locations per female were determined using the Home Range Tools for ArcGIS extension (Rodgers et al., 2005). Also, KR density (with 50% and 95% contours) for all fisheries locations was produced with the purpose of identifying the core areas of fisheries effort (operation). The 25% for sea lions and 50% for CBTF contour was used to highlight core regions of utilization distribution, whilst 50–95% contours showed areas of decreasing usage, respectively.

2.4. Diet characterization

Scats were collected at Isla de Lobos (Fig. 1) during summer January 2009. Scat samples were washed through a 0.5 mm mesh sieve and prey hard parts recovered were compared with a reference collection, were identified to the lowest possible taxon; and hard parts digested beyond recognition were not included in our analysis (Abilhoa and Correa, 1993; Barros-Lemos and Albihoa, 1993; Clarke, 1936; Correa and Vianna, 1993; Torno, 1976; Volpedo and Echevarría, 2000). The number of individuals of a particular fish species (NF) found in scat sample was calculated following Koen Alonso et al. (1998) as $\mathrm{NF}=\mathrm{LO}+0.5\mathrm{NO}$, if $\mathrm{LO}>\mathrm{RO}$, or as $\mathrm{NF}=\mathrm{RO}+0.5\mathrm{NO}$, if $\mathrm{RO}>\mathrm{LO}$, were, LO is the number of left otoliths, RO is the number of right otoliths, and NO is the number of unidentified otoliths. The minimum number of cephalopods consumed was estimated from the maximum number of lower beaks recovered for each species (Koen Alonso et al., 1998) since only lower beaks are used to identify the Family and upper beak were separated as unclassified. To estimate prey size, otoliths with no erosion to medium erosion (grade of erosion 0–2) were measured using digital calipers. Thereafter, size of prey consumed was estimated from regression equations of total prey length (TL_p) and otoliths length (OL) developed for each fish taxa. Biomass was estimated from regressions between total length (TL) and mass of prey (Bugoni and Vooren, 2004). To determine the importance of each prey species the following indexes were calculated: the percent frequency of occurrence (FO%, percentage of samples in which a taxon was observed); percentage by number (N%, percentage of the total prey number across all samples); percentage of biomass (W%, percentage of biomass of each prey that contributes to the total biomass); and index of relative importance ($\mathrm{IRI}=(\mathrm{N\%}+\mathrm{W\%})\times\mathrm{FO}$).

2.5. Coastal Bottom Trawl and Artisanal Fisheries data

The Uruguayan Coastal Bottom Trawl Fisheries (CBTF) targets mainly whitemouth croaker and striped weakfish (Uruguay Dirección Nacional de Recursos Acuáticos, 2010). The fleet is restricted to fishing within 7 nm from the coastline and includes a total of 33 boats ranging between 19 and 31 m (loading capacity of 85–240 gross tons, and 290–680 horse power). The fishing technique utilized by this fleet corresponds to pair trawling (i.e. two boats, each with one towing cable). Each fishing vessel is equipped with a vessel monitoring system (VMS), obtaining GPS position, course and speed of bottom trawl fishing vessels on an hourly basis. Data on CBTF and artisanal landings and CBTF satellite locations were obtained from DINARA. For the purpose of mapping the fishing effort of the CBTF fleet, GPS position obtained from VMS of the whole Uruguayan fleet was filtered by speed (3.5–4 nm that was an indication of fishing activity). Filtered locations were plotted on a grid (cell size 10 km × 10 km) in ArcMap$^{\mathrm{TM}}$ 9.3 GIS and the number of location per cell was an indication of fisheries effort (number of VMS per 100 km^2). The artisanal fishing fleet that operates within 7 nm of the coast is characterized by vessels that are not larger than 10 m or 10 gross registered tons. The distribution of fishing effort in the artisanal fishery along the 500 km of the Uruguayan coast was estimated based on fortnightly surveys of fisherman conducted over a three month period during the 2009 austral summer.

2.6. Niche overlap

We used the Morisita–Horn index ($C\lambda$) to calculate the niche overlap between SASL and the CBTF (Horn, 1966; Morisita, 1959):

$$C\lambda = 2\sum_{i=1}^{n} p_{ij}p_{ik} \Big/ \sum_{i=1}^{n} p_{ij}^2 + \sum_{i=1}^{n} p_{ik}^2$$

where, $C\lambda$ is the index of overlap of diet between predator (j) and predator (k), P_{ij} is the proportion of prey i that is consumed by predator (j), P_{ik} is the proportion of prey i that is consumed by predator (k) and n is the total number of prey. The values of $C\lambda$ range between 0 and 1, a value of 0 means that diets are different, and a value of one diet are identical (Horn, 1966; Smith and Zaret, 1982). The degree of overlap was determined according to Langton's (1982) scale: low overlap, 0–0.29; medium overlap, 0.30–0.65; and high overlap, greater than 0.66.

2.7. Spatial resource overlap

The degree of resource overlap between SASL and the Uruguayan fisheries was quantified using a niche-overlap index (MacArthur and Levins, 1967) and modified by Trites et al. (1997) and further developed by Kaschner et al. (2001) into a Resource overlap/fisheries impact index:

$$a_{jl} = \left(\left(\frac{2\sum_k p_{l,k}p_{j,k}}{\sum_k p_{l,k}^2 + p_{j,k}^2}\right)(\varrho_l C_j)\right)\Big/(\mathrm{NF})$$

where a_{jl} express the quantitative overlap between fishery j and sea lion l in each cell sharing the resource k, and $p_{l,k}$ and p_{jk} describes the proportion that each of the k resource contributes to the average diet of sea lions l or the catch composition of the fisheries j. This term is multiplied with the product of the total average food consumption of sea lion l ($b_{d=}$estimated annual prey biomass, see Section 2.7.1 for details) and the total fisheries' annual catches within each cell. The result is normalized using a normalization factor (NF) defined as the product of the total food consumption of sea lions and total fisheries catches adjusted by a division by a scaling factors of 10^9 (Kaschner et al., 2001). To construct the Resource overlap/fisheries impact index, a food consumption model (estimates of SASL food resource utilization) and a spatial food consumption model was created following Kaschner et al. (2001) work and modified accordingly as described below.

2.7.1. Food consumption model

We used a simple generic food consumption model developed by Trites et al. (1997) for marine mammals to generate estimates of the total daily consumption and specified by food type, for adult SASL females population from Isla de Lobos:

$$\varrho_i = \sum N_s W_s R_s$$

where N_s is the number of individuals by sex s, W_s is the mean individual weight by sex and R_s is the total food consumption by food type and by sex for an individual of weight W_s. Main model input parameters for the model were as follows: (1) abundance estimates of females at Isla de Lobos, (2) female mean body mass, (3) daily food consumption and by food type (R_s), and (4) diet composition. The most recent female SASL abundance estimates were obtained from surveys conducted by DINARA in 2009 (Dirección Nacional de Recursos Acuáticos, 2012). We used the Von Bertalanffy growth curves available for SASL population in Patagonia that allow us to estimate the body mass for each age class and consequently the mean body mass of adult SASL females in Uruguay (García, 1997). Diet composition was obtained from the present study and daily food consumption for adult SASL female was available in Winship et al. (2006), which was estimated using a bioenergetic model (M) developed by Winship et al. (2002). Whereas food consumption by prey species was estimated using the equation:

$$R_s = \sum_{j=l}^{s} \mathrm{pDC}_{js} M_s$$

where pDC_{js} is the proportion of prey species j in the diet of sex s, and the second product of the equation is the daily food consumption (M_s) of sex s (adult SASL female) predicted from a bioenergetic model (Winship et al., 2002, 2006). Estimate of total daily consumption (ϱ_i) and consumption of specific prey species by SASL females from Isla de Lobos was multiplied by 365 days to estimate the total annual food consumption (C_{sasl}), and total annual consumption of individual prey species.

2.7.2. Spatial food consumption model

To extrapolate the satellite-tracking data collected in this study to the SASL females population at Isla de Lobos we applied a simple distance-based foraging models (normal probability density function) developed by Goldworthy et al. (2003), that assume that seals forage within a set range (mean foraging distance and standard deviation) from their colony:

$$f(D_d) = \frac{1}{\sigma\sqrt{2\pi}} e^{-\left(\frac{D_d-\mu}{2\sigma}\right)^2}$$

where f is the probability of an animal from a given colony foraging at a particular cell (d), and it was estimated by calculating the distance (D) from the cell to the colony and the mean (μ) and standard deviation (σ) of foraging distance (km). We used ArcMap^{TM} 9.3 to plot shape files of bathymetry and overlaid with a 10×10 km^2 grid cell (100 km^2) in projected coordinate (Mercator World). The coordinates (latitude and longitude) of each cell (center point) were obtained, and the distance from Isla de Lobos to each point was calculated. The estimated annual prey biomass (kg/100 km^2) consumed by SASL from Isla de Lobos at each cell (b_d) was calculated using the following formula developed by Goldworthy et al. (2003) but modified to account for one colony:

$$b_d = C_{sasl} \frac{f(D_d)}{\sum_{d=1}^{d=N_d} f(D_d)}$$

where N_d is the total number of cells and C_{sasl} is total annual prey consumption by adult SASL females. The estimated prey biomass consumed at each grid cell (10×10 km^2) by sea lions and foraging areas of SASL from Isla de Lobos were manually digitized as shape file polygons using ArcMap^{TM} 9.3 GIS tool.

3. Results

3.1. Diving behavior

Seven of the 10 TDRs deployed on SASL females were recovered between 16 and 44 days after initial deployment during which a total of 91 foraging trips and 50,847 dive records were identified (Table 1). Dive parameters are summarized in Table 2. The distribution of dive depth and dive duration was unimodal at 20 m and 1.5 min, respectively (Fig. 2a, b). Eighty-four percent of all dives performed were between 1.0 and 2.5 min in duration (Fig. 2a). Approximately 70% of dives were between 15 and 25 m, 23% between 5 and 10 m, and 7% were between 30 and 55 m (Fig. 2b). Visual examination of the temporal distribution of the 50,847 dives recorded indicates that SASLs dove regardless of the time of day, exhibiting no obvious diel pattern in dive depth or dive frequency (Fig. 3). However, the statistical analysis indicated

Table 1
Maternal foraging trip and attendance duration (mean ± SD), and summary of dives records of lactating South American sea lions (*Otaria flavescens*) during the austral summer at Isla de Lobos, Uruguay. NA=no data available, time–depth recorder or satellite data was not recovered.

Female ID	Body mass (kg)	Body length (cm)	Total no. of dives recorded	No. of dives/ trip	Length of dive records (days)	No. of foraging trips	Foraging trip duration (days)	Haul-out duration (days)
H1	159.2	189.0	NA	NA	NA	5	2.7 ± 0.5	0.8 ± 0.6
H2	115.6	176.0	8807	880	39	10	1.6 ± 0.8	1.5 ± 0.5
H3	160.2	200.0	6332	575	37	11	1.7 ± 0.5	1.2 ± 0.2
H4	101.8	166.0	7824	300	35	26	0.7 ± 0.5	0.7 ± 0.5
H5	97.6	168.0	7605	691	34	11	1.7 ± 0.8	1.2 ± 0.7
H6	120.2	195.0	9009	450	37	20	0.9 ± 0.7	0.9 ± 0.3
H7	128.2	190.0	10,001	909	44	11	2.4 ± 0.8	1.6 ± 0.8
H9	142.8	185.0	NA	NA	NA	8	2.2 ± 0.7	1.9 ± 1.4
H10	152.2	179.0	1269	634	16	2	1.9 ± 0.8	2.6
Mean	125.1 ± 23.8	182 ± 13.3	7264 ± 2891	635 ± 219	35.6 ± 8.8	12 ± 7	1.5 ± 0.9	1.1 ± 0.8

Table 2
Dive parameters (mean ± SD and maximum) of seven lactating South American sea lions (*Otaria flavescens*) during the austral summer at Isla de Lobos, Uruguay. (cADL=calculated Aerobic Dive Limit; %IDZ (inter-depth zone) proportion of benthic dives/dives to the same depth of the total dives performed by the individual sea lion; PDI=post-dive interval; TVDT=total vertical depth travelled).

Female ID	Dive depth (m)		Dive duration (min)		Bottom time (min)		Transit time (min)		Rate (m/s)		PDI (min)	Dive rate (dives/h)	cADL (min)	Percent dives > cADL	Percent IDZ	TVDT (km)
	Mean	Max	Mean	Max	Mean	Max	Mean	Max	Descent	Ascent						
H2	23 ± 7	50	1.7 ± 0.5	4.8	0.9 ± 0.4	3.0	1.1	2.7	0.9 ± 0.3	0.9 ± 0.3	1.1	21.5 ± 8.8			71	398
H3	17 ± 6	35	2.1 ± 0.8	5.0	1.2 ± 0.7	3.8	0.8	4.5	0.7 ± 0.3	0.7 ± 0.3	2.3	14.4 ± 7.1	4.5	0.02	68	215.9
H4	18 ± 6	35	1.7 ± 0.6	4.2	1.1 ± 0.5	3.5	0.8	2.8	0.9 ± 0.3	1. ± 0.3	1.6	18.8 ± 9.5	4.8	0.02	68	279.5
H5	23 ± 8	57	2.1 ± 0.7	4.6	1.3 ± 0.6	4.0	0.7	2.7	1.1 ± 0.3	1.0 ± 0.4	1.7	16.1 ± 6.9	4.3	0.0	88	342.7
H6	23 ± 8	78	1.7 ± 0.6	4.4	0.8 ± 0.5	3.8	0.7	2.9	0.9 ± 0.3	0.9 ± 0.3	1.5	19.7 ± 8.3	4.3	0.1	54	406.6
H7	19 ± 6	36	2.1 ± 0.8	5.4	1.2 ± 0.7	4.0	0.8	3.2	0.8 ± 0.3	0.7 ± 0.3	1.9	16.1 ± 7.5	4.5	0.0	68	371.1
H10	29 ± 11	55	2.5 ± 0.8	4.8	1.3 ± 0.7	3.5	0.8	3.9	0.8 ± 0.3	0.8 ± 0.3	1.8	13.9 ± 4.7	4.6	0.2	71	74.2
Mean	21 ± 8	57	1.9 ± 0.7	5.4	1.1 ± 0.6	3.9	0.8	4.5	0.9 ± 0.3	0.9 ± 0.3	1.7		4.7	0.1	69	298.3 ± 120

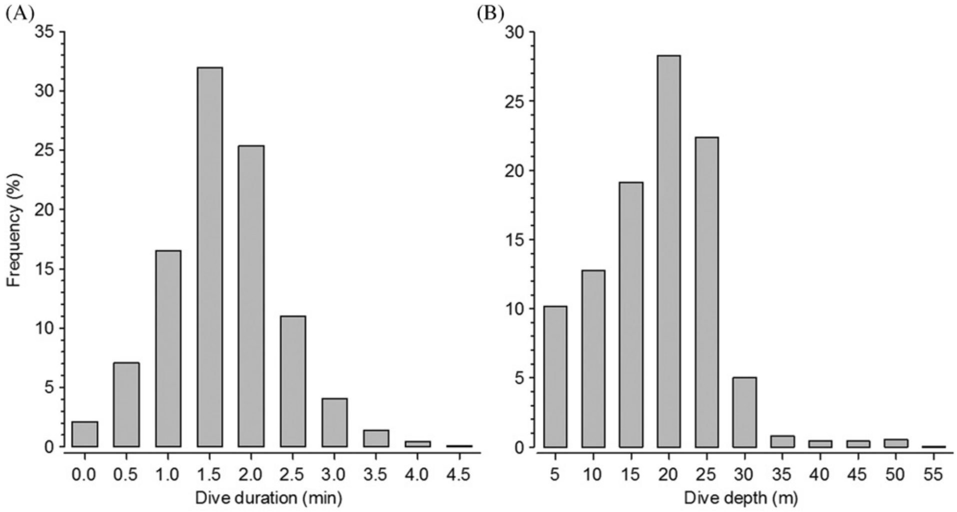

Fig. 2. Frequency distribution of the number of dives in relation (A) dive duration (min) and (B) maximum dive depth (m) for seven lactating South American sea lions (*Otaria flavescens*) during the austral summer at Isla de Lobos, Uruguay.

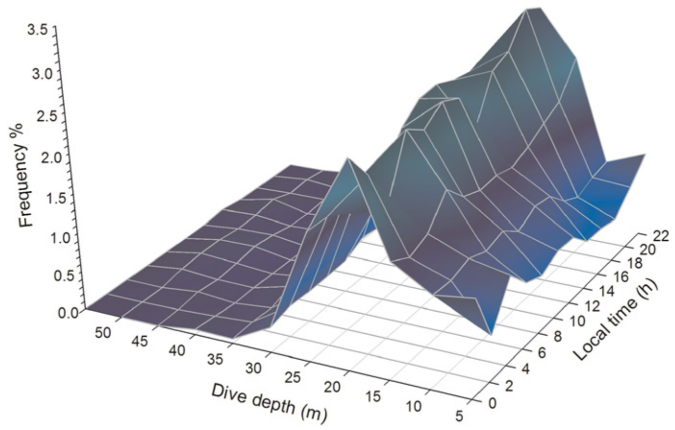

Fig. 3. Frequency distribution of the number of dives in relation to time of day (h) and maximum dive depth (m) for seven lactating South American sea lions (*Otaria flavescens*) during the austral summer at Isla de Lobos, Uruguay.

significant differences but without a biological significance. SASL dove significantly deeper at night (18.7, 33.1–70.4 m, mean, 95% confidence interval, $F_{1,6990}=3.97$, $P=0.046$) than during the day (18.4, 33.4–70.1 m), whereas dives were significantly longer during daytime hours (2.15, 1.43–2.86 min, $F_{1,6991}=8.59$, $P=0.0034$) compared with night dives (2.12, 1.41–2.84 min). As well, bottom time was significantly greater during the night (1.39, 0.81–1.97 min, $F_{1,6974}=26.77$, $P=0.0001$) than during the day (1.34, 0.76–1.92 min).

3.2. *Utilization distribution*

Eight of the 10 satellite telemetry tags (five SPOT5 tags and three Rechargeable Fastloc^{TM} GPS dataloggers) were recovered, yielding 4256 filtered locations over a 16–44 day period. A total of 2801 locations were obtained after sub-sampling one location per hour. The maximum distance travelled on a foraging trip from Isla de Lobos colony ranged between 37.8 and 135.5 km, whereas the total distance travelled (sum of all the foraging trips for each individual) ranged from 249 to 1062 km (Table 3). Female SASL foraged exclusively over the continental shelf, with individuals showing different dispersal patterns (Fig. 4). Most lactating SASL travelled west/ southwest or south/southeast of Isla de Lobos, although two individuals travelled northwest and along the coast (Fig. 4). The home ranges of lactating SASL were confined exclusively to waters over the continental shelf and the total area of utilization distribution was 3199.5 km^2 (95% MCP, Fig. 5). KR and peeled MCP 95% estimates were variable between individual and the mean ($\pm$SD) estimated home ranges areas accounted for 342 ± 251 km^2 for 50% KR, 565 ± 414 km^2 for 65% KR and $2224\pm1{,}639$ km^2 for MCP 95% (Table 3). The center of females 50% KR was located near and surrounding the breeding colony (Fig. 5).

3.3. *South American sea lion diet*

Prey species length and mass were estimated from the measurement of otoliths with no or low erosion (Bugoni and Vooren, 2004). A total of 73 scat samples were processed and 58 samples contained prey hard parts. One hundred and one otoliths from teleost fish and 42 cephalopods beaks were found. The most abundant prey species in the diet of SASL during summer were cephalopods (Family *Omastrephidae)* and striped weakfish. However, the principal contribution by biomass was accounted by whitemouth croaker (46.7%), largehead hairtail (*Trichiurus lepturus*) (24.0%), Brazilian codling (*Urophysis brasiliensis*) (17.0%) and Argentine croaker (*Umbrina canosai*) (8.1%). Collectively these four species accounted for >95% of the estimated reconstructed prey biomass (Table 4). The maximum length for striped weakfish found in the diet of sea lions was less than the minimum length permitted to be landed in the fisheries, although, regulation allows for a percentage of smaller sized fish. In the case of whitemouth croaker, the length of this species observed in the diet of SASL (31.9 cm) and the minimum length (32 cm) allowable that can be landed by the fisheries were similar. There are no fisheries regulations for minimum size that can be landed for king weakfish, Argentine croaker or Brazilian codling.

3.4. *Niche and resource overlap/fisheries impact indexes*

During the austral summer the Morisita–Horn (M–H) niche overlap index value indicated a high degree of overlap between the diet of SASL and the prey items targeted by the artisanal

Table 3
Metrics for foraging trip distances and home ranges sizes estimated with kernel method (KR) using the 50% and 65% isoclines and the peeled minimum convex polygon method (MCP 95%) for eight lactating South American sea lions (*Otaria flavescens*) from Isla de Lobos, Uruguay. Autocorrelation is measured with the Schoeners index (see Section 2). Means presented ± SD.

Female ID	total no. of locations	No. days deployed	Max. distance from colony (km)	Distance travelled (km)		KR (km^2)		95% MCP (km^2)	Schoeners index
				Total	Per trip	50%	65%		
H1	265	21	81.8	863.6	172.7 ± 61.4	290.2	493.1	3063.1	0.01
H2	444	39	127.0	1015.1	145.0 ± 70.9	563.3	942.9	4103.6	0.009
H3	22	37	118.5	576.7	52.4 ± 45.1	424.5	669.9	156.0	0.74
H4	538	35	66.6	503.8	21.9 ± 23.5	31.9	48.8	433.4	0.009
H5	592	34	135.5	1062.0	106.2 ± 61.0	475.3	821.9	4794.4	0.005
H6	454	37	37.8	249.0	35.6 ± 26.6	93.2	140.9	570.7	0.0027
H9	413	43	88.7	1053.1	131.6 ± 87.6	119.3	205.5	1298.8	0.0087
H10	73	16	109.7	330.5	165.2 ± 85.5	739.4	1196.2	2374.3	0.02
Mean			98.60 ± 31.3	706.7 ± 332.7	62.2 ± 63.0	342.1 ± 251.2	564.9 ± 413.9	2224.3 ± 1638.9	

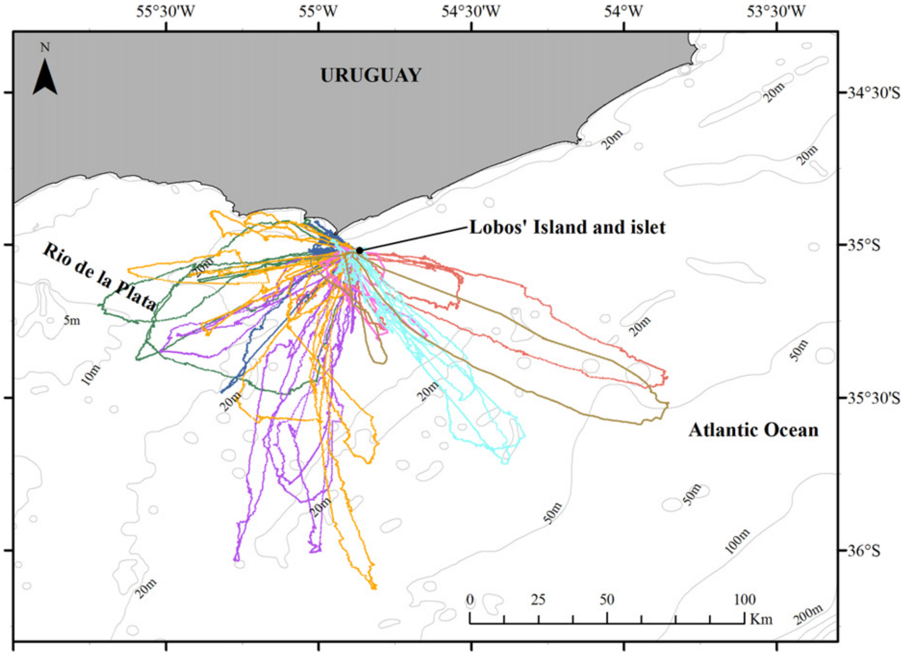

Fig. 4. Satellite locations from 8 (each color represents a track for an individual female) lactating South American sea lions (*Otaria flavescens*) instrumented at Isla de Lobos, Uruguay during the austral summer, 2009. Depth (isobaths, light gray lines) data was collected in 2002 by FREPLATA-Proyecto de Protección Ambiental del Río de la Plata y su Frente Marítimo and data layer was obtained from www.freplata.org.

fisheries (M–H = 0.84) and the CBTF (M–H = 0.79). The mean body mass of an adult female SASL (110.3 ± 3.29 kg), implies a daily food consumption of 6–7 kg day^{-1} according to the model of Winship et al. (2006). Thus, the total daily consumption and total food consumption for the year 2009 for the entire adult female population from Isla de Lobos was estimated in 298 t/day and 108,862 t, respectively (Table 4). The annual and daily prey consumption density estimated was 1.4 t/year/km^2 and 0.004 t/day/km^2, respectively (Fig. 6). The spatial distribution of the CBTF fishery effort showed an operational area of 97,800 km^2 (Fig. 7). The reported CBTF landing for year 2009 was 35,511 t (Table 4) and reported a lower daily catch per km^2 (0.0018 t/day/km^2) than SASL. During 2009, the main species targeted by CBTF were whitemouth croaker, followed by striped weakfish and king weakfish (Table 4). Argentine croaker and Brazilian codling were caught by the fleet but in minor quantities. The Resource Overlap/Fisheries Impact index indicated a spatial and temporal overlap between lactating SASL foraging areas and artisanal fisheries and CBTF operational areas (Fig. 8).

4. Discussion

This study is the first to estimate the core-use areas and home ranges of lactating SASL in Uruguay, and quantify the spatial–temporal resource overlap with fisheries. Our results showed that summer core-use areas of lactating SASL were restricted to near the breeding site with foraging occurring exclusively on the continental shelf. Like other lactating otariids, SASL are central place-foragers and are restricted to foraging relatively close to their colony (Costa, 1993; Houston et al., 2007). Thus the resource overlap with fisheries may have the potential to create sub-optimal foraging conditions for breeding females. As with any colonial breeding species there will be local depletion of resources near the colony (Ashmole, 1963), but this local depletion will become worse if the AF or CBTF fisheries operate in this area. As local prey are depleted, lactating females will have to work harder, stay at-sea longer and/or travel farther, requiring the expenditure of more energy resulting in reductions in the milk energy delivered to her pup (Boyd et al., 1994; Costa, 2008).

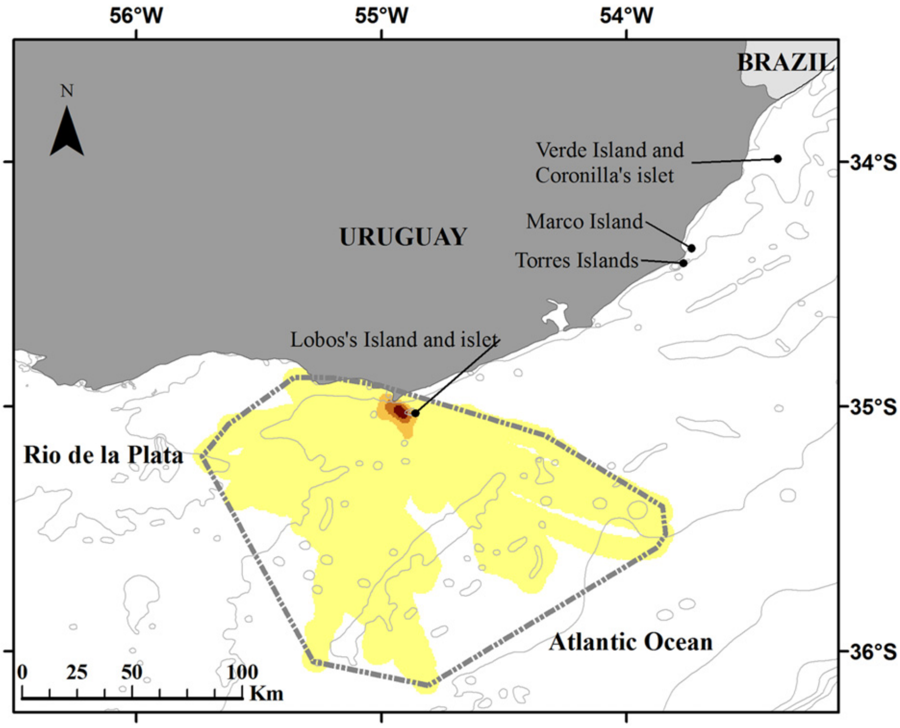

Fig. 5. Kernel density estimates (KR) and peeled minimum convex polygon (MCP) for eight adult lactating South American sea lions (*Otaria flavescens*) satellite-tracked from Isla de Lobos in 2009. Core-use areas and overall home ranges for sea lions are shown in dark brown (25% KR) and in lighter brown (50%, 75%, 99.99%) and shown in light dashed line (95% MCP), respectively.

Table 4
Estimate of the composition of the total annual Uruguayan artisanal fishery and coastal bottom trawl fishery catches, and diet composition and prey quantity of South American sea lion's (*Otaria flavescens*), and comparison of consumption of overlapping prey species. Composition of the South American sea lions diet expressed as % of frequency of occurrence (FO%, percentage of scat in which a prey was observed), % number (*N*%, percentage of the total prey number across all samples), % biomass (*W*%, percentage of the number of prey times the average body mass), and index of relative importance (IRI/100). NA was not possible to obtain biomass since no length-body mass regression is available.

Prey and catch species		**Diet composition of SASL**				**Total catch *t* (%)**[a]		**Seal consumption *t* (%)**	**Consumption of overlapping prey *t***	
Common name	**Scientific**	**FO%**	***N*%**	***W*%**	**IRI**	**Artisanal**	**Trawling**		**Fisheries**	**Sea lions**
Brazilian codling	*Urophysis brasiliensis*	15.79	3.73	17.0	3.27	181 (10.0)	188 (0.5)	18,507 (17)	369	18,507
Largehead hairtail	*Trichiurus lepturus*	31.58	9.94	23.98	10.7			26,105 (23.98)		
White mouthcroaker	*Micropogonias furnieri*	10.53	8.70	46.66	5.83	1379 (76.4)	22,349 (62.9)	50,795 (46.66)	23,728	50,795
Striped weakfish	*Cynoscion guatucupa*	31.58	13.04	0.72	4.34	177 (9.8)	6177 (17.4)	784 (0.72)	6354	784
Argentine seabass	*Acanthistius brasilianus*	10.53	6.83	NA	–			NA		
Argentine croaker	*Umbrina canosai*	10.53	3.73	8.10	1.24	51 (2.8)	1989 (5.6)	8818 (8.10)	2040	8818
Argentine conger	*Conger orbignyanus*	5.26	1.24	NA	–		10 (0.0)	NA		
Argentine hake	*Merluccius hubbsi*	10.53	3.11	3.54	0.70			3854 (3.54)		
Squid	*Loliginidae*	10.53	11.18	NA	–		1585 (4.5)	NA		
King weakfish	*Macrodon ancylodon*	–	–	–	–	16 (0.9)	3213 (9.0)	–		
Argentine anchoita	*Engraulis anchoita*	–	–	–	–			–		
Searobin	*Prionotus* sp.	–	–	–	–			–		
Cephalopods	*Omastrephidae*	5.26	38.51	NA	–			NA		
Total catch/prey						**1804**	**35,511**	**108,862**	**32,491**	**78,868**

[a] *Source*: Uruguay Dirección Nacional de Recursos Acuáticos (2010).

4.1. *Limitations of the study*

Given the continued decline in this population, there are only two small breeding aggregations amenable to research at Isla de Lobos. As it was important to minimize disturbance to this small colony we were limited to a small sample size. We therefore assumed that these data are representative of all female SASL at Isla Lobos over the entire year using a simple spatial model. In terms of fisheries information we were limited by the type of the data that are collected by the fisheries regulatory agency (DINARA), data on the spatial distribution of fisheries catch were not available. Furthermore, this study didn't investigate the biomass of the resource and resource allocation. These are limitations to consider in the interpretations of this research. Further research in this area should be focus toward, such as (i) increasing the sample size of the various data set, (ii) determining fish stock size to facilitate quantitative resource biomass and allocation, (iii) extent the study period to cover the entire year, and (iv) conduct telemetry and diet study in breeding colonies located in Marcos Island and Torres Islands to quantify the extent of the resource overlap with the fisheries in those locations.

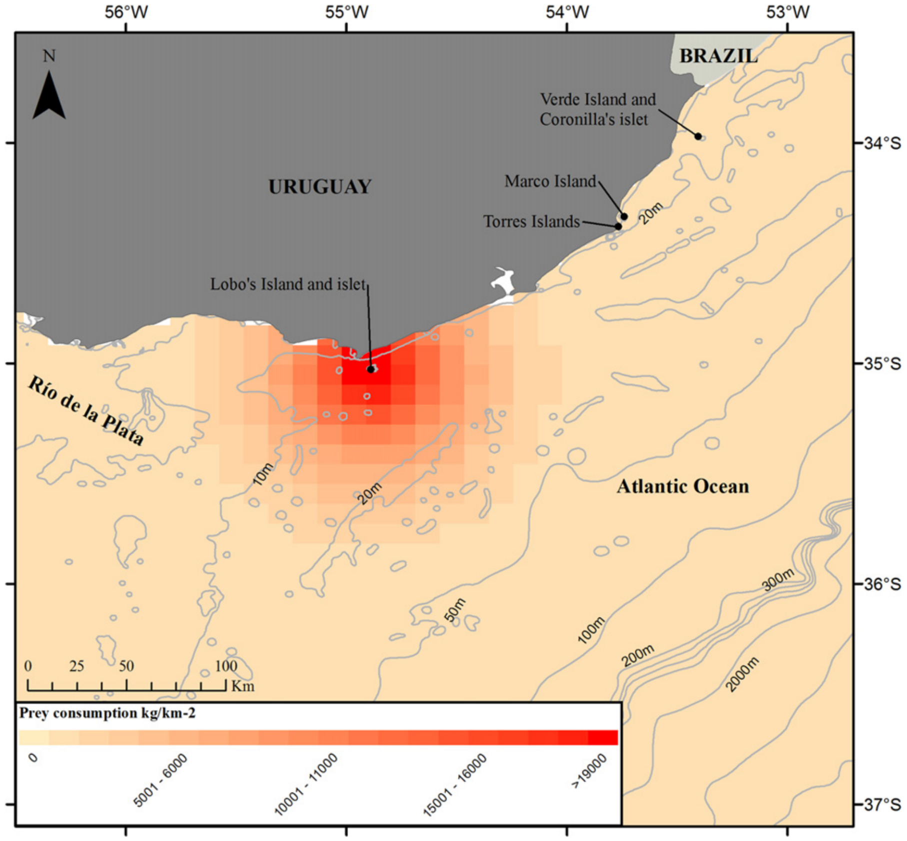

Fig. 6. The estimated annual spatial distribution of prey consumption of adult lactating South American sea lions (*Otaria flavescens*) from Isla de Lobos in 2009 on the continental shelf of the Rio de la Plata and Atlantic Ocean.

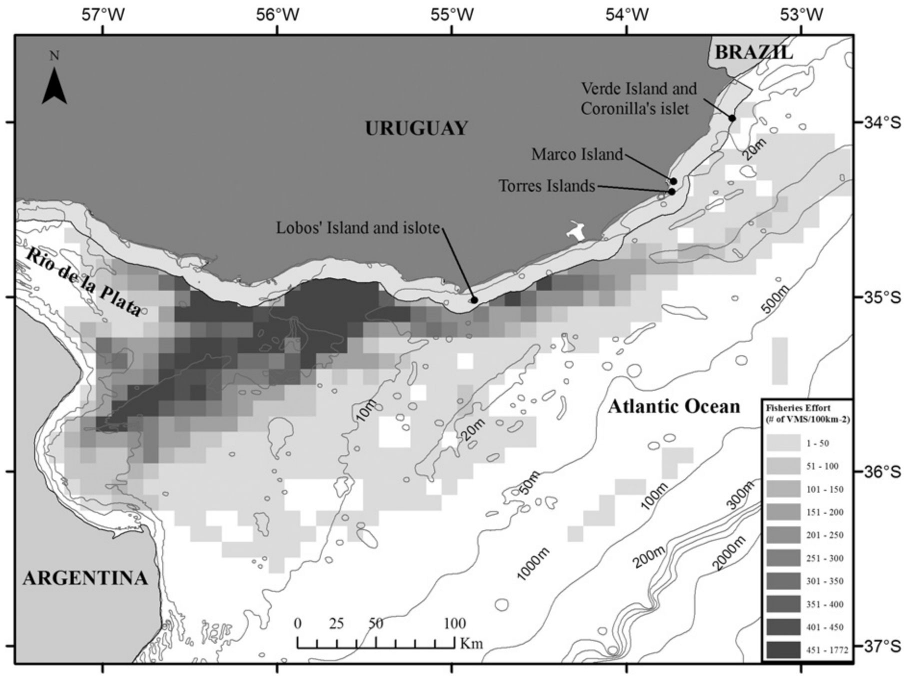

Fig. 7. Spatial distribution of the Uruguayan coastal bottom trawls fisheries effort in the Rio de la Plata estuary and Atlantic Ocean during 2009. Trawl fisheries exclusion zone (7 nm off the coast) is shown. Coastal bottom trawling Fishing effort is represented as number of satellite position (Vessel-Monitoring-System) by cell (cell size 10×10 km^2 i.e. 100 km^2 resolution). Fisheries data provided by Fisheries Technology Lab, DINARA, MGAP. Depth (isobaths, light gray lines) data was collected in 2002 by FREPLATA-Proyecto de Protección Ambiental del Río de la Plata y su Frente Marítimo (www.freplata.org).

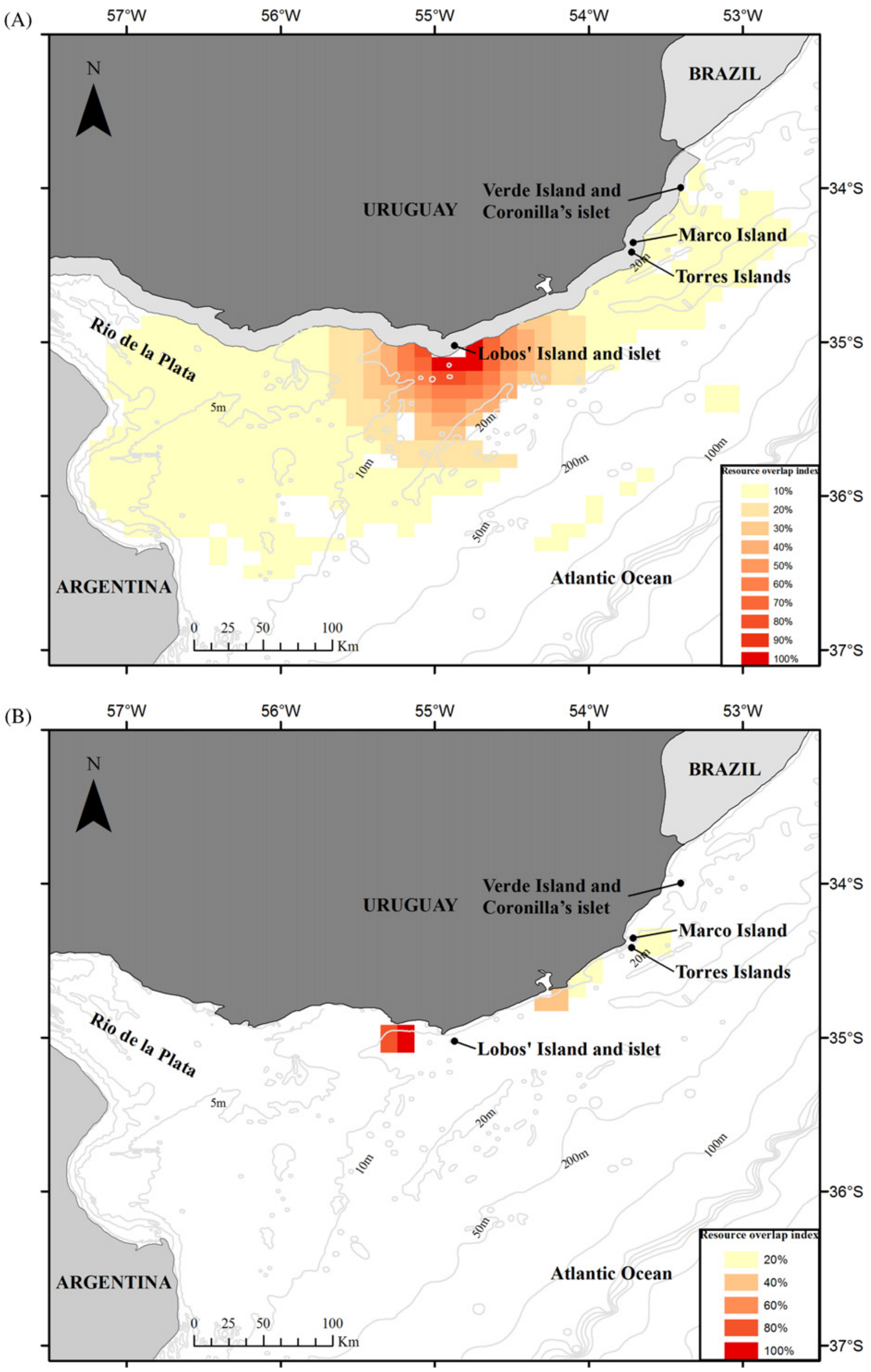

Fig. 8. Spatial distribution of resource overlap between adult lactating South American sea lions (*Otaria flavescens*) satellite-tracked from Isla de Lobos and (A) coastal bottom trawl fisheries (CBTF) fleet and (B) artisanal fisheries fleet for 2009. Overall home ranges for sea lions (peeled minimum convex polygon 95%) are shown in light gray dashed line. In (A), CBTF exclusion zone (light gray, 7 nm off the coast) is shown. Depth (isobaths, light gray lines) data were collected in 2002 by FREPLATA-Proyecto de Protección Ambiental del Río de la Plata y su Frente Marítimo (www.freplata.org).

4.2. Foraging behavior and locations

The diving behavior of lactating SASLs from Isla de Lobos was characterized by short, shallow benthic dives, with a large proportion of time spent at the bottom (Table 2). In addition, they exhibited high IDZ values meaning consecutive dives were consistently to the same depth (mean = 69%, Table 2) which is typical for benthic divers. Lactating sea lion spend more than half (54.8%) of their foraging trip diving without exceeding their cADL (Table 2). This may suggest, consistent with Costa's model of foraging behavior modification (Costa, 2008), that lactating SASLs have a window to alter their foraging behavior (increase foraging time and push their diving limits) without changing the duration of their foraging trips to accommodate for changes in prey availability or nutritional requirements.

Diving within physiological limits is characteristic of pelagic and/or generalist otariids such as California sea lions (*Zalophus californianus*) and Antarctic fur seals (*Arctocephalus gazella*) (Boyd and Croxall, 1992; Feldkamp et al., 1989; Weise and Costa, 2007). In contrast, it has recently been reported that benthic foraging

Steller sea lions (*Eumetopias jubatus*) do not exceed their aerobic dive limits (Rehberg et al., 2009). On the other hand, other otariid central place foragers such as Australian sea lions (*Neophoca cinerea*) and New Zealand sea lions (*Phocarctos hookeri*) are considered extreme divers since they push or exceed their cADLs up to 68% (Costa and Gales, 2000, 2003; Chilvers et al., 2006). These two sea lions species, are therefore, less likely to have the capacity to increase their foraging effort in response to shortage in food availability as a result of environmental conditions and/or competition with fisheries (Costa et al., 2004). The cADL calculation in the present study was based only on estimates of SASLs O_2 stores (Costa et al., 2001, 2004), and can be confirmed only by collection and analyses of blood and muscle samples. However, given the extremely shallow and short duration of SASL dives and their large body size, it is likely that they rarely challenge their oxygen stores.

The foraging locations of SASL were limited exclusively to the coastal environment, here defined as extending to the 50 m isobaths (Angelescu and Prensky, 1987; Prenski and Sánchez, 1988), within the continental shelf, and not exceeding travel distances of 135.5 km from the rookery (Figs. 6 and 7). It is possible that females do not venture further away from the rookeries in search for alternate food resources because they are limited by the demands or fasting abilities of their pup.

4.3. *Spatial resource overlap with the Uruguayan fisheries*

This research is the first to investigate the spatial–temporal resource overlap between SASL and the Uruguayan fisheries. The M–H index value indicated a high trophic overlap between the diet of SASL and commercial fisheries catch; this is a result of CBTF targeting several of the main prey species consumed by sea lions such as whitemouth croaker, stripped and king weakfish (Table 4). Food resource overlap between SASL and industrial fisheries has been reported in Falkland Island and Patagonia. Foraging locations of SASL overlapped with the trawl fleet targeting Argentine hake in Patagonia and sea lions in the Falkland Island have shown resource use overlap with the *Loligo* trawl fisheries (Campagna et al., 2001; Thompson et al., 1998). Despite these findings none of these studies have determined the spatial and temporal overlap in consumption of prey species. The Resource Overlap/Fisheries Impact here indicated a spatial resource overlap between lactating SASL and CBTF (Fig. 7a).

The present study is the first to report a high overlap in resource exploitation between SASL and the artisanal fisheries in Uruguay. The overlap is in species targeted; however, the overlap in prey size was minimal. Artisanal fisheries in Uruguay target mainly whitemouth croaker, Brazilian codling and weakfish (Uruguay Dirección Nacional de Recursos Acuáticos, 2010) that are the main prey items in the diet of SASL (Table 2). Our results contrast those of Szteren et al. (2004) who reported a low overlap in consumption of prey species between SASL and the artisanal fishery catches. One of the main differences with our study is that we calculated the overlap based on the prey biomass composition while they used the prey numeric composition that may bias the estimate toward smaller but more abundant species in the diet of sea lions. Furthermore, Szteren et al. (2004) included landing data collected during trips ($n=14$) onboard artisanal fishing boats, while the current work included the landings from the whole artisanal fleet.

The Resource Overlap/Fisheries Impact index indicated that the overlap between sea lions and the artisanal fisheries was located west of Isla de Lobos (Fig. 7b). The spatial diet overlap occurred with the artisanal fisheries operating in the Rio de la Plata with no overlap with the fisheries operating to the east (Atlantic Ocean) of Isla de Lobos (Fig. 7b). Artisanal fishermen operating in the Atlantic Ocean consistently report interactions with SASL; given the distances involved it is likely that these interactions are with sea lions from the colonies at Marco and Torres Islands (Fig. 1). In summary, our results indicate that there is a spatial and diet overlap between sea lion and artisanal fisheries operation during the austral summer in the Rio de la Plata. Lowry and Frost (1985) suggest that a four-stage process is required to establish the indirect effects of fishery. Firstly, stocks of prey species must be significantly depleted beyond the predatory effect of marine mammals. Secondly, the consequential changes in abundance of the prey must affect amounts consumed by the marine mammal. Thirdly, such a change should affect the marine mammal's life or behavior. Finally, these changes should affect the population characteristics of the marine mammal. There is a shortage of information on all of these areas (Lowry and Frost, 1985).

We estimate that female SASL from Isla de Lobos consumed annually (108,862 t) approximately 3.1 times as much prey as the CBTF landings (35,511 t) (Table 4). Furthermore, if we take into account the annual consumption of overlapping prey, SASL consumed 2.5 times more than the artisanal and CBTF fisheries (Table 4). We have no evidence to support the hypothesis that there is a negative effect on the recovery of sea lion population as a result of the spatial–temporal resource overlap between sea lion and the fisheries. Nonetheless, current or increased levels of fishery exploitation may lead to increased competition for finite food resources and may result in changes in the distribution and availability of preferred SASL prey in proximity to rookery location. If this occurs, sub-optimal foraging condition may develop for a central place forager such as a lactating SASL, where increased foraging costs may alter pup provisioning, consequently affecting female reproductive success (Boyd et al., 1998, 1997; Campagna et al., 2001; Staniland et al., 2007; Thompson et al., 1998). In turn, this may preclude recovery of SASL and may even lead to population decline.

4.4. *Conclusions*

Our observations on the foraging behavior of lactating SASLs, shows that there is a relatively large spatial resource overlap between SASLs and the Uruguayan fisheries. We were able to identify "hot spot" where there is considerable overlap/interaction between SASLs and fisheries. Given that the SASL population is declining our data could be used to establish small regions where fishing activities could be curtailed or eliminated. A reduction in fishing activities within these regions could aid in the recovery of the SASLs at Isla de Lobos. These results should be considered in the management of the Uruguayan fisheries and to the conservation of the Uruguayan sea lion population that consequently could aid to solve the conflict between sea lions and the fisheries.

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Corrigendum

Corrigendum to “Foraging behavior of lactating South American sea lions (*Otaria flavescens*) and spatial–temporal resource overlap with the Uruguayan fisheries” [Deep-Sea Res. II 88–89 (2013) 106–109]

Federico G. Riet-Sapriza [a,*], Daniel P. Costa [b], Valentina Franco-Trecu [a], Yamandú Marín [c], Julio Chocca [c], Bernardo González [c], Gastón Beathyate [c], B. Louise Chilvers [d], Luis A. Hückstadt [e]

[a] *Proyecto Pinnípedos, Cetáceos Uruguay, Sección Etología, Facultad de Ciencias (UDELAR), Iguá 4225, CP 11400, Montevideo, Uruguay*
[b] *Department of Ecology and Evolutionary Biology, University of California, 100 Shaffer Road, Santa Cruz, CA 95060, USA*
[c] *Laboratorio de Tecnología Pesquera, Dirección Nacional de Recurso Acuáticos, M.G.A.P., Constituyente 1497, C.P. 11200, P.O Box 1612, Montevideo, Uruguay*
[d] *Aquatic & Threats Unit, Department of Conservation, P.O. Box 10-420, Wellington 6011, New Zealand*
[e] *Ocean Sciences Department, University of California, 100 Shaffer Rd, Santa Cruz, CA 95060, USA*

The authors of Riet-Sapriza et al. (2013) regret that after publication of the original manuscript an error was found in the estimation of lactating South American sea lions prey consumption and led to an overestimation of the daily and annual prey consumption.

In this corrigendum the amendments include:

1. Results sections

The corrected Table 4 is shown below.

The sentences (page 112) in the original manuscript states:

‘Thus, the total daily consumption and total food consumption for the year 2009 for the entire adult female population from Isla de Lobos was estimated in 298 t/day and 108,862 t, respectively (Table 4). The annual and daily prey consumption density estimated was 1.4 t/year/km^2 and 0.004 t/day/km^2, respectively (Fig. 6).’

These sentences should be changed to:

‘Thus, the total daily consumption and total food consumption for the year 2009 for the entire adult female population from Isla de Lobos was estimated in 2.75 t/day and 1004.88 t/year, respectively (Table 4). The daily prey consumption and annual consumption density estimated was estimated in 0.0009 t/day/km^2 and 0.31 t/year/km^2, respectively (Fig. 6).’

2. Discussion sections

The sentences (page 116, subheading 4.3. ‘Spatial resource overlap with the Uruguayan fisheries’) in the original manuscript states:

‘We estimate that female SASL from Isla de Lobos consumed annually (108,862 t) approximately 3.1 times as much prey as the CBTF landings (35,511 t) (Table 4). Furthermore, if we take into account the annual consumption of overlapping prey, SASL consumed 2.5 times more than the artisanal and CBTF fisheries (Table 4).’

These sentences should be changed to:

‘We estimate that female SASL from Isla de Lobos annual prey consumption (1004.88 t) was approximately 97% less than the CBTF landings (35,511 t) (Table 4). Furthermore, if we take into account the annual consumption of overlapping prey, female SASL consumed (728 t) 98% less than the total artisanal and CBTF fisheries catch (32,491 t) (Table 4).’

The authors regret the mistake and would like to apologize for any inconvenience caused. We are very thankful to Dr. Arliss Winship for his suggestion and assistance to correctly estimate the sea lion prey consumption.

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[*] Corresponding author.

E-mail address: frietsapriza@gmail.com (F.G. Riet-Sapriza).

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Table 4
Estimate of the composition of the total annual Uruguayan artisanal fishery and coastal bottom trawl fishery catches, and diet composition and prey quantity of South American sea lion's (*Otaria flavescens*), and comparison of consumption of overlapping prey species. Composition of the South American sea lions diet expressed as percentage of frequency of occurrence (FO%, percentage of scat in which a prey was observed), % number (*N*%, percentage of the total prey number across all samples), % biomass (*W*%, percentage of the number of prey times the average body mass), and index of relative importance (IRI/100). NA was not possible to obtain biomass since no length-body mass regression is available.

Prey and catch species		**Diet composition of SASL**				**Total catch (t) (%)**[a]		**Sea lion consumption (t) (%)**	**Consumption of overlapping prey (t)**	
Common name	**Scientific**	**FO%**	***N*%**	***W*%**	**IRI**	**Artisanal**	**Trawling**		**Fisheries**	**Sea lions**
Brazilian codling	*Urophysis brasiliensis*	15.79	3.73	17.0	3.27	181 (10.0)	188 (0.5)	171 (17.0)	369	171
Largehead hairtail	*Trichiurus lepturus*	31.58	9.94	23.98	10.7	–	–	241 (23.98)	–	–
White mouthcroaker	*Micropogonias furnieri*	10.53	8.70	46.66	5.83	1379 (76.4)	22,349 (62.9)	469 (46.66)	23,728	469
Striped weakfish	*Cynoscion guatucupa*	31.58	13.04	0.72	4.34	177 (9.8)	6177 (17.4)	7 (0.72)	6354	7
Argentine seabass	*Acanthistiusbrasilianus*	10.53	6.83	NA	–	–	–	NA	–	–
Argentine croaker	*Umbrina canosai*	10.53	3.73	8.10	1.24	51 (2.8)	1989 (5.6)	81 (8.10)	2040	81
Argentine conger	*Conger orbignyanus*	5.26	1.24	NA	–		10 (0.0)	NA	–	–
Argentine hake	*Merluccius hubbsi*	10.53	3.11	3.54	0.70	–	–	36 (3.54)	–	–
Squid	*Loliginidae*	10.53	11.18	NA	–	–	1585 (4.5)	NA	–	–
King weakfish	*Macrodon ancylodon*	–	–	–	–	16 (0.9)	3213 (9.0)	–	–	–
Argentine anchoita	*Engraulis anchoita*	–	–	–	–	–	–	–	–	–
Searobin	*Prionotus sp.*	–	–	–	–	–	–	–	–	–
Cephalopods	*Omastrephidae*	5.26	38.51	NA	–	–	–	NA	–	–
Total catch/prey						**1804**	**35,511**	**1004.88**	**32,491**	**728**

[a] Source: Uruguay DINARA (2010).

Reference

Uruguay DINARA, 2010. Boletín Estadístico Pesquero 2009/ Uruguay. Dirección Nacional de Recursos Acuáticos. MGAP-DINARA, Montevideo, pp. 52.

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INTERNAL AND EXTERNAL DRIVERS LEADS FORAGING BEHAVIOUR IN SYMPATRIC OTARIID SPECIES

Valentina Franco-Trecu[1,2*], Pablo Alarcón[3], Juan Manuel Morales[3] and Pablo Inchausti[2]

[1]Proyecto Pinnípedos, Sección Etología, Facultad de Ciencias, Universidad de la República, Iguá 4225, Montevideo 11400, Uruguay.

[2]Departamento de Ecología y Evolución, Centro Universitario Regional Este (CURE) Universidad de la República, Tacuarembó S/N, Maldonado 20000, Uruguay.

[3]Laboratorio Ecotono. INIBIOMA, Universidad Nacional del Comahue-CONICET, Quintral 1250, Bariloche 8400, Argentina.

* Corresponding author:

Phone: 00598 25258618

Fax: 00598 25258617

pinnipedosuy@gmail.com

Author Contributions: VFT and PI formulated the idea, VFT conducted fieldwork, PA and JMM collaborated in imaging analysis, VFT, PI and PA performed statistical analyses, VFT, PI, PA and JMM wrote the manuscript

Abstract

Mammals foraging behaviour is influenced and constrained by internal drivers (e.g. body condition, reproductive status), external processes (e.g. local environmental conditions, species interactions) and combinations thereof. We studied the foraging behaviour (space use and diving behaviour) of SAFS females during the early lactation and how it changed among feeding trips. We also compared the SAFS foraging behaviour with a sympatric species, the South American sea lion (SASL), in the same area in Uruguay. We found that reproductive status and body condition determined the distances travelled, the extent of the foraging area used, and the variability in diving behaviour among individual SAFS females during their first foraging trip. We also found that individual home range sizes were inversely correlated between consecutive foraging trips. Given the differences found in the foraging areas and diving patterns between SASL and SAFS, we believe that interspecific interactions are an unlikely explanation for the contrasting population trends (that are unique in their geographic ranges) of these species in Uruguay. Instead, we believe that these contrasting trends are more likely to result from the combined influence of internal drivers (body condition and avoidance of infanticide) and external constraints (harvesting and shallow bathymetry) on the females' foraging behaviour.

Keywords: *Arctocephalus australis*, diving behaviour, foraging area, internal drivers, *Otaria flavescens*

INTRODUCTION

Maximizing individual reproductive success and achieving high population growth rate require that individuals efficiently gather resources and successfully invest them in reproduction. Gathering foraging resources is the outcome of a sequence of individual behavioral decisions under the ecological, morphological and physiological constraints that shape individual foraging tactics (Krebs and Davies 1991; Stephens et al. 2007; Stephens and Krebs 1986). Different features of foraging behaviour are influenced and constrained by internal drivers (e.g. age, body condition, reproductive status), external processes (e.g. local environmental conditions, species interactions) and combinations thereof (Forchhammer et al. 2001; Morales et al. 2010; Stephens et al. 2007; Tiedemann et al. 2014) depending on the species' ecology, reproductive cycle and previous breeding success (Martin et al. 2013; Nathan et al. 2008). Mammalian reproductive females often meet the high energetic demands of gestation and lactation by increasing the amount and/or quality of resources ingested (Bardsen et al. 2008; Speakman 2008; Thompson et al. 2012).

Classical competition theory postulates that the stable coexistence of sympatric predator species in stable environments requires at least some level of differentiation of their trophic niches (Levins 1979; Tilman 1987). Understanding the proximate mechanisms that lead to differences in the foraging behavior and its inter-individual variation between sympatric species is a key feature in the management and conservation strategies (e.g. Bolnick et al. 2011; Cohen et al. 2014; Riet Sapriza et al. 2013). Nevertheless, obtaining a direct quantitative understanding of the feeding habits of wild marine animals has been mired with difficulties inherent in gathering unbiased and relevant data at appropriate spatial and temporal scales (Chiaradia et al. 2014; Franco-Trecu et al. 2013). Over the last 30 years, ecologists have increasingly used telemetric technologies to describe habitat use by wild marine species and to understand its proximate determinants (e.g. Costa et al. 2007; Costa et al. 2010). Satellite-based technology and dive recorders have allowed quantify the extent and intensity of use of the 3D foraging areas used by marine predators over time, and highlight the main factors determining their habitat selection and trophic preferences (e.g. Costa et al. 2007; Jeglinski et al. 2013; Villegas-Amtmann et al. 2013).

Uruguay has the largest colony of the South American fur seal, *Arctocephalus australis* (SAFS) with a current size of *c.a.* 100,000 individuals that was reached after

60 years of steady increase (see Table 1, Franco-Trecu 2015). After SAFS females give birth to one pup in December (austral summer), they begin to alternate foraging trips at sea with nursing bouts ashore for almost a year (Vaz-Ferreira 1982). Otariid (fur seal and sea lion) are income breeders that sustain their high cost of long lactation with current energetic income (Boyd 2000). However, the storage of energy at the time of giving birth is an important feature for the maximization of pup survival (Boyd 2000; Roff 1992) that constitutes an important internal driver affecting the individual foraging behaviour of reproductive females (Boyd 2000; Houston et al. 2007). The total duration and the distance travelled during maternal foraging trips are constrained by their pups fasting ability remaining on the rookery, such that the foraging behavior of females with poor body condition may result in a sub-optimal energy deliver to their pups (Boyd et al. 1994; Trillmich and Weissing 2006).

The Uruguayan SAFS population breed in sympatry with the South American sea lion, *Otaria flavescens* (SASL), whose overall abundance has declined to less than 10,000 individuals over the same time period (Franco-Trecu 2015). Both species were subject to intense harvesting between 1873 and 1991 in Uruguay and elsewhere in the South West Atlantic that led to important declines in their abundances (Crespo and Pedraza 1991; Sielfeld 1999). The underlying causes for these post-harvesting contrasting trends of SAFS and SASL in Uruguay (Pedraza et al. 2009) that are unique in the geographic ranges of both species (Crespo et al. 2009; Dans et al. 2009) remain unknown. Given that breeding areas are not limiting for the current size and recent population trends of either species, it is reasonable to seek trophic-based explanations related with their foraging zones or the trophic resources consumed for the contrasting population trends of these species in Uruguay.

An early comparison of the diet compositions based on scat analyses suggested a high degree of trophic overlap of sympatric SASL and SAFS in Uruguay during their reproductive seasons (Szteren et al. 2004). However, assessing diet composition and trophic overlap using scat analysis is hampered by the strong biases of this method (Davies-Mostert et al. 2010; Klare et al. 2011; Wachter et al. 2012). More recent comparisons of diet compositions based on stable isotope analyses found no trophic overlap in isotopic space between the two species (Franco-Trecu et al. 2012; Franco-Trecu et al. 2014; Franco-Trecu et al. 2013). These more recent comparisons also showed that SASL fed on preys at higher trophic levels, used more nearshore resources and had a higher degree of individual trophic specialisation than SAFS (See Table 1, Franco-Trecu et al. 2012; Franco-Trecu et al. 2014). While the analysis of diving behaviour and habitat use showed that SASL's foraging areas overlap with areas used by coastal fisheries (Riet Sapriza et al. 2013) that have lead to conflicts with artisanal fishermen (Franco-Trecu et al. 2009; Riet Sapriza et al. 2013; Szteren and Páez 2002), there are no comparable studies of habitat use and foraging behavior for SAFS in the same area.

Body condition index and body mass are proxies commonly used as indicators of the individual energetic reserves that are assumed to be related to individual fitness (Krebs and Singleton 1993). We first studied the foraging behaviour (mainly, the space use and diving patterns) of SAFS females during the early lactation and the extent to which it varied among individuals. Our second aim was to assess whether and how SAFS females' foraging and diving behavior changed among the successive feeding trips during the breeding season when a substantial part of pup mortality occurs (Franco-Trecu 2010). Finally, we compared the SAFS foraging behaviour and habitat use with those of SASL in the same area (Riet Sapriza et al. 2013) to assess the potential of interspecific competition for trophic resources to explain the contrasting population trends of both species in Uruguay. Also, we wanted to validate the results of feeding habits obtained using indirect methods based on stable isotopes (See Table 1, Franco-Trecu et al. 2012; Franco-Trecu et al. 2014). Given that SAFS is an income breeder, we hypothesized that body condition can influence foraging behavior of SAFS females and constrain their selection of foraging areas immediately after parturition when pups have the strongest dependence of their mothers for energy and protection (i.e. Kuhn and Costa 2014).

MATERIALS AND METHODS

Study Areas

We worked in Isla de Lobos (35°01'S, 54°50'W), the main SAFS rookery in Uruguay that is located at five nautical miles from the mainland in the easternmost part of the Río de la Plata estuary. Isla de Lobos is part of a rather shallow continental shelf that reaches a maximum depth of 200 m at *c.a.* 100 nautical miles from the rookery. The Río de la Plata estuary has a large and highly dynamic mixing of seawater and freshwater due to the confluence of the Brazil and Falkland currents together with the Parana, Paraguay and Uruguay river discharges that generate high primary productivity that supports large industrial and artisanal fisheries (Ortega and Martinez 2007).

Data Collection

Satellite tracking and diving behavior data

We captured ten randomly selected SAFS breeding females with a hoop net in December 2011. All captured animals were lead to a cage and sedated by injecting them with ~1.5 ml of Midazolan 0.5% (Midapine®, Vetcross Laboratory) into their gluteal muscle regions. Each captured female was weighted and fitted with a smart position and transmitting (SPOT5 model) Argos tag (Wildlife Computers, USA) and a Sensus Ultra (ReefNet) attached to a neoprene patch that was glued to the fur on the lower back using quick set epoxy. These logging instruments were recovered approximately after *ca.* 30 days by recapturing all tagged individuals and sedating them with a dosage of ~ 1.5 ml Midazolam (0.5%) administered with a Dan-Inject Rifle (Børkop, Denmark). After sedation, we restrained the animals with a hoop net to allow the removal of the instruments by cutting through the neoprene mounting patch leaving behind the epoxy mount that would later fall off during molting. Because of the low recovery rate of Reefnet devices in 2011 (30%), we equipped ten reproductive SAFS females in December 2012 only with Sensus Ultra (ReefNet) devices to record their diving performance. Both years, we conducted daily scan samplings (Martin and Bateson 1991) of the study site on an hourly basis (7-10 and 17-20hs) to record the presence of all marked females in the study area. All procedures of animal manipulation were submitted and approved as valid according to the national laws in animal welfare by the Ethics Committee in Animal Experimentation (CHEA) of the Universidad de la República, Uruguay.

Data Analysis

Space use analysis

We analyzed a telemetry dataset that included 471 high-quality locations (i.e. ARGOS classes 3, 2, 1 and 0) from nine of the 10 satellite telemetry tags. We firstly studied the foraging areas at the population level by pooling all 471 locations to compute a fixed-kernel home range estimator to describe the intensity of space use during the study period (Worton 1987). Additionally, we estimated the individual home range sizes using 95% minimum convex polygons (95% MCP). To evaluate changes in foraging behavior during the early lactation period, we compared the home range sizes (95% MCP), the total distance travelled and the maximum distance from the colony between the first and the second foraging trips of each SAFS female. To assess individual variation in space use of SAFS females, we calculated the percentage of each individual 95% MCP that overlapped with those of the other individuals. All the above calculations were performed using the adehabitat package (Calenge 2006) for the R free software (R Core Team 2013).

Diving behaviour

The Reefnet devices recorded the water pressure every five seconds and thus they allowed a fine profile of individual diving behaviour. The SAFS diving data was analyzed with the diveMove library (Luque 2007; Luque and Fried 2011) of the free software R (R Core Team 2013). This library allowed visualize individual dives, and estimate the maximum depth, the durations and speeds of the descent, bottom and ascend phases that are a basic summary of each dive (Luque 2007). All dives reaching depths of less than 5 m were excluded from the analyses (Tremblay and Cherel 2003) because these shallow dives typically occur when female otariids are travelling (Blake 1983; Williams 2001). We characterized the individual diving behaviour using the following variables: transit time (defined as the descent plus ascent duration of each dive), diving time (estimated as the sum of the transit time and the time at the bottom) and the descent, bottom and ascent speeds of each dive. Whenever the latter three speeds exceeded 2.5 m/s, they were considered unfeasible and eliminated from the analyses. We also calculated the bottom to dive time ratio and used it as an indicator of dive type: pelagic dives whenever the ratio was closer to zero and benthic dives when it tended towards one. The sum of transit and bottom distances of each dive was used as a proxy of diving effort. We characterized the SAFS individual diel pattern by the proportions of day and night dives, and by comparing the maximum depth, the diving effort, the bottom to dive time ratio, the bottom times and the diving times for all SAFS females. For each of these response variables, we formulated separate generalized linear mixed models (GLMM) with day and night, the foraging trips (first *vs* second) and their interaction as categorical fixed effects, and individual identity as a random effect, and a first-order continuous autocorrelation function to model the temporal autocorrelation of each response variable at the individual level (Pinheiro and Bates 2000). We used the function glmmLDTS (Ver Hoef et al. 2010) to fit all the generalized linear mixed models in the free software R (R Core Team 2013). The Aerobic Dive Limit (min) (ADL) for all tagged females was calculated from 1.57*body mass (kg)$^{0.22}$ (Gentry et al. 1986). We estimated the proportion of dives exceeding the SAFS physiological limits as the ratio between the number of dives longer than ADL and total number of dives of each female. The durations of the foraging trips of each female were calculated from the

Reefnet diving records, and from the combination of satellite records and daily scans performed of the study area. We used lineal regression models to assess relationship between females body mass (here used as proxy of body condition) with the home range size (95% MCP), the maximum and the total distances traveled as well as with the mean and standard deviation of the other diving variables (i.e. bottom time, dive time, deep, transit time and dive effort). We also evaluated whether individual home range sizes (95% MCP) between consecutive foraging trips were correlated.

RESULTS

Space use analysis

The SAFS home range at the population level was 60,789.9 km^2 (95% Kernel, Fig. 1) and 78,752.06 km^2 (95% MCP) that was mainly extended southwards (Fig. 1). The individual home range varied between 6,892.9 km^2 and 46,958.3 km^2 (see overall mean and SD in Table 1). Most foraging trips occurred toward the S-SW of Isla de Lobos (Fig. 1), with the maximum distance and total distance travelled varying widely among females (Table 1). All SAFS females had high home-range overlap with the others (mean: 95.6%, range: 71% - 100%). Similarly, they had very similar space use patterns, with their core foraging areas neatly divided into a foraging areas near the rookery after parturition (first trip), and areas of open waters on located at (on average) 531 km S-SW from Isla de Lobos in their second foraging trips (Fig. 2). The areas of individual home range sizes varied between 2 and 3,203 km^2 during the first foraging trip and between 7,990 and 45,786 km^2 in the second one (see Table 1).

Diving Behavior

We recovered three and nine Reefnet deployed on SAFS females in 2011 and 2012, respectively. These twelve Reefnet records lasted on average 20 days (SD = 5) per female, and included a total of 25 foraging trips and 49,906 individual dives. The main descriptors of diving behaviour for each SAFS female are given in Table 2. The longest dive lasted 5.25 min, while 45% of all dives lasted between 0.08 and 0.50 min, 45% between 0.51 and 1.75 min of duration. We found that the mean ADL of SAFS was 3.6 min (SD = 0.1), and that only a very small proportion of individual dives exceeded the ADL (mean = 0.20 ± 0.06, see Table 2). Almost 60% of all dives recorded had a bottom time shorter than 0.25 min, 30% between 0.26 and 1.00 min, and the 10% remaining was between 1.01 and 4.75 min. The maximum depth of approximately two third of the dives was less than 20 m, 31% between 21 and 60 m, and only *c.a.* 5% were deeper than 61 m (Fig. 2b). The GLMM showed that the maximum depth, diving effort, bottom to dive time ratio, bottom times and diving times significantly differed between day and night, and between the first and the other trips with significant interactions (see Table 3). Regarding the diel pattern, lactating SAFS dove significantly deeper during daytime (18.2 m) than during the night hours (12.6 m) ($P \ll 0.001$) during the first foraging trip, but the maximum depths barely differed between day and night during the subsequent trips (day= 14.4 m; night= 14.9 m). Similar patterns were observed for the diving effort (see Table 3). However, the bottom time, diving time and its ratio were always lesser during the night than during the day for all foraging trips (see Table 3). The duration of the first foraging trip (7.3 ± 4.9 days) was shorter than subsequent trips (13.3 ± 4.3 days, $t = -5.66$, $P \ll 0.01$). The mean duration of first attendance on land lasted for 3.3 days (SD = 1.5).

SAFS individual body mass was positively correlated with the total distance traveled (r = 0.67, $P = 0.02$), the maximum distance traveled (r = 0.77, $P = 0.01$) and the 95% MCP area of the first foraging trip (r = 0.63, $P = 0.04$). However, there was only a negative association between the body mass and the 95% MCP (r = 0.71, $P = 0.005$) during subsequent foraging trips. Individual home range sizes (95% MCP) between first and second foraging trip was marginally ($P = 0.07$), and negative correlated (-0.08, r = 0.45).The heterogeneity (as measured by the standard deviation) of the bottom time (r = 0.79, $P = 0.001$), the dive time (r = 0.77, $P = 0.002$), transit time (r = 0.67, $P = 0.01$), dive effort (r = 0.71, $P = 0.006$) and maximum deep (r = 0.71, $P = 0.005$) were all positively correlated with SAFS body mass only for the first foraging trip.

Sympatric species

The comparison between the foraging behavior of SAFS and SASL females in Isla de Lobos during the breeding season showed several key differences (Table 4). SAFS females traveled farther and for longer duration from the rookery (and hence had larger average home range), dove predominantly at night and deeper than the larger bodied SASL females. Only a small proportion of the dives of both species were limited by their aerobic capacities (Table 4). Although both species on average exploited similar depths, their diving patterns were clearly different, in that SASL had a more benthic and SAFS a more pelagic diving behavior (see Table 4). Bottom to dive time ratios were significantly different between species, while the mean to SAFS was 0.4 to SASL was 0.6 ($t = -4.9$, $P \ll 0.01$). In general, SAFS's dives were noticeably more heterogeneous than those of SASL. For instance, averaged across all individuals equipped of each species, the SD of the maximum depths of all dives of the tagged SAFS individuals was 2.5-fold greater than for SASL.

DISCUSSION

We found that while SAFS females constrained the first feeding trip to areas near the rookery, probably due to their reproductive status (newborn pup). Also, females body condition determined: the extent of the individual foraging area used, the distances traveled and the variability in individual diving behaviour during this first trip. However, SAFS females that had a larger individual foraging area during the first foraging trip tended to restrict the size of the foraging area during the second trip. Although many features of the foraging behaviour differed between sympatric SASL and SAFS, the latter used trophic resources at the same average depth and showed greater deep range than former despite of a four-fold difference in their body sizes.

SAFS foraging behaviour and internal drivers

Much like other fur seal species (i.e. Costa 1993; Houston et al. 2007), SAFS are pelagic foragers that carry out short, pelagic dives mostly during the night (Table 1). Only a small fraction of the SAFS foraging trips occurred close to the rookery, with other important areas being on the break of the continental shelf at about 500 km from the breeding colony. In Otariids, satisfying the energetic needs of lactation and pup care can reduce females' foraging efficiency and steeply increase their energetic demands (Boyd 2000; Houston et al. 2007). The foraging behaviour of female income breeders such as SAFS is shaped by the spatial-temporal variation of food resources and also by their individual body condition in relation to the high energetic demands during lactation (Boyd 2000). Despite the high importance of early lactation for otariid pups, females SAFS have a very low lactating frequency during the perinatal period (i.e., the time span between pup birth and the departure in the first foraging trip) (Franco-Trecu et al. 2010). This low frequency of early lactation bouts in SAFS may be related to the limited capacity of the pup stomach during the perinatal period (Arnould and Hindell 2001), and to the suppressing effect of frequent lactation bouts on the prolactine concentration and the occurrence of the postparturition estrous (Yoshimura et al. 1994). It is likely that stronger needs of maternal care shortly after parturition constrained SAFS females to forage closer to the rookery during their first foraging trip (see Table 3 and 4, Fig. 2).

Lactating female otariids feed their pup using energy gathered from remote resources and hence they typically face decisions regarding how far away searching for trophic resources and how much assimilated energy can they provide to their pups without hampering their survival (Houston et al. 2007). Therefore, the foraging behaviour of otariid females with poor body conditions may have a sub-optimal energy delivery to their pups (Boyd et al. 1994). Beyond the general trend during the SAFS first foraging trip, there was a high inter-individual variation in the foraging distances travelled, individual home range sizes and diving behaviour (Table 1 and 2). At the beginning of the breeding season, the SAFS body condition differed between individual SAFS females and may have become an important constraint of their foraging subsequent behaviour. Overall, SAFS lactating females with lower body mass travelled shorter distances from the rookery during their foraging trips and had smaller home ranges than heavier females. It is thus likely that their weaker body condition hindered the energetic provisioning of pups during the perinatal period. Also, heavier SAFS females showed greater variation in depth, time and effort of dive than the lighter females, indicating that a better body condition allowed the former to exploit a wider range of resources and environments. However, females that used a large home ranges during the first foraging trip may have impaired their pup body condition or survival (that could not be statistically detected because of the small number of equipped SAFS females) that in turn constrained the home range sizes during their second foraging trip.

There is mounting evidence that the complex interactions among the spatio-temporal variation of resource abundance, female age, body mass, individual experience and pup behaviour can all affect and to some extent co-determine the foraging decisions during the post-partum period of otariids. For instance, the differences in the trip duration, the distances traveled, and other dive variables among years were related to (and explained by) the temporal variability in the foraging habitat of *Z. californianus* (Kuhn and Costa 2014). Arnould and Hindell (2001) suggested that pup appetites might influence the maternal foraging time budgets by limiting the total amount of milk that their mothers can deliver during each attendance. The duration of the maternal foraging trips in *A. pusillus doriferus* increase with pup age and with their sucking ability and stomach capacity (Arnould and Hindell 2001). In the northern fur seal, *Callorhinus ursinus*, larger females spent less time in ashore visits, spent a greater proportion of time at sea diving, and had longer dive bouts compared to smaller females (Skinner et al. 2012). It has been suggested that body size may only influence female fur seal foraging behavior when they are forced to dive at or near their limits of their physiological tolerance (Costa et al. 2001). However, in our case female body size influenced foraging behaviour although SAFS females only dove over their aerobic limit in 0.1% of dives.

Otariid foraging tactics also may shift with age as females gain experience. The latter could explain why younger, smaller female northern and Antarctic fur seals made longer trips compared to larger and older individuals (Goebel 1988; McDonald et al. 2009). In addition, older Steller sea lion (*Eumetopias jubatus*) mothers had significantly longer periods of nursing before taking their first foraging trip, thus suggesting the possible role of experience in enhanced physical condition (Burkanov et al. 2011). Besides being the energy currency that can be transferred to the pup, the amount of fat reserves can also enhance neutral buoyancy and reduce the energetic cost of traveling in a phocid species (Adachi et al. 2014). Regardless of the proximate mechanism involved, we think that it is clear the role of body condition in constraining the foraging areas exploited and the diversity of diving behaviour by SAFS females.

Finally, because each SAFS female showed a high spatial overlap with other females, each individual did not contribute significantly to the home range size at the population level (Table 1). These findings are consistent with the results based on stable isotopes analysis of whiskers since SAFS individuals used more extensive and overlapped niche areas than SASL (Franco-Trecu et al. 2014). They also suggest that with regards to its trophic behaviour, SAFS can be considered a generalist species made up by generalist individuals (Franco-Trecu et al. 2014),

Sympatric species

Classical competition theory predicts that sympatric competitors would coexist provided that each species consumes different food resources, forage in different areas or times or that they are differentially constrained by other environmental factors or affected by other ecological processes (Begon et al. 2006). Combining biologging and diving data, we have shown that there is a general segregation of the trophic areas and diving behaviour of the sympatric SASL and SAFS in Uruguay (see Fig. 3). Summer foraging areas of SAFS females were mainly located at long distances (up to 736 km) from Isla de Lobos where depth is more than 200m (Fig. 1). In contrast with our prediction, we found that SAFS females used coastal areas during the first foraging trip, especially so for females having a poorer body condition (Fig. 2). While the coastal foraging areas used by SAFS females during their first trip could induce a limited overlap with SASL foraging area during a 2 - 3 weeks time period, it is unlikely that such overlap could generate direct competition between the two species. On the one hand, the main foraging zones of SAFS and SASL are largely spatially segregated (Fig. 1 and 3), and although the two species forage at similar depths, they had different diving behaviour (pelagic *vs.* benthic, Table 4). On the other, studies of diet composition based on stable isotopes showed that the two species actually consume different principal prey species (Franco-Trecu et al. 2013) as it can be expected because of their different diving behaviour.

Whenever two Otariid species coexist in sympatry (usually a sea lion and a fur seal), the large-bodied sea lion always has the smaller population size and more benthonic feeding habits than the more abundant, small-bodied, pelagic fur seal (Franco-Trecu et al. 2014; Páez-Rosas et al. 2012; Villegas-Amtmann et al. 2013; Waite et al. 2012). To our knowledge, Isla de Lobos is an exception since the fur seal and the sea lion actually forage at similar average depths in the water column, regardless of the fact that SAFS dives exploited a larger range of depths (maximum depth 191 m) during its longer foraging trips (overall mean 10 ± 5.5 days) that allowed them to reach areas of higher depths at the break of the continental shelf (Fig. 1). Despite of the four-fold difference in female adult body sizes, there was a three-fold difference in the maximum depth in favor of the small-bodied SAFS (Table 4). The latter results from the flat and shallow (maximum depth of 50 - 70 m) topography of the Uruguayan continental shelf that reaches the 200-1000 m isobaths only at *ca.* 200 km from the coast. Given that SASL females are constrained to forage near the rookery (avoidance of pup's infanticide would be another internal driver, see below), they cannot exploit food resources at higher depths since the benthonic zone in SASL's foraging area is in the continental shelf (Riet Sapriza et al. 2013). Given its larger body size and its associated greater swimming performance, it would seem surprising that SASL is circumscribed to a small foraging area near the rookery and that only 0.2% of SASL female dives lasted longer than its ADL. While SAFS pups are capable of enduring long periods of fasting (Franco-Trecu 2010), SASL pups can withstand fasting periods of only ~2 days on average (VF-T unpublished data). Because infanticide of SASL pups by adult and subadult males (Campagna et al. 1988) can have an important effect in low-density colonies (Drago et al. 2011; Franco-Trecu et al. in press), we believe that the combination of these two internal drivers (tolerance to fasting and the avoidance of pups infanticide) may constrain SASL females to make only short foraging trips (1.5 ± 0.9 days) limiting the extent of their foraging areas (Riet Sapriza et al. 2013).

Conclusions

Negative post-harvesting trends of local populations of sea lions is a widespread phenomenon (Gerber and Hilborn 2001) that has been attributed to the low availability of food resources due to their overexploitation by coastal fisheries (Alleway et al. 2014; Milessi et al. 2005; Pauly et al. 1998). Besides, many subtropical and temperate coastal areas used by Otariids worldwide are subject to the impact of pollution associated to the nautical activities and ports in areas with high human population densities whose effects compound those of low resource abundance in these habitats (Bulleri and Chapman 2010; Clausen and York 2008; Davenport and Davenport 2006).

Given the differences found in the foraging areas used, the diving patterns and the feeding habits between SASL and SAFS, we believe that it is very unlikely that interspecific interactions could underlie the contrasting population trends of these sympatric species observed in Uruguay. Instead, we believe that the contrasting trends in Uruguay are likely to result from the combined influence of internal drivers (body condition and avoidance of infanticide) and external constraints (anthropogenic impacts and shallow bathymetry) of females' foraging behaviour. SASL females foraging behaviour would be constrained by male pup's infanticide, which determining the use of foraging areas with low quality benthic resources, and where direct (resource competition) and indirect (by-catch) interactions with coastal fisheries (Franco-Trecu et al. 2009; Riet Sapriza et al. 2013; Szteren and Páez 2002). Also, SASL commercial exploitation was realized in newborn pups during 15 year, killing ~3,000 pups per year (Ponce de León 2000). In contrast, in SAFS harvesting was done principally on adult males (Ponce de León 2000), having low impact on the population, because it is a polygynous species. In addition, SAFS mostly consume energetically rich, pelagic food found in foraging areas that, by being much farther away from the coast, are less likely to have been affected by anthropogenic activities.

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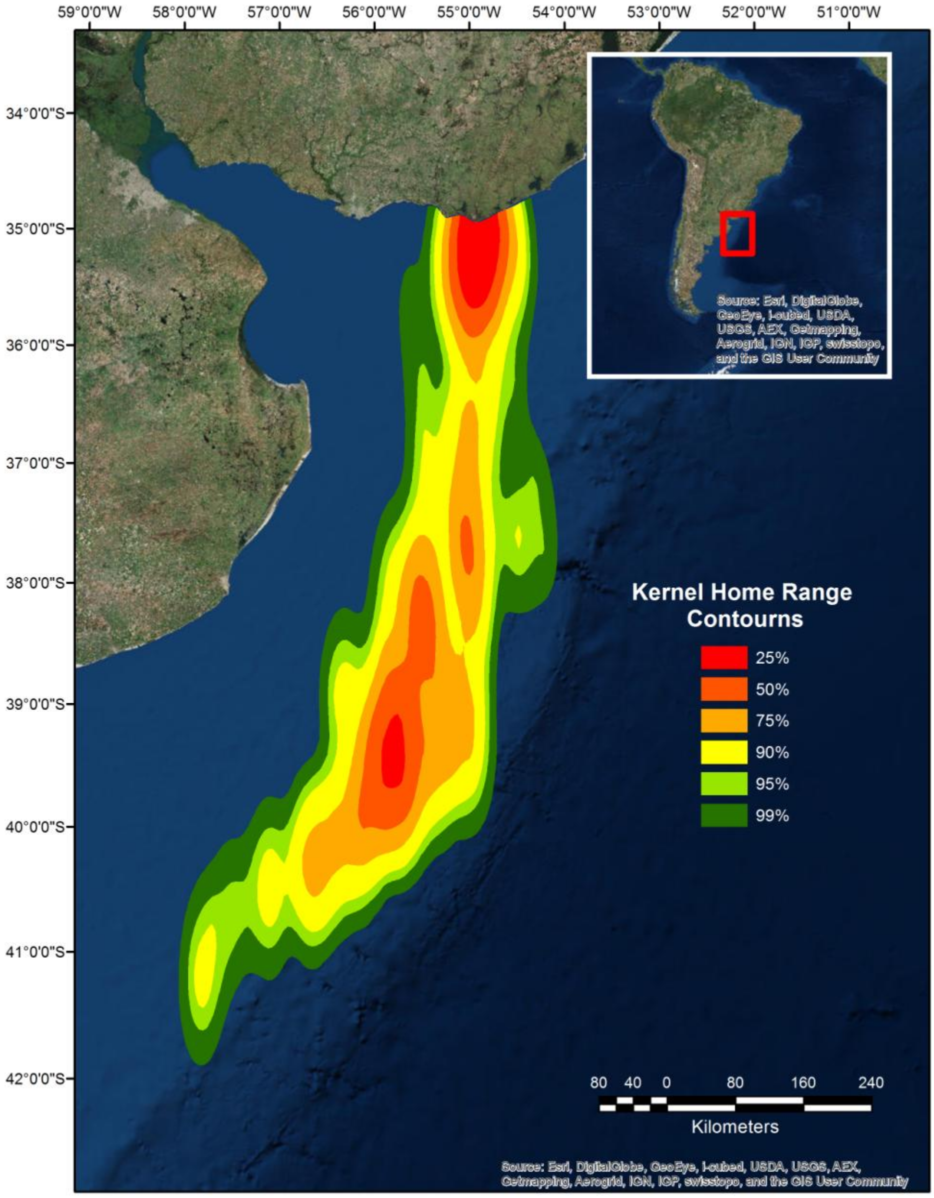
Figures legends

Figure 1. Kernel density plot including satellite relocations from individuals females of South American fur seal, *Arctocephalus australis*, captured in the Isla los Lobos, Uruguay. Density contours encompass that proportion of time spent by the individuals in the area (see colour references).

Figure 2. Home ranges of South American fur seal females, *Arctocephalus australis*, captured in the Isla los Lobos, Uruguay during the first foraging trip (green line) and the subsequent ones (red line). Home ranges were computed as the minimum convex polygons including the 95% of relocations.

Figure 3. South American sea lion (*O. flavescens*) 95% minimum convex polygon home range and individual females trajectories during the first month of breeding season at Isla de Lobos, Uruguay. From Riet-Sapriza et al. 2013.

Figure 1.



Source: Esri, DigitalGlobe, GeoEye, i-cubed, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community

Source: Esri, DigitalGlobe, GeoEye, i-cubed, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community

Figure 2.

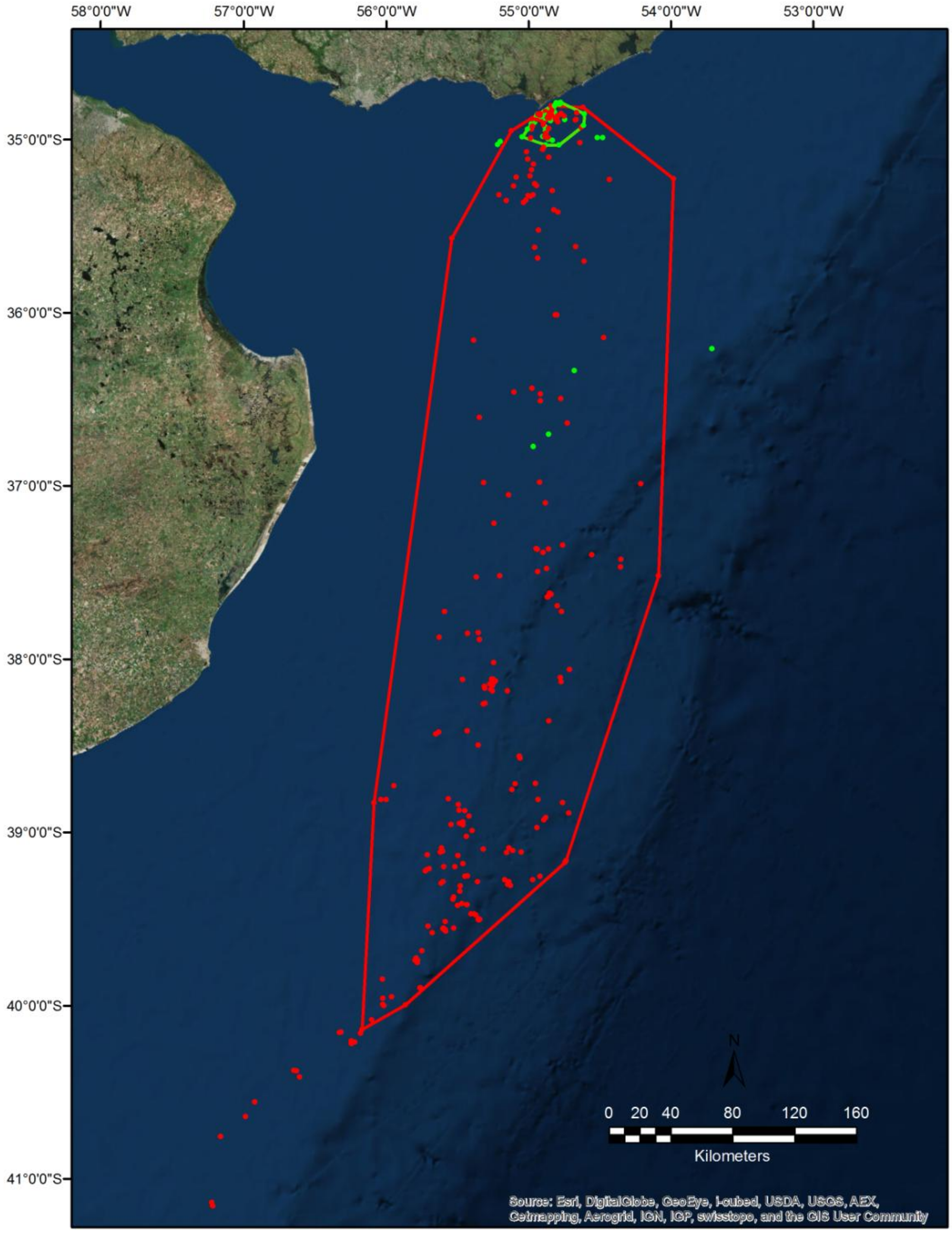

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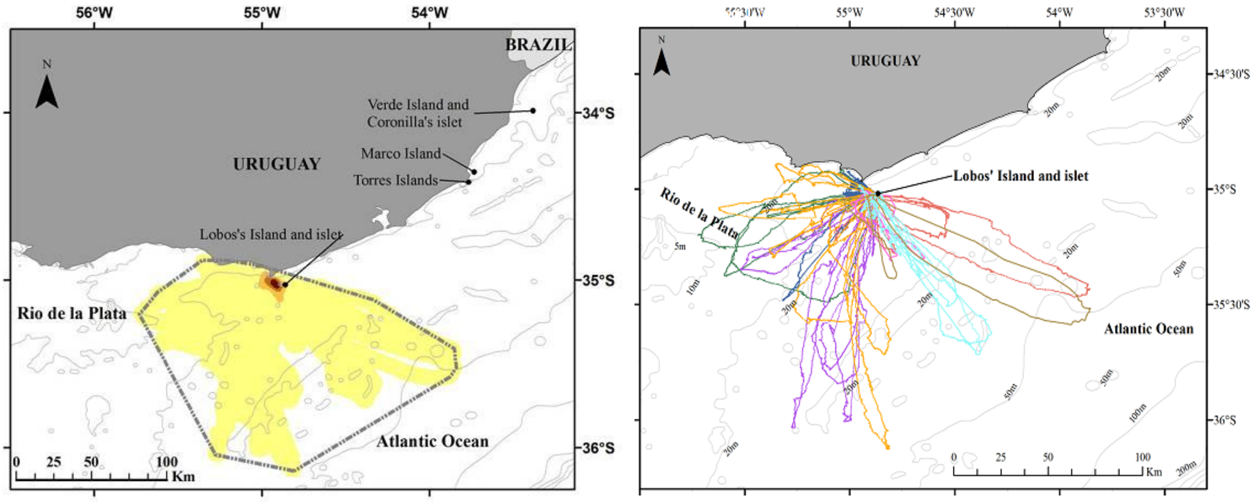
Figure 3.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50m
35°30'S
Atlantic Ocean
100m
36°S
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200m

Table 1. Summary statistics of key variables describing the use of foraging habitat by female South American fur seals (SAFS) in Isla de Lobos, Uruguay in January 2011. The variables describing the foraging behaviour were obtained by tagging each female with an Argos satellite transmitter. For each female is shown its total length, body mass, the number of Argos valid locations, the maximum distance traveled from the rookery, the total distance traveled (all trips combined), the home range (95% minimum convex polygon) during the first and subsequent foraging trips, and the % of overlap between SAFS females.

							MCP 95% km2		
Fem ID	Total length (cm)	Weight (Kg)	Location	days	Max dist (Km)	Total dist (Km)	1st trip	Others	% Overlap
181	125	38.5	38	24	451	1310	29	29729	100
182	134	46.5	56	32	476	1296	3203	21170	100
184	126	46.0	31	32	500	846	1302	22080	95
185	140	41.5	21	17	459	512	34	7990	100
186	135	46.0	75	46	551	966	38	38146	98
187	136	42.5	90	31	612	1622	330	32697	100
188	134	40.5	63	35	493	1438	209	36189	97
189	125	40.0	60	31	736	919	128	45786	71
190	123	38.5	37	38	504	1188	2	37954	99
Mean	131	42.2	52	32	531	1122	586	30193	96
SD	6	3.2	22	8	91	342	1063	11453	9

Table 2. Summary statistics of key variables describing individual diving behaviour by female of South American fur seals in Isla de Lobos, Uruguay during January 2011. Results for each variable are presented as means ± sd, except for the maximum depth of all dives and the proportion of night dives. The variables describing the diving behaviour obtained from the set of individual Reefnet records of each tagged female are: the ascent and descent rates (both in m/s), the bottom time, total dive time (total duration of a dive) and transit time (all in min), the ratio between the bottom time and dive time (ratio bt/dt), the dive effort, the average depth and the maximum depth of all dives (both in m), the aerobic dive limit (ADL; defined as the maximum duration of a dive set by the individual aerobic capacity as calculated from Gentry et al. (1986)), and the percentage of all individuals dives longer than the ADL.

ID	#dives	Ascent rate	Descent rate	Bottom time (bt)	Dive time (dt)	bt/dt	Transit time	Depth	Dive effort	Maximum depth	Prop. Night dives	ADL (min)	% dives > ADL
140	3558	1.6 ± 0.5	1.6 ± 0.5	0.3 ± 0.4	0.7 ± 0.7	0.4 ± 0.3	0.3 ± 0.4	19.1 ± 17.4	39.5 ± 36.4	102	0.6	3.6	0.2
141	3039	1.5 ± 0.6	1.4 ± 0.5	0.5 ± 0.4	0.9 ± 0.8	0.5 ± 0.2	0.5 ± 0.5	21.7 ± 21.2	46.7 ± 44.7	122	0.5	3.7	0.3
142	4844	1.6 ± 0.5	1.5 ± 0.5	0.4 ± 0.4	0.9 ± 0.8	0.4 ± 0.3	0.4 ± 0.4	21.6 ± 21.5	46.0 ± 45.7	144	0.5	3.7	0.2
144	4754	1.7 ± 0.5	1.6 ± 0.5	0.3 ± 0.4	0.5 ± 0.6	0.4 ± 0.3	0.3 ± 0.3	13.7 ± 13.4	28.4 ± 28.5	103	0.4	3.4	0.2
145	6466	1.7 ± 0.5	1.6 ± 0.5	0.3 ± 0.3	0.7 ± 0.6	0.4 ± 0.3	0.3 ± 0.4	20.3 ± 18.5	42.2 ± 38.9	152	0.5	3.5	0.1
146	6158	1.6 ± 0.6	1.6 ± 0.5	0.4 ± 0.4	0.8 ± 0.6	0.4 ± 0.3	0.4 ± 0.4	20.7 ± 18.6	43.5 ± 39.3	106	0.3	3.5	0.1
147	4007	1.6 ± 0.5	1.4 ± 0.5	0.4 ± 0.3	0.7 ± 0.5	0.5 ± 0.2	0.3 ± 0.2	16.2 ± 10.7	34.9 ± 24.0	109	0.7	3.4	0.2
148	3530	1.5 ± 0.6	1.4 ± 0.6	0.3 ± 0.4	0.8 ± 0.8	0.4 ± 0.2	0.4 ± 0.5	18.4 ± 22.1	37.9 ± 45.6	160	0.6	3.8	0.2
149	2760	1.5 ± 0.6	1.5 ± 0.5	0.5 ± 0.5	0.9 ± 0.9	0.4 ± 0.3	0.5 ± 0.5	23.4 ± 26.4	49.6 ± 54.9	150	0.5	3.6	0.3
182	2401	1.7 ± 0.5	1.5 ± 0.5	0.4 ± 0.4	0.8 ± 0.7	0.3 ± 0.3	0.4 ± 0.4	22.9 ± 21.9	47.5 ± 45.3	191	0.8	3.7	0.3
184	4595	1.6 ± 0.5	1.5 ± 0.4	0.5 ± 0.5	0.9 ± 0.6	0.5 ± 0.2	0.4 ± 0.3	24.5 ± 19.2	51.9 ± 40.9	145	0.6	3.6	0.2
190	3705	1.7 ± 0.5	1.6 ± 0.4	0.5 ± 0.4	1.0 ± 0.6	0.5 ± 0.2	0.5 ± 0.4	31.0 ± 19.9	66.0 ± 42.4	142	0.8	3.5	0.2

Table 3. Generalized linear mixed models (GLMM) of key variables describing individual diving behaviour by female of South American fur seals in Isla de Lobos, Uruguay during January 2011. Dependent variables was logarithm of dive effort, maximum depth of all dives (both in m), the ratio between the bottom time and dive time (bt/dt), the bottom time, total dive time (total duration of a dive). Estimates and statistical significance of the fixed factors (diel and travel and their interactions) and the variance of the random effect (individual identity) are shown for each analysis.

model	*intercept*	*diel (nigth)*	*travel (others)*	*diel*travel*	*var (random effect)*	*p value*
log(diving effort) ~ diel*travel	3.65	-0.40	-0.23	0.40	0.82	< 0.01
log(max depth) ~ diel*travel	2.90	-0.37	-0.23	0.40	0.76	< 0.01
bt/dt ~ diel*travel	0.48	-0.11	-0.03	0.05	0.08	< 0.01
log(bt) ~ diel*travel	-1.22	-0.83	-0.46	0.60	3.20	< 0.01
log(dt) ~ diel*travel	-0.30	-0.50	-0.37	0.43	1.16	< 0.01

Table 4. Summary characteristic to describing the population dynamic and foraging habitat for South American fur seals (SAFS) and South American sea lion (SAFS) females in Isla de Lobos, Uruguay.

	SASL	**SAFS**	**Source**
Adult female body size (Kg)	140	40	1
Annual pup population trend (period)	- 4.5% (1993 - 2001)	2% (1988 - 2005)	2
Estimated Abundance (individuals)	12,000	300,000	2, 3
Trophic habits (ratio bottom to dive time)	Benthic (0.6 ± 0.06)	Pelagic (0.4 ± 0.06)	4, 5, 6, this study
Mean dive depth (m) (sd)	21 (8)	29.8 (20.1)	6, this study
Maximum dive depth (m)	78	191	6, this study
Diel pattern	both	> night	6, this study
Mean proportion of dives longer than the ADL	0.1 (0.08)	0.21 (0.07)	6, this study
Total 95% home range	3,199.50	78,752.10	6, this study
Maximum distance travelled from colony (km)	135	736	6, this study
Mean Foraging trip duration (days) (sd)	1.5 (0.9)	10 (5.5)	6, this study
Feeding habit/diet breadth	specialist	generalist	5

[1]Reeves et al. 2005, [2]Páez 2006, [3]Páez 2000, [4]Franco-Trecu et al. 2013, [5]Franco-Trecu et al. 2014, [6]Riet-Saprisa et al. 2013

ESPECIALIZACIÓN TRÓFICA A NIVEL INDIVIDUAL Y SEGREGACIÓN SEXUAL EN EL LOBO FINO (Arctocephalus australis) Y EL LEÓN MARINO SUDAMERICANO (Otaria flavescens)

Objetivo específico:

2. Evaluar la existencia de estrategias alimenticias a nivel individual en el lobo fino y león marino sudamericano (*A. australis y O. flavescens*), evaluando la diferenciación entre sexos

Hipótesis

En ambientes variables, los individuos generalistas presentan un éxito mayor que los individuos especializados, ya que los primeros son capaces de amortiguar mejor los cambios relacionados con la presencia y abundancia de potenciales especies presa (Bolnick et al. 2007). Considerando los tamaños y tendencias poblaciones del lobo fino y león marino en Uruguay, a nivel inter-específico proponemos que el lobo fino tendrá un menor grado de especialización trófica individual que el león marino. De esta forma el lobo fino atenúa los cambios ambientales (variación de los recursos tróficos en el tiempo) de forma más eficiente, lo que se traduce en una tasa de crecimiento poblacional positiva, inversamente a lo que ocurre con el león marino. A nivel intra-específico se espera, en ambas especies, que las hembras presenten hábitos alimenticios más estables o constantes debido a las restricciones impuestas por el amamantamiento de las crías (ej. uso de áreas de forrajeo restringidas a zonas relativamente próximas a las colonias), mientras los machos, fuera del período reproductivo, podrían realizar grandes desplazamientos hacia zonas más productivas, utilizando un rango de recursos tróficos más amplio a lo largo del año.

RESUMEN

En los últimos años se ha vuelto cada vez más claro que el nicho trófico de muchas especies de vertebrados no puede asumirse homogéneo, ya que los individuos de la población pueden diferir sustancialmente en el uso de recursos (Araujo et al. 2011; Bolnick et al. 2003; Bolnick et al. 2002). Muchas poblaciones catalogadas como generalistas, con un amplitud de nicho extensa, no son más que la sumatoria de individuos especializados en distintas porciones del eje de nicho (Bolnick et al. 2003; Bolnick et al. 2002). La especialización trófica individual es cada vez más reconocida como un proceso ecológico y evolutivo con importantes influencias en la dinámica poblacional y en la estructura de las comunidades de vertebrados (Bolnick et al 2003;. Araujo et al 2011), y ha sido reportada en diversidad de especies (Brodersen et al. 2012; Matich et al. 2011; Newsome 2009; Vander Zanden et al. 2010; Woo et al. 2008). En el caso de otáridos, la especialización trófica a nivel individual podría estar relacionada con la segregación espacial de las zonas de alimentación cuando las especies viven en simpatría (Jeglinski et al. 2013; Páez-Rosas et al. 2012). En general las investigaciones sobre especialización individual en otáridos se han basado únicamente en hembras, limitando las inferencias que puede ejerer la diversificación individual a nivel poblacional, aunque estudios recientemente han incluido ambos sexos (Kernaléguen et al. 2012). Las poblaciones simpátricas de otáridos que se reproducen en Uruguay (*Otaria flavescens* y *Arctocephalus australis*) presentan tendencias poblacionales opuestas (Páez 2006) con una clara segregación alimenticia (ver capítulo 1). Para evaluar la especialización individual en ambas especies y sexos (n=17) se utilizó el análisis de isótopos estables de $\delta^{13}C$ y $\delta^{15}N$ en vibrisas. Se seleccionó este tejido de crecimiento continuo ya que el mismo integra una ventana temporal aproximada de 2-3 años (n=414 porciones). Se utilizaron modelos lineales generalizados mixtos (Pinheiro and Bates 2000) para evaluar las diferencias entre especies, sexos y su interacción (efectos fijos), así como de la identidad (efecto aleatorio) sobre los valores de $\delta^{13}C$ y $\delta^{15}N$. La selección de modelos fue realizada empleando el Criterio de Información de Akaike (AIC), considerando un ΔAIC>2 como indicador de diferencias en el soporte empírico entre los modelos (Bolker 2007). Estimamos el área de nicho isotópica a nivel poblacional e individual a través de la estimación de Kernel al 95% y al 25% (Worton 1987). A su vez evaluamos el solapamiento de dichas áreas entre los individuos de cada especie. El modelo seleccionado para el $\delta^{13}C$ mostró que la especie, el sexo y su

interacción tuvieron un efecto estadísticamente significativo, mientras que para el $\delta^{15}N$ solo se detectaron diferencias estadísticamente significativas entre especies. A nivel intra-especifico, los machos de lobo fino presentaron mayor área de nicho trófico que las hembras y mayor cantidad de área exclusiva. En el león marino las hembras no sólo tuvieron mayor área de nicho trófico que los machos, sino que también mayor exclusividad. A nivel individual el promedio de las área de nicho trófico fue significativamente mayor para el lobo fino que para el león marino (al 95 y 25%: $P < 0.01$). Además el solapamiento entre individuos fue significativamente mayor entre los individuos de lobo fino (95%: 0.67 ± 0.23; 25%: 0.28 ± 0.31) que entre los de león marino (95%: 0.50 ± 0.19; 25%: 0.14 ± 0.26) ($P << 0.001$). Los resultados encontrados sugieren que los 4 grupos (especies y sexos) se alimentan en diferentes áreas, pero con similar nivel trófico. En el lobo fino, el efecto de la competencia intra-específica, dado su tamaño poblacional (~300mil) (Páez 2000), podría estar conduciendo la disminución de la especialización (con individuos compartiendo los recursos secundarios). Esto último se reflejaría en la expansión del nicho trófico a nivel individual y poblacional, pero en una menor diferenciación entre individuos del lobo fino. Por otro lado, la batimetría y la restringida capacidad de ayunar de las crías del león marino limitarían las distancias que las hembras de esta especie podrían desplazarse durante sus viajes (ver capítulo 1), y por lo tanto la diversidad de recursos tróficos que las hembras de esta especie pueden explotar. De esta forma, el grado de especialización trófica individual de las dos especies de otáridos en Uruguay resultaría de la acción de diferentes mecanismos. Es importante conocer los niveles de especialización individual en los depredadores tope porque desempeñan un papel importante en la estructura y la dinámica de sus comunidades, ya sea a través de efectos directos sobre sus presas o vía indirecta sobre las especies de niveles tróficos más bajos (Estes et al. 1998; Shurin et al. 2002).

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ORIGINAL PAPER

Individual trophic specialisation and niche segregation explain the contrasting population trends of two sympatric otariids

Valentina Franco-Trecu · David Aurioles-Gamboa · Pablo Inchausti

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Abstract Individual specialisation is increasingly recognised to be an ecological and evolutionary process having important consequences for population dynamics of vertebrates. The South American fur seal (SAFS) and the South American sea lion (SASL) are two otariid species with similar ecology that coexist in sympatry in the Uruguayan coast. These two species have contrasting trends and widely different population sizes. The underlying reasons for these population trends, unique in their geographical ranges, remain unknown. We studied the foraging ecology of these otariid species over 2 years at the individual- and population levels using the isotopic ratios (δ^{13}C–δ^{15}N) in whiskers of both sexes. We compared the isotope ratios between species and sexes and used several metrics to characterise the degree of overlap and distinctiveness in the use of isotopic niche space at the individual- and population levels. Interspecific trophic niche overlap was minimal, thus ruling out interspecific competition as the cause for the contrasting population trends of both species. At the intraspecific level, both species had sexual segregation in their foraging areas, but each species had a large overlap in the isotopic niches between sexes. While SAFS had a wider niche and generalist individuals, SASL had the narrower niche with a higher degree of individual specialisation. Behavioural constraints during the breeding season, intraspecific competition and a major dependence on resources of the Uruguayan coastal shelf may explain why SASL had a higher trophic individual specialisation and a larger vulnerability in a heavily exploited habitat by fisheries and, by consequence, a locally declining population trend.

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V. Franco-Trecu
Proyecto Pinnípedos, Sección Etología, Facultad de Ciencias,
Universidad de la República, Iguá 4225, 11400 Montevideo,
Uruguay

D. Aurioles-Gamboa
Laboratorio de Ecología de Pinnípedos Burney J. Le Boeuf,
Centro Interdisciplinario de Ciencias Marinas, Instituto
Politécnico Nacional, Ave IPN s/n, CP 23096, La Paz,
Baja California Sur, Mexico

P. Inchausti (✉)
Departamento de Ecología y Evolución, Centro Universitario
Regional Este (CURE), Universidad de la República,
Tacuarembó S/N, 20000 Maldonado, Uruguay
e-mail: pablo.inchausti.f@gmail.com

Introduction

The ecological niche, defined as a *n*-dimensional hypervolume containing the relevant variables that explain the persistence of a species or a local population, (Hutchinson 1957) is a keystone concept in ecology. It is involved in a wide range of topics ranging from the behaviour and physiology of individual organisms to the structure of communities and ecosystem functioning (Chase and Leibold 2003). However, it has become increasingly clear that the niches of many vertebrate species cannot be assumed to be homogeneous because individuals can substantially differ in their resource use (Bolnick et al. 2003). For instance, many generalist populations that use a wide diversity of resources when examined at the population level are actually an ensemble of specialised individuals that segregate in the niche space (Bolnick et al. 2003, 2007).

Individual specialisation is increasingly recognised to be an ecological and evolutionary process having important influences on population dynamics and community structure of vertebrates (Bolnick et al. 2003; Araujo et al. 2011). Trophic specialisation at the individual level has been found in many species such as fish (Brodersen et al. 2012), sharks (Matich et al. 2011), birds (Woo et al. 2008), sea turtles (Vander Zanden et al. 2010) and carnivores (Newsome et al. 2010a). Top predators often play an important role in the structure and dynamics of their communities either through direct effects on their prey or via the indirect impact on species at other trophic levels (Estes et al. 1998; Shurin et al. 2002). In the case of otariids, trophic specialisation could arise because of the individual-level differentiation of resource use and the spatial segregation of foraging areas (Franco-Trecu et al. 2012; Páez-Rosas et al. 2012; Jeglinski et al. 2013). However, to our knowledge, there has been little research on trophic specialisation of otariids including both sexes (Kernaléguen et al. 2012), thus limiting the inferences on the individual behavioural strategies at the population level.

Uncovering the existence of individual strategies in resource use requires showing the consistent differentiation among individuals of a population. In recent years, stable isotopes analysis (SIA) of different tissues has emerged as a key method to investigate the differences in the foraging ecology of pinnipeds (Aurioles-Gamboa et al. 2006; Páez-Rosas et al. 2012; Franco-Trecu et al. 2013). In marine food webs, the prey-to-consumers isotopic (δ^{15}N and δ^{13}C) enrichment change in a predictable manner in accordance with the specific dietary fractioning (Hobson et al. 1994; Post 2002; Newsome et al. 2007). The δ^{15}N and δ^{13}C are used to estimate the trophic position (Post 2002) and the feeding sources used by the predators (DeNiro and Epstein 1978; Bearhop et al. 2004) at different temporal scales depending on the moment of production and the turnover rate of the tissue analysed (Dalerum and Angerbjörn 2005). The SIA of metabolically inert tissues such as tooth dentine and whisker keratin with continuous growth, represent sequential archives that allow inferring foraging strategies at individual level over long periods of time (Zhao and Schell 2004; Kernaléguen et al. 2012; Elorriaga-Verplancken et al. 2013).

Two sympatric otariid species breed in South American coast: the South American fur seal (SAFS), *Arctocephalus australis*, and the South American sea lion (SASL), *Otaria flavescens* . While the Uruguayan SAFS population has steadily increased over the last 17 years, with a current estimated size of 300,000 individuals, the SASL has declined in the same period, and its current population size is about 12,000 individuals (Páez 2006). The underlying reasons for these contrasting trends (Pedraza et al. 2009) that are unique in the geographical ranges of both species (Crespo et al. 2008; Dans et al. 2009) remain unknown. Both species can be considered central place foragers since females regularly return to the rookery to feed the pups (Pyke 1984; Stephens and Krebs 1986). Lactating females from both species must maintain a steady energy supply to their offspring that feed exclusively on mother's milk for several months. Based on faecal analysis, the SAFS and SASL have been characterised as generalist predators whose diets have similar species composition (Naya et al. 2000, 2002; Szteren et al. 2004). However, using SIA in pup's different tissues, Franco-Trecu et al. (2012) showed that these species were segregated in the isotopic space because SASL breeding females exploited nearshore resources whereas SAFS's used offshore resources during pre- and post-partum periods. Nevertheless, the only study dealing with these two species (Franco-Trecu et al. 2012) evaluated trophic differentiation at the population level without considering potential differences of feeding strategies at the individual level.

In this paper, we test the existence of trophic strategies at the individual- and population levels for two sympatric pinniped species with similar diets (Szteren et al. 2004) having different population trends. We used stable isotope values of δ^{13}C and δ^{15}N in whiskers of the SASL and SAFL from Isla Lobos Uruguay to integrate the spatial and trophic dimensions of the ecological niche of individuals over a long period of time. Considering the estimated growth rates for other otariids species of 0.10–0.17 mm d^{-1} (Hirons et al. 2001), the time period comprising the whiskers analysed was of approximately 2–3 years. We hypothesised that females of both species would have less variable foraging strategies due to restrictions imposed by maternal care. On the other hand, males could exploit other marine environments including different preys after the breeding season, which would result in males of both species having more distinct and wider isotopic niches than in females over time. Regarding the trophic segregation between SASL and SAFS found by Franco-Trecu et al. (2012) using data for females, we hypothesise that by including isotopic data from the males, the trophic segregation between these two species should decrease. Finally, given that generalist individuals (or populations) often access a wider range of trophic resources and achieve higher fitness (at both individual- and population levels) than specialist individuals in temporally or spatially variable environments (Bolnick et al. 2007), we expect the SAFS population to have a higher trophic niche area and a lower degree of individual specialisation. In contrast, the SASL is expected to have a smaller niche area, stronger resource use specialisation with a larger variety of individual trophic strategies.

Materials and methods

Study site, sample collection and treatment

The SAFL and SASL breed on rocky islands of the Uruguayan continental shelf that are the northernmost breeding sites of both species. Their main rookery is Isla de Lobos

(35°01'S, 54°50'W) located at the easternmost part of the Río de la Plata estuary where a highly dynamic mixing regime results from the mixing of freshwater and seawater because of the convergence of the Brazil and Falklands currents (Ortega and Martinez 2007).

Whiskers of five SASL and five SAFS randomly chosen lactating females were obtained in January 2009 and December 2009, respectively. Lactating females were captured with a hoop net and sedated using ~2 ml of midazolan 0.5 % (Vetcros) in the case of SAFS, while SASL were anaesthetised using isoflurane gas mixed with oxygen (0.5–2.5 %) using a portable-field vaporizer (see Riet-Sapriza et al. 2013). Whiskers of adult males of both species were collected from dead animals incidentally captured in January 2009 (SASL, $n = 3$) and January 2010 (SAFS, $n = 4$). All procedures of animal manipulation were submitted and approved by the Ethics Committee in Animal Experimentation, Universidad de la República, Uruguay, as valid according to the national laws in animal welfare.

Each whisker was washed with distilled water and phosphate-free soap to remove impurities and divided into approximately 55 fragments, adjusting to the total length of the whisker. To minimise the effect of a strong autocorrelation in the comparison of isotopic profiles, we processed every other fragment of each whisker obtaining a total of 414 fragments of the two sexes and species. Each whisker fragment was immersed in a 1:1 hexane–acetone solution to extract lipids and left until total evaporation (Zeppelin and Orr 2010). We then subsampled each whisker to obtain fragments of *ca*. 0.8 mg (high-precision microbalance Mettler Toledo MX5, precision = 1 μg) that were stored until isotope determination.

We used a mass spectrometer of continuous flow (CF-IRMS) coupled to an elemental Analyzer PDZ Europe ANCA-GSL (Stable Isotope Laboratory, University of California at Davis) to determine natural carbon and nitrogen abundance and their isotopic ratios with an analytical precision of ±0.2 ‰ for both isotopes. The resulting isotope ratios for each whisker segment were converted and reported to the conventional values delta (δ) in parts per thousand (‰), according to: $\delta X = [(R/R_{st}) - 1] \times 1{,}000$, where X stands for ^{13}C or ^{15}N, R is the heavy–light stable isotope ratio of the sample ($^{15}N/^{14}N$ or $^{13}C/^{12}C$), and R_{st} is the heavy–light stable isotope ratio in reference standards, which were the atmospheric N_2 (air) for ^{15}N and for ^{13}C *relative to the Pee Dee Belemnite* (*PDB*) *standard*.

Data analysis

Average isotopic content at species level

We used linear mixed models (Pinheiro and Bates 2000) with Gaussian distributions and identity link functions to examine the differences between species, sex (both as fixed effects) and their interactions on the average content of $\delta^{13}C$ and $\delta^{15}N$ values. These models had individual identity as a random effect to account for repeated measures of each response variable on the different fragments of each whisker. This random effect allowed evaluating the extent to which the individuals' isotopic value differentiated from the average profile of the species. We used a continuous autocorrelation function (Pinheiro and Bates 2000) to model the serial correlation of the set of values of the response variables at the individual level. The statistical significance of fixed effects in the mixed models was assessed using Bayesian methods (details in Baayen 2008). Starting from the global model (all fixed effects and their interactions), subsequent models were generated by the stepwise removal of non-significant terms and assessing each simplification with the Akaike information criterion (AIC) using the $\Delta AIC > 2$ criterion (Bolker 2007). All models considered were subject to the customary residual analyses (Pinheiro and Bates 2000) and were found to have a satisfactory fit (results not shown).

Isotopic niche space use

We characterised the individual use of the isotopic space defined by $\delta^{13}C$ and $\delta^{15}N$ using statistical methods developed for home-range analysis (Layman et al. 2007; Sepúlveda et al. 2012). Home ranges are commonly characterised by a set metrics that delimit the zone of its maximum use (minimum convex polygon) or estimate the probability of finding an individual in a given area typically using an adaptive kernel (Worton 1987; Newsome et al. 2012) that minimised the effect of temporal autocorrelation (Fieberg 2007). The percentages of the overall area in the isotopic space used by an individual had a similar interpretation to their common use in home-range analysis. While the 95 % kernel extent denotes the overall area of the isotopic space (resources and foraging areas) used by each individual (or group) over time regardless of frequency of use, the 25 % kernel extent refers to the fraction of the isotopic space that is frequently used and thus likely to be important for a randomly chosen individual. We further characterised the individual- and population-levels patterns of the use of niche space using two metrics. First, we measured the isotopic niche width for each species and sex using the convex hull area calculated as the total area of individual values in the isotopic space encompassed by the minimum convex polygon (Cornwell et al. 2006; Layman et al. 2007). Second, we calculated the individual- and group-levels niches in the isotopic space using the 25 and 95 % kernel density estimates (Sepúlveda et al. 2012) that were employed to estimate their degree of niche overlap at each level. The latter was estimated using the proportion of each individual (or group) home range (HR) i covered by the home range of another individual (or group) j defined as $HR[i,j] = A[i,j]/A[i]$, where $A[i,j]$ is the area of the intersection between the home ranges of individuals (or group) i and j, and $A[i]$ is the area of the home range of individual (or group) i. We separately compared the magnitude of overlap in the kernel densities at 25 and 95 % between species and sexes using linear mixed models as described above.

We quantified individual specialisation using Bolnick et al.'s (2002) S index (=WIC/TNW) that assesses the proportion of the total niche width (TNW) of a population (or group) that can be attributed to the within individual component (WIC). When the population is made of largely generalist individuals, WIC is a large proportion of TNW (the opposite being true in a population of specialist individuals) (Bolnick et al. 2002). We estimated the WIC as the average of individual kernel densities at 25 as 95 % and the TNW as the total kernel density at the species level. We considered 1−S as the proportion of the TNW explained by variation among the individual niches (WIC) (Bolnick et al. 2003).

All statistical analyses were carried out in R (R Development Core Team 2008) using the splancs and tripack libraries (Jombart 2008) to obtain the convex hulls, adehabitat (Calenge 2006) for kernel density analysis, nlme (Pinheiro et al. 2013) and lme4 (Bates et al. 2011) for mixed models, and languageR (Baayen 2008) to assess the statistical significance of the fixed effects using Bayesian methods.

Results

The average lengths of the whiskers analysed were 132.7 mm (SD = 26.2) and 123.0 mm (SD = 14.3) for SASL and SAFS, respectively. There were significant differences in the mean whisker δ^{13}C content between of males and females depending on the species (see interaction sex*species in Table 1). While the average δ^{13}C was significantly higher for SAFS females compared with males of the same species, the opposite was true for SASL. Mean δ^{15}N values significantly differed between species (but not between sexes), with SASL having higher values than SAFS (Tables 1, 2). For both δ^{13}C and δ^{15}N, the most parsimonious linear mixed models included a slowly decaying autocorrelation at the individual level of 0.92^{γ} with γ being the distance in mm between the fragments analysed

Table 1 Linear mixed models for whisker δ^{13}C and δ^{15}N value

		Intercept (p value)	Species (SASL) (p value)	Sex (males) (p value)	Species*sex (p value)	AIC	Anova (p value)
δ^{13}C	Sex*species	−15.30 (0.00)	2.50 (0.00)	0.40 (0.02)	−0.80 (0.002)	361.3	0.002
	Sex + species	−15.16 (0.00)	2.15 (0.00)	−0.01 (0.93)	–	369.0	
	Sex*species (corCAR1)	−15.30 (0.00)	2.53 (0.00)	0.48 (0.01)	−0.94 (0.002)	206.9	<0.0001
δ^{15}N	Sex*species	17.14 (0.00)	2.84 (0.00)	0.50 (0.18)	−0.58 (0.28)	900.8	
	Sex + species	17.26 (0.00)	2.59 (0.00)	0.25 (0.36)	–	900.0	0.3766
	Species	17.36 (0.00)	2.59 (0.00)	–	–	898.8	<0.0001
	Species (corCAR1)	17.38 (0.00)	2.59 (0.00)	–	–	823.4	<0.0001

Estimates and statistical significance of the fixed factors (sex and species and their interactions) are shown for each variable. The analysis considered the "contrast treatment" option whereby each level of the fixed effects and their interactions was compared with the reference levels: SAFS for species and females for sex. The averages of δ^{13} C and δ^{15}N (and their standard error) for each combination of Species and sex can be obtained from the fitted coefficients of the fixed effects. The p values correspond to the statistical significance of each coefficient of the fixed effects in each model. The AIC are the values of the Akaike information criterion of each model and ANOVA p values of the comparison of the deviances between models. The selected models (lowest AIC) for each isotope are in bold and include continuous first order autocorrelation modelled as 0.92^{γ}, where γ is the distance in mm between consecutive fragments analysed of a whisker

Table 2 Ranges in δ^{13}C and δ^{15}N, convex hull area and kernel density (25 and 95 %) by groups

Group	δ^{13}C (mean, range)	δ^{15}N (mean, range)	Convex hull area 95 %	Kernel 25 % area	Kernel 95 % area
SAFS males	−14.9 (−16.6, −13.7)	17.6 (14.3, 20.2)	8.80	0.76	8.44
SAFS females	−15.3 (−16.6, −14.1)	17.2 (14.1, 19.1)	6.80	0.57	7.00
SASL males	−13.2 (−14.8, −12.3)	19.9 (19.1, 21.3)	3.70	0.23	2.54
SASL females	−12.8 (−13.9, −12.2)	20.0 (18.5, 21.6)	3.50	0.56	4.39

SAFS South American fur seal, *SASL* South American sea lion. Linear model CH-Kernel at 95 %: $y = 0.57 + 0.92*x$ ($p = 0.055$; $R^2 = 0.90$)

of each whisker (Table 1). This decaying function implied that the correlation of isotope readings separated by more than 23 mm (corresponding to four analysed whisker fragments) would not be significantly different from zero (i.e. statistically independent from each other).

SAFS males had the largest niche area in the isotopic space (in units of squared delta isotopic contents) as estimated by the convex hull area (8.8), followed by SAFS females (6.8), SASL males (3.7) and SASL females (3.5) (Fig. 1a). The isotopic niche areas estimated by kernel density had similar ranking, but SASL female areas were larger than those of SASL males (see Table 2, Fig. 1b). At intraspecific level, 85 % of SAFS females' isotopic niche areas were used by males of the same species, whereas the latter had a more exclusive niche areas that were shared in 75 % by SAFS females (Fig. 1b). In contrast, SASL niche areas had the opposite pattern: 79 % of males' isotopic niche areas were also used by females, and but only 54 % of females' niche areas were used by SASL males (Fig. 1b). At the interspecific level, the individual isotopic niches of females of both species did not overlap whereas those of males only had a small overlap of 16 % for the SASL and 5 % for the SAFL (Fig. 1b). These findings suggest the existence of trophic segregation between species that is similar between sexes (Fig. 1 a, b).

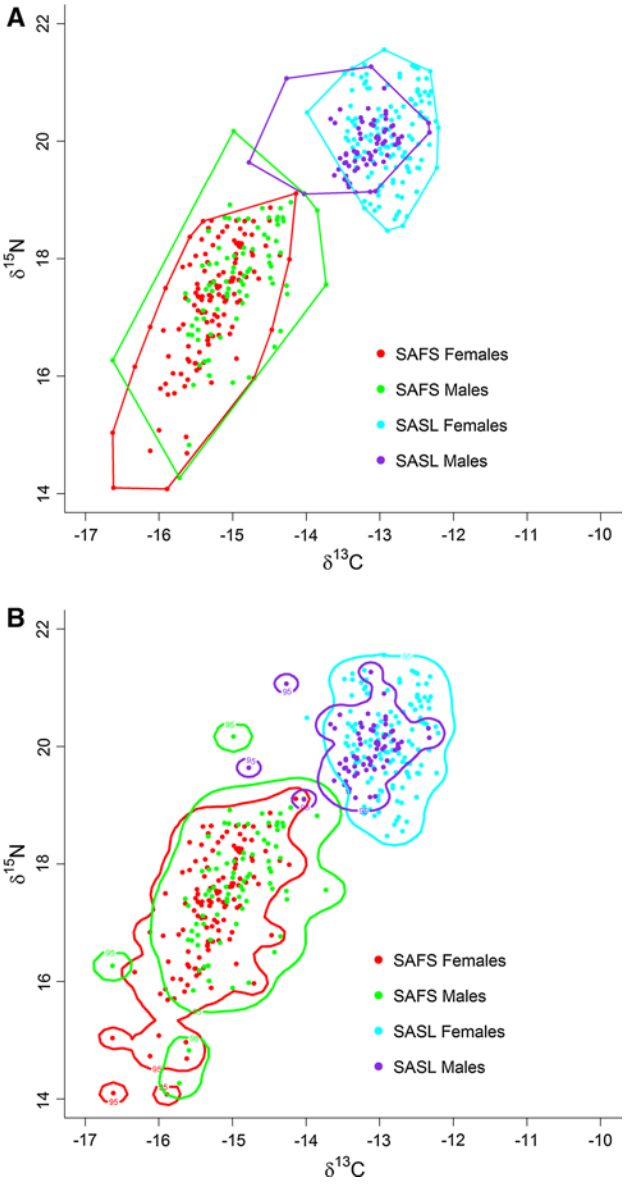

Fig. 1 Isotopic niche area (δ^{13}C, δ^{15}N) for South American fur seal (SAFS) and South American sea lion (SASL) females and males estimated by **a** convex hull areas and **b** kernel densities at 95 %. *Dots* represent the isotopic values of successive fragments analysed of a whisker for all individuals of each species and sex

At the individual level, the average isotopic niche areas calculated as 25 and 95 % kernel densities were significantly wider for SAFS than for SASL (25 %: $T = 3.93$, $p = 0.003$; 95%: $T = 4.18$, $p = 0.002$, Fig. 2). In addition, the average overlap between the individual niche areas also calculated as 25 and 95 % kernel densities was significantly higher for SAFS than for SASL (Fig. 2; Table 3). The individual specialisation index (S) was much greater for SAFS than for SASL both at the 25 % (0.963 vs. 0.591) and 95 % kernel densities (0.812 vs. 0.588). These results suggest that the SAFS population was composed by generalist individuals since only between 3.7 and 18.8 % of the TNW could be explained by variation among the individual niches (calculated as $1-S$). In contrast, the SASL population was made of individuals with a medium level of trophic specialisation because 40.9 and 41.2 % of the TNW was due to the differences among individual niches for 25 and 95 % kernel densities, respectively.

Discussion

We assessed the individual long-term dietary specialisation from two sympatric otariid species using the isotopic ratios in their whiskers (incorporating 2–3 years, see Results). Our results indicate that the isotopic niches of SASL and SAFS have different sizes and that these species have degrees of individual trophic specialisation in the Uruguayan coast. We found that SAFS had a larger trophic niche resulting from generalist individuals, whereas SASL has a smaller niche, and its individuals had a higher degree of trophic specialisation. Characterising individual specialisation and foraging strategies requires having longitudinal data (of isotope profiles, in our case) of the same individual over sufficient length of time. Our sample sizes in terms of individuals may seem limited to some (but they are actually comparable with other studies with otariids: Cherel et al. 2009). However, facing the unavoidable trade-off between having many but more coarsely analysed individual data or

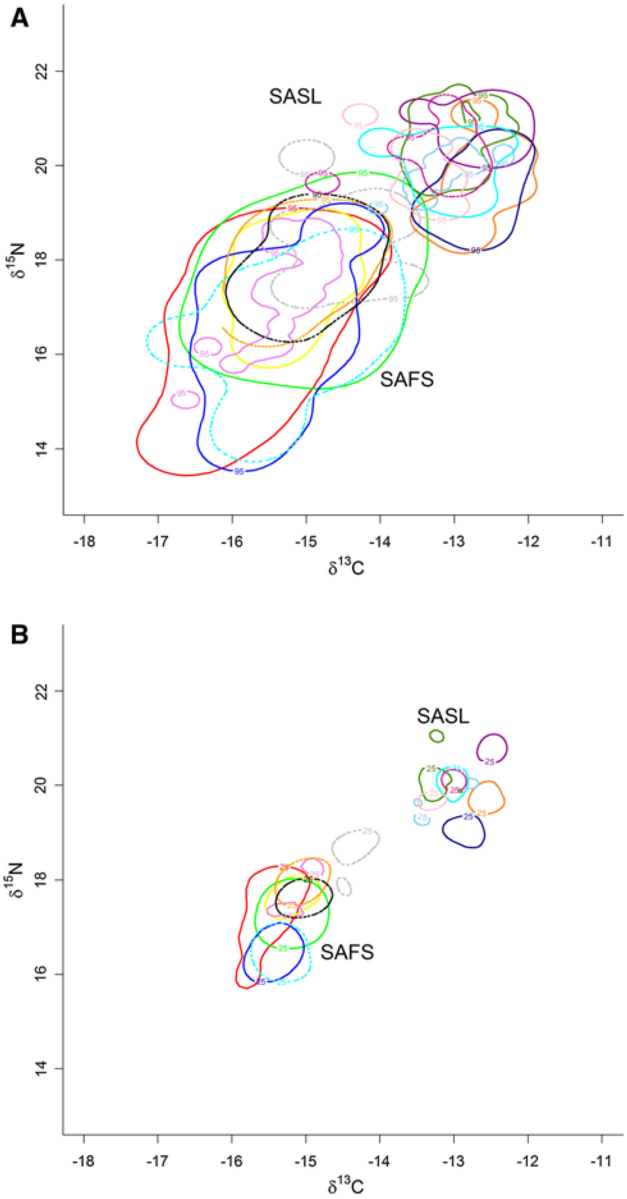

Fig. 2 Individual isotopic niche areas (δ^{13}C, δ^{15}N) estimated by kernel density for South American fur seal (SAFS) and South American sea lion (SASL) at (**a**) 95 % and (**b**) 25 % kernel densities with individuals having different colours

Table 3 Linear mixed models for intraspecific overlap between pairs of individual niche areas in the isotopic space estimated by the 25 and 95 % kernel areas

	Intercept (*p* value MCMC)	Sp (SASL) (*p* value MCMC)
95 % Kernel overlap model	0.665 (0.00)	−0.165 (0.02)
25 % Kernel overlap model	0.284 (0.00)	−0.141 (0.05)

Estimates are shown with their statistical significance as determined by Markov chain Monte Carlo (MCMC). The analysis considered the "contrast treatment" option showing the average intraspecific overlap of South American fur seals as the Intercept and its average difference with the South American sea lion (SASL) as Sp

having relatively fewer but more finely analysed isotopic profiles over time, we think that the latter choice may best yield the detailed characterisation of individual profiles over 2–3 years required to test our hypotheses.

Sexual segregation

The existence of overall trophic segregation by sex has already been shown in other species with sexual size dimorphism (Forero et al. 2002; Beck et al. 2007; Cherel et al. 2007; Kernaléguen et al. 2012). Regarding δ^{13}C, as it has also been observed in other aquatic environments (France 1995; Newsome et al. 2010b), in Uruguay offshore prey species (deeper waters) have lower δ^{13}C value than nearshore (Franco-Trecu et al. 2012). Our results showed that sexual niche segregation more likely occurred in the use of distinct diversity of foraging habitats as reflected by the δ^{13}C values and that the differences between sexes in each species varied significantly and in opposite direction along the δ^{13}C axis (see significant interaction in Table 1). These results were expected since both SASL and SAFS have sexual dimorphism in body size with males being three times larger than females. Then, differences in δ^{13}C contents between sexes may reflect physiological (body mass) or behavioural (parental care) differences. Had males of both species used their higher diving capacity to exploit larger three-dimensional foraging areas, and considering that they are not involved in postnatal care, they could feed farther away from the rookery than females (Campagna et al. 2001) and have exploited wider ranges and more exclusive foraging habitats in δ^{13}C (Bearhop et al. 2004).

While SASL males had a lower δ^{13}C values than females of the same species, the opposite was true for SAFS. Although the range of δ^{13}C was wider for males of both species, we found a large overlapping in the overall areas of isotopic niches between the sexes of both SASL and SAFS (Fig. 1a, b). As reported for other pinniped species (e.g. Weise and Costa 2007), adult females of these species may turn out to have larger mass-specific muscle and total oxygen stores than adult males of similar size. The latter may explain the seemingly surprising result that males, despite not being linked to the colonies, have a similar foraging behaviour than females of California sea lion (*Zalophus californianus*). However, it remains to be explained why the average values of δ^{13}C between sexes in these two species differed in opposite directions. We hypothesise that SASL males could be preferentially foraging on more pelagic resources or at more southern areas than SASL females, with the opposite being true for SAFS. In this regard, there have been sightings of SASL males marked in Mar del Plata, Argentina (38º00'S, 57º33'W) breeding in Isla de Lobos (Giardino et al. 2009) and of SAFS males marked in our study site that were stranded in southern Brazil (VFT unpublished data).

The interpretation of the differences in the isotopic niche areas between sexes may change depending on the method used to quantify them. While niche metrics obtained from convex areas may be influenced by extreme values and thus show biased segregated patterns (Jackson et al. 2011), those based on the kernel density method are more robust and would then be a better representation for the species (or group) use of the isotopic space (Sepúlveda et al. 2012). Contrary to our expectations based on the sexual dimorphism in body size of both species that would allow males to exploit larger preys often at higher trophic levels, the results for δ^{15}N showed that both sexes of SASL and SAFS exploited preys at similar trophic levels (Table 1; Fig. 1). In both species, females had wider ranges of δ^{15}N (see Table 2) that are associated with a higher consumption of preys at lower trophic levels than males'. The difference in kernel niche area between SASL sexes was related to the wider range of δ^{15}N of females (see Table 2). SASL pup physiology imposes restrictions on their mothers (see below) to feed in areas close to the rookery at depth smaller than the diving capacity associated with their large body size (Riet Sapriza et al. 2013) probably consuming preys at lower trophic levels.

Species segregation

We found a strong trophic segregation between species for both δ^{15}N and δ^{13}C (Fig. 1). This result confirms that SASL generally consume preys of higher trophic levels in nearshore areas than SAFS (Franco-Trecu et al. 2012). However, the small intraspecific segregation between sexes for δ^{13}C led to a small overlap between species on this axis (Fig. 1). The spatial segregation of trophic niches between sympatric species is well known to minimise interspecific competition (Begon et al. 2006). The trophic segregation between SASL and SAFS in the Uruguayan coast implies either the absence or the release from competition of these species. Therefore, the contrasting trends and population abundances between SAFS and SASL would be unrelated to interspecific competition. Another potential cause for the limitation of SASL feeding area is the higher SAFS abundance in the area which would restrict the SAFS to coastal waters, although testing this idea would require an historical approach that the available data in the study area do not allow. In a study conducted at the San Benito Islands, the stable and larger population of the California sea lion (*Zalophus californianus*) share breeding habitat with the less abundant Guadalupe fur seal (*Arctocephalus townsendi*). In this case, the sea lion showed clearly coastal feeding habits with a large component of fish species in its diet, whereas the fur seal fed mostly on squids (Aurioles-Gamboa and Camacho-Ríos 2007). In another case, the Galapagos sea lion (*Zalophus wollebaeki*) and Galapagos fur seal (*Arctocephalus galapagoensis*) both have reduced populations and clearly separated feeding grounds and feeding habits (Páez-Rosas et al. 2012). While the case of SAFS and SASL is one in which one species significantly overpasses the other in abundance, it is possible that the density of the SAFS may have some effect on the feeding areas of the SASL. Nevertheless, we think that the patterns we found for SAFS and SASL essentially resemble other cases in which the sea lion feed mostly in coastal waters while the fur seal concentrates its feeding in pelagic waters.

Individual specialisation

There is strong evidence of individual trophic specialisation for many vertebrate species (Bolnick et al. 2003, 2007, 2011) mostly at very short time scales (Woo et al. 2008). In pinnipeds, most evidence is restricted to breeding females that possess fidelity to foraging areas over time (Bonadonna et al. 2001; Chilvers et al. 2005), actively select prey species (Bowen et al. 2002) and have individually distinct diving patterns (Villegas-Amtmann et al. 2008).

The SAFS and SASL had contrasting degrees of individual trophic specialisation. While the SAFS population had a large trophic niche area and was comprised of generalist individuals, SASL has a smaller trophic niche area that was exploited by individuals with a higher degree of individual specialisation. The latter is reflected in the low degree of overlapping between individual niche areas (Fig. 2) and by the index $1-S$ (proportion of the TNW that could be explained by variation among the individual niches, WIC) for SASL showing that more than 40% of SASL's niche area at the population level corresponded to differentiated niche areas at the individual level. This value of 1-S for SASL lies within the range of values (average = 21 %; range: 0; 62 %) found reported by Bolnick et al.'s (2003) compilation of 79 studies of individual specialisation. The individual-level diversification of the trophic niches here reported for both species concerns a relatively long period of approximately 2–3 years, according to the typical growth rates of pinniped whiskers (Hirons et al. 2001).

Despite of its currently low and declining population size in Uruguay, we believe that SASL's higher degree of individual specialisation may be related to high intraspecific competition. SASL mainly forages in coastal areas that are heavily exploited by both industrial and artisanal fisheries with whom SASL has been shown to have an important degree of spatial overlapping and shared use of fish resources (Riet Sapriza et al. 2013). There have been declining trends in the CPUE for the main fish species in the Uruguayan coastal areas (Vasconcellos and Haimovici 2006), with the fisheries of many target species being declared overfished (Milessi et al. 2005; Defeo et al. 2009). In a context of resource reduction due to intense competition with coastal fisheries that mainly target whitemouth croaker (*Micropogonias furnieri*, an important prey for SASL (Riet Sapriza et al. 2013), SASL individuals could be forced to diversify their resource use (indicated by $\delta^{15}N$) and their foraging areas (indicated by $\delta^{13}C$) so as to minimise the strength of intraspecific interactions (Kobler et al. 2009). However, why did SASL not enlarge its foraging area? While SAFS pups are capable of enduring long periods of fasting (Franco-Trecu 2010), SASL pups can withstand fasting periods of 2 days on average (VFT unpublished data). It is known that infanticide of SASL pups can have an important effect in low-density colonies (Drago et al. 2011), but this behaviour has not been reported for SAFS. The combination of these two features (tolerance to fasting and infanticide) may constrain SASL females to make only short foraging trips and have frequent returns to the rookery; thereby, limiting the extent of their foraging areas (Riet Sapriza et al. 2013). Moreover, the extent and shallowness of the Uruguayan continental shelf (being approximately 200 km with an average depths of 20–30 m) may further constrain the access of SASL females to pelagic resources with higher nutritional value (Drago et al. 2010a) for which they should make longer foraging trips and remain absent for longer periods from the rockery. In contrast, the diets of SASL populations living in areas with narrower and deeper continental shelf are largely comprised of pelagic resources (Hückstädt et al. 2007; Drago et al. 2010b). We believe that the combined influence of behavioural traits and the wide and shallow bathymetry of the Uruguayan continental shelf are key factors shaping the foraging strategies of SASL females. The isotopic specialisation at the individual level in SASL and a major dependence of SASL on resources of the Uruguayan coastal shelf may explain why SASL had a higher trophic individual specialisation, larger vulnerability in a heavily exploited habitat by fisheries and by consequence a declining population trend that is unique in its geographical range. In contrast, the relatively lower individual specialisation found for SAFS would be related with a wider trophic niche at the population level may explain their breeding success and survival rates underlying its observed population trend over the past 17 years (Páez 2000, 2006).

Conclusions

In sum, we have evaluated the trophic segregation of two sympatric otariid species having contrasting population trends. At the interspecific level, the trophic niche overlap (including both sexes) was rather minimal, which rules out interspecific competition as the cause of the observed population trends of SASL and SAFS in Uruguay. At the intraspecific level, we evaluated the trophic segregation between sexes and individuals. The sexual segregation in the use of foraging areas (indicated by $\delta^{13}C$) found for both species were opposite for males of SASL and SAFS. This difference probably reflects that capacity or preference of males of each species to exploit different foraging areas. Finally, the species (SAFS) with larger abundance and positive population trend had the largest niche area and showed little individual trophic specialisation, whereas that with smaller abundance and negative population trend (SASL) had the smallest niche area but with a higher individual trophic specialisation. The combined behavioural constraints related to breeding and some key features of the Uruguayan coastal shelf may help explain the contrasting population trends of these sympatric otariid species.

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TÁCTICAS REPRODUCTIVAS INDIVIDUALES EN MACHOS DEL LOBO FINO (Arctocephalus australis) Y LEÓN MARINO SUDAMERICANO (Otaria flavescens)

Objetivo específico:

3a. Evaluar la clasificación de los sistemas de apareamiento del lobo fino y de león marino en Uruguay.

3b. Evaluar la presencia de tácticas reproductivas en los machos de ambas especies a partir de variables comportamentales y su efecto en el éxito reproductivo obtenido (análisis de paternidad).

Hipótesis

El sistema de apareamiento definido para el león marino sudamericano es de defensa de territorio y de hembras, limitando a los machos a defender un número acotado de hembras (Campagna and Le Boeuf 1988). Por otro lado, en el lobo fino, a pesar de que su sistema de apareamiento está clasificado como harem - defensa de hembras (Vaz-Ferreira and Ponce de Leon 1987; Vaz-Ferreira 1956), se ha observado que las hembras de esta especie se desplazan libremente por la colonia durante el período reproductivo (Franco-Trecu et al. 2009). Se espera que estas diferencias comportamentales afecten la varianza en el éxito reproductivo de los machos, determinando que en el león marino exista una menor disparidad en el acceso a cópulas, mientras en el lobo fino el acceso a las cópulas más heterogéneo determine una mayor varianza en el éxito reproductivo individual. Se espera que machos de ambas especies desarrollen tácticas reproductivas alternativas con un éxito reproductivo menor a las dominantes.

RESUMEN

El comportamiento reproductivo de los machos en los sistemas de apareamiento poligínicos mayoritariamente consiste en la monopolización de las hembras receptivas (poliginia de defensa de hembras), o de los recursos que pueden atraer indirectamente a las hembras (poliginia de defensa de recursos) (Emlen and Oring 1977). En los sistemas poligínicos, el éxito reproductivo masculino está determinado en gran medida por el número de eventos de apareamiento que los machos obtienen (Bateman 1948, Trivers 1972), lo que generalmente está ligado a la táctica reproductiva adoptada. En varias especies de mamíferos, las tácticas reproductivas han sido asociadas a rasgos individuales como la experiencia reproductiva previa, la condición corporal (Harcourt et al. 2007), o el rango social ocupado dentro de la población (Rodríguez-Llanes et al. 2009, Wiszniewski et al. 2011). Las tácticas reproductivas individuales se describen en relación a diferentes categorías de comportamiento tales como residente vs. vagabundo o dominante vs. subordinado (Young et al 2007; McGuire & Getz 2010) y son clasificadas en función del éxito reproductivo obtenido. Los machos dominantes y más competitivos alcanzan un éxito reproductivo mayor, mientras las tácticas alternativas adoptadas por aquellos individuos que no satisfacen los costos involucrados en la táctica dominante, obtienen un éxito reproductivo menor (Wolff 2008). En este sentido, la distribución espacial de los machos reproductores en la colonia puede proporcionar pistas importantes para comprender como las interacciones sociales pueden afectar el sistema de apareamiento, la existencia de tácticas de apareamiento alternativas y su éxito asociado en la población (Emlen and Oring 1977, Davies and Hartley 1996).

Los pinnípedos presentan una amplia variedad de sistemas de apareamiento yendo desde la monogamia serial a la poliginia extrema (Atkinson 1997). Los otáridos presentan una amplia variación en el grado de poliginia (Cassini 1999), convirtiéndolos en un buen modelo para evaluar la presencia de diferentes tácticas reproductivas y el éxito individual en los machos. Las colonias reproductivas de los otáridos son altamente densas generando un escenario de fuerte competencia entre los machos por el acceso y la monopolización de las hembras, sincrónicas en su receptividad sexual (Cassini 1999). En este contexto, de alta competencia intra-sexual, la maximización del éxito reproductivo individual podría conducir a la aparición de comportamientos flexibles que determinan tácticas reproductivas alternativas (Taborsky et al. 2008). En los otáridos, la alta densidad local y la distribución espacial de los machos reproductores no solo afecta

el éxito reproductivo individual, sino que también la frecuencia de las interacciones agonísticas (Cassini and Fernandez-Juricic 2003; Cassini and Vila 1990; Earley and Dugatkin 2010; Sutherland 1996). Estas interacciones incluyen exhibiciones o rituales, así como agresión física (Bohorquez-Herrera et al. 2014; Campagna and Le Boeuf 1988), para obtener y mantener los territorios y en muchos casos restringir el movimiento de las hembras durante el estro (Heath 1989). Sin embargo, estos enfrentamientos provocan un aumento de la temperatura corporal que implica altos costos energéticos para los machos (Bohorquez-Herrera et al. 2014; Matsuura and Whittow 1974). Dependiendo de la especie, distintos mecanismos permiten a los machos mantener un equilibrio térmico (Wartzok 1991; Whittow et al. 1972), que en algunos casos limita la ocurrencia de comportamientos agresivos (Bohorquez-Herrera et al. 2014). Esto se observa en el león marino de California (*Zalophus californianus*) (Bohorquez-Herrera et al. 2014), ya que temperaturas estivales superiores a 30ºC dificultan su capacidad de lograr un equilibrio térmico (Whittow et al. 1972).

Para cumplir con los objetivos propuestos, se realizaron muestreos en dos zonas reproductivas de Isla de Lobos. Para **el lobo fino** se tomaron muestras del ~ 50% de los machos reproductores durante la temporada de cría de 2010 y del 85% de las crías nacidas durante la temporada de cría siguiente en el área de estudio. Los análisis de paternidad se realizaron con 10 marcadores de microsatélites. La paternidad fue determinada para el 47% (n = 220) de las crías con un nivel de confianza del 80% y 95%. En el lobo fino el 80% (n = 36) de los potenciales padres tuvieron al menos un descendiente (media = 3 ± 2,9; rango = 0 - 13), sin diferencias significativas (Welch $t = -1{,}92$, $P = 0{,}064$) en los valores medios entre machos territoriales (3,4 ± 3,1) y satélites (1,9 ± 1,5). A partir de las ubicaciones individuales de los machos (media=39; SD = 12; rango: 18-55) y hembras (media = 44; SD = 18; rango: 13-91) de lobo fino marcadas en el área de estudio, se obtuvo que el área utilizada por las hembras fue significativamente mayor (105,8 ± 44 m^2) que la utilizada por los machos (2,9 ± 2,3 m^2; Mann-Whitney $U = 0$, $P < 0{,}005$). Además los *home range* de los machos no se solaparon entre sí, mientras las hembras se solaparon entre ellas así como con los territorios de varios machos. La varianza en el éxito reproductivo, estimada a partir de la paternidad, para todos los machos de lobo fino fue de 8,17, mientras que para los machos periféricos tuvo un valor de 2,4 y para los territoriales fue de 9,8. Los modelos para explicar el efecto de diversas variables en el éxito reproductivo de machos de lobo fino mostraron que el mismo varió significativamente entre machos territoriales y satélite, relacionándose significativamente con el número de cópulas, el tiempo de residencia ponderado, y las frecuencias de interacciones machos-macho y macho-hembra con complejas interacciones entre sí. Aunque la frecuencia de interacciones macho-macho se asoció positivamente con el éxito reproductivo en los machos territoriales, la misma tuvo un efecto opuesto en los machos satélites. En contraste, la frecuencia de interacciones macho-hembra tuvo un efecto negativo en el éxito reproductivo de los machos territoriales y satélites. El tiempo de residencia se asoció positivamente con el éxito en los machos territoriales, pero los machos satélites tuvieron mayor éxito cuando sus residencias fueron menores a la media. Finalmente, el número de cópulas de machos de lobo fino se relacionó positivamente con el éxito en ambas tácticas reproductivas. Evaluamos diferentes categorías reproductivas por medio de árboles de regresión, utilizando el éxito reproductivo como variable de respuesta. Se generaron 4 grupos de machos con diferente éxito reproductivo asociado a diferentes variables. El grupo 1, estuvo compuesto por machos territoriales, que tuvieron las mayores residencias, frecuencias de interacciones macho-macho y número de cópulas, con el mayor éxito reproductivo (5,2 ± 3,9; n = 8). El grupo 2 con la mayor frecuencia de interacciones macho-hembra, estuvo compuesto por machos territoriales, siendo el grupo que alcanzó el menor éxito reproductivo (0,83 ± 0,75; n = 7). Los grupos 3 y 4 tuvieron las menores residencias, bajo número de cópulas, diferenciándose únicamente en la táctica adoptada. Mientras el grupo 3 estuvo compuesto solo de machos territoriales (3,4 ± 1,7, n = 12), el grupo 4 lo estuvo por machos satélites (1,88 ± 1,6; n = 9).

En el caso del **león marino**, las observaciones y muestreo se realizaron en enero y febrero de 2011. Se tomaron muestras del ~73% de los machos reproductivos en la zona de estudio y del 83% (*n* = 65) de las crías nacidas en la siguiente temporada (2012). La paternidad para los machos de león marino se determinó para el 80% (52 de 65) de las crías nacidas en 2012, que fueron asignados al 83% (19 de 23) de los padres potenciales. El número promedio de crías por macho fue de 2,5 (SD = 1,6; rango = 0 - 5). La residencia media de los machos con territorio fue de 12 días (SD = 7,0, rango = 1-25 días) siendo en la mayoría de los casos continua. En base al registro de las posiciones individuales de los machos territoriales (*n* = 29) en la colonia, éstos fueron clasificados en dos grupos de acuerdo a su ubicación (machos que ocuparon un territorio en línea de marea y los que ocuparon territorios internos con piscina). Por medio de los registros comportamentales, se obtuvo que mientras los machos de la línea de marea se movieron en función de la variación del nivel del mar (no diaria), los que ocuparon las piscinas internas permanecieron en sus posiciones fijas durante todo el período de permanencia. Por un lado, los machos de los territorios ubicados en la línea de marea monopolizan grupos de hembras (*female-defense polygyny*) en territorios flotantes (territorios que cambian de posición en el tiempo) (Alcock et al. 1978; Barrows 1983; Wilson 1975). Por otro lado, los machos de los territorios internos con pileta defienden territorios fijos (territorios en un mismo lugar a lo largo de la residencia) (Dewsbury 1978), estableciendo un sistema de apareamiento de defensa de hembras y de recursos (Emlen and Oring 1977). En este sentido encontramos que el sistema reproductivo del león marino en Uruguay consiste en la coexistencia de dos tipos de poliginia (Isvaran 2005; Taborsky et al. 2008). Dado que el éxito reproductivo fue diferente entre los dos grupos de machos con diferentes tipos de poliginia, éstas podrían asimilarse a dos tácticas reproductivas, siendo la de los machos de línea de marea (con mayor éxito reproductivo) la táctica dominante y la de los machos de territorios internos la táctica subordinada. La varianza en el éxito reproductivo para todos los machos fue de 2,6, mientras que para los machos de la línea de marea fue de 1,4, para los de territorios internos con piscina fue 1,1. Si bien los machos de la línea de marea podrían tener un beneficio relacionado con la termorregulación, la residencia promedio (mean ± SD) no varió entre ubicaciones (t = -0.75, P = 0.46). Debido a que durante el pico de cópulas (última semana de enero) la distancia media entre machos de la línea de marea fue significativamente menor (2,5 ± 1,6 m) que para los machos de las piletas internas (5,1 ± 3,7 m) (t = -3,8, $P < 0.001$) es posible que el beneficio que implica para los primeros la termorregulación se contraponga con altos niveles de agresión entre vecinos. Sin embargo, encontramos que únicamente los machos de la línea de marea tuvieron altos niveles de parentesco durante la mayor parte de la temporada de cría (G_{test} = 10,36; P = 0,016), sugiriendo una estructura de parentesco entre machos a una escala fina.

En relación a los sistemas de apareamiento, la alta varianza en el éxito reproductivo de los machos del lobo fino, la alta sincronía reproductiva de las hembras y el patrón de uso del espacio sugieren que el sistema de apareamiento de esta especie es consistente con un lek. Por otro lado, aunque los sistemas poligínicos de defensa de recursos y de hembra ya se han descrito para otras poblaciones del león marino (Campagna and Le Boeuf 1988; Cappozzo and Perrin 2009; Cassini and Vila 1990), cada población exhibió un sistema de apareamiento simple o "puro", y no una mezcla con las dos tipos de poliginia que encontramos en la Isla de Lobos. La flexibilidad del sistema de apareamiento del león marino no se limita a las poblaciones del Atlántico, ya que en Perú se ha definido un sistema de apareamiento de lek (Soto and Trites 2011). En Chile se han reportado cambios en el sistema de apareamiento entre temporadas reproductivas relacionados a cambios en la morfología de la playa (Paves et al. 2005). Se propone que factores ecológicos y demográficos como el estrés térmico, la topografía y el tipo de sustrato de la sitio de reproducción, así como los movimientos de las hembras y la densidad poblacional son claves para determinar el sistema de apareamiento del león marino del sur (Arnold and Duvall 1994; Carranza 2000; Davies 1991).

Como era de esperar se encontró que el sistema de apareamiento más laxo, como es el del lobo fino, presentó una mayor varianza en el éxito reproductivo (8,2) frente a la estimada para un sistema de defensa de hembras/recursos, como ocurre en el león marino (2,6), donde los machos tienen limitada la capacidad de monopolizar hembras. Sin embargo, las varianzas de ambas especies se encuentran entre las más elevadas que han sido reportadas para otras poblaciones de pinnípedos (González-Suárez and Cassini 2014). Esto probablemente se relacione con la presencia de tácticas alternativas en ambas poblaciones, que presentaron elevado éxito reproductivo. Incluso en el lobo fino se reportaron 3 categorías dentro de la táctica dominante donde una de ella tuvo incluso menor éxito que la táctica alternativa. En esta tesis, se ha cuantificado por primera vez el éxito reproductivo de las tácticas alternativas en machos de otáridos.

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Original Article

Sex on the rocks: reproductive tactics and breeding success of South American fur seal males

Valentina Franco-Trecu,[a] Paula Costa,[b] Yolanda Schramm,[b] Bettina Tassino,[c] and Pablo Inchausti[d]
[a]Proyecto Pinnípedos, Sección Etología, Facultad de Ciencias, Universidad de la República, Iguá 4225, Montevideo 11400, Uruguay, [b]Facultad de Ciencias Marinas, Universidad Autónoma de Baja California, Km 103 carretera Tijuana-Ensenada, 22860 Ensenada, Baja California, Mexico, [c]Sección Etología, Facultad de Ciencias, Universidad de la República, Iguá 4225, Montevideo 11400, Uruguay, and [d]Departamento de Ecología y Evolución, Centro Universitario Regional Este (CURE), Universidad de la República, Tacuarembó S/N, Maldonado 20000, Uruguay

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Males of polygynous mammalian species may adopt different reproductive tactics to accomplish female fertilization, with dominant males often attaining a higher reproductive success than those adopting alternative breeding tactics. We worked on the largest breeding colony of the South American fur seal to determine its mating system and quantify the breeding success of male reproductive tactics using behavioral data and paternity assignment. We sampled ~50% of reproductive males during the 2010 breeding season and 85% of pups born during the following breeding season. Paternity analyses were made with 10 microsatellite markers, and 80% ($n = 36$) of the candidate fathers had at least 1 offspring (mean = 2.9, range = 0–13). Paternity was determined for 47% ($n = 220$) of pups at 80% and 95% confidence levels. We assessed the importance of different behavioral variables (tenure, copulation, and agonistic interactions) and reproductive tactics (territorial/satellite) in South American fur seal male breeding success using generalized linear models. We used regression trees to assess the homogeneity of breeding success within each reproductive tactic. The relatively high variance in South American fur seal male breeding success and the relatively high reproductive synchrony of breeding females and their distinctive pattern of space suggest that the mating system is consistent with a lek. We found that the territorial reproductive tactic was actually composed of 3 distinct categories and that a surprisingly high proportion of territorial males had a lower breeding success than the alternative satellite male reproductive tactics. This is the first study in otariids that has assessed the breeding success of male alternative reproductive tactics.

Key words: ***Arctocephalus australis*, breeding success, mating system, paternity, reproductive tactics.**

INTRODUCTION

Polygyny, whereby males mate with a group of females in successive attempts, is the most common mammalian mating system (Clutton-Brock 1989). The degree of spatial aggregation and of synchrony in female sexual receptivity are key factors determining the degree of polygyny in a population because they determine the extent to which individual males may monopolize mating events (Emlen and Oring 1977; Ims 1990; Shuster and Wade 2003). In most polygynous systems, males monopolize the access to receptive females either directly (female-defense polygyny) or indirectly (resource-defense polygyny) (Emlen and Oring 1977). However, in lekking systems, males cluster to defend very small territories that rarely contain significant resources but that are located in areas commonly used by females (Clutton-Brock 1989; Fiske et al. 1998; Shuster and Wade 2003).

Even within a given polygynous mating system, mammalian males may adopt different behavioral reproductive tactics (Gross 1996; Oliveira et al. 2008). These alternative breeding tactics have been associated with individual traits such as previous breeding experience, body condition (Harcourt et al. 2007), the formation of social alliances, or to differences in social rank within the breeding population (Rodriguez-Llanes et al. 2009; Wiszniewski et al. 2011). Often, individual reproductive tactics aimed at accomplishing female's fertilization have been described as distinct and

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Address correspondence to V. Franco-Trecu. E-mail: pinnipedosuy@gmail.com.

contrasting behavioral categories such as resident versus wanderer or dominant versus subordinate (Young et al. 2007; McGuire and Getz 2010). However, these reproductive tactics may also be classified depending on the achieved breeding success. The dominant and most competitive males actually may attain high breeding success, and an alternative tactics adopted by those individuals unable to meet the costs involved in the dominant reproductive tactic would generally achieve a lower breeding success (Wolff 2008).

Males of many mammalian species may change reproductive tactics depending on the resource abundance, population density (Schradin et al. 2012), and foraging strategies (Corlatti et al. 2013). Although some studies have assessed the fitness benefits of each reproductive tactic using behavioral observations (McGuire and Getz 2010), these assessments need to be complemented by molecular methods because of the generally biased nature of behavioral data when estimating breeding success (Westneat 2000; Pörschmann et al. 2010). The use of molecular methods has allowed evaluating the relationship between reproductive tactics and male breeding success in fishes (Rezucha et al. 2012; Cogliati et al. 2013; Richard et al. 2013), lizards (Keogh et al. 2012), and birds (Jiguet and Bretagnolle 2014). However, to our knowledge, the quantification of the breeding success of alternative reproductive tactics in mammals has been limited to one ungulate species, *Capra ibex* (Willisch et al. 2012), and meerkats (Young et al. 2007).

Pinnipeds (otariids, true seals, and walrus) exhibit a wide span of mating systems ranging from serial monogamy to extreme polygyny (Atkinson 1997). Otariid species (fur seals and sea lions) are known to exhibit a wide variation in the degree of polygyny (Cassini 1999), thus making them into a good model system to assess males' reproductive tactics and their individual breeding success. Otariid breed in high-density rookeries where there is the potential for strong competition among males for the access and monopolization of breeding females that typically are highly synchronous in their sexual receptivity (Cassini 1999). In these conditions, the large body size of males would appear as a trait under intense sexual selection to directly promote behavioral dominance and territorial exclusion and enhance a longer tenure that would allow maximizing individual breeding success (Le Boeuf 1986). However, in the context of high intrasexual reproductive competition, the maximization of individual breeding success may lead to the emergence of a flexible mating behavior and/or of other behavioral traits involved in alternative reproductive tactics (Taborsky et al. 2008).

The South American fur seal (*Arctocephalus australis*) breeds along the South American coasts, and the Uruguayan rookery is the largest breeding colony of this species (Páez 2006). Parturition and mating occur in the Austral summer between late November and mid-January (Franco-Trecu et al. 2010), when females give birth to a pup conceived during the previous season and a few days later enter in postpartum estrus. Approximately 10 days after parturition (called perinatal period hereafter), females leave the colony toward the sea for the first foraging trip. Pregnancy in South American fur seal lasts 11–12 months, including 3–5 months of embryonic diapause (Katz et al. 2013). Although South American fur seal mating system was initially identified as a female-defense polygyny (Vaz-Ferreira 1982), we have observed along 9 years of field surveys that individual males do not monopolize groups of females, but rather they defend small territories for periods of time lasting on average 13 days (see Results). Under this scenario, females would seem to choose males for mating, and this could favor alternative male reproductive tactics to establishing and defending territories in the rookery.

Although the occurrence of male alternative reproductive tactics has been reported in pinnipeds (Kiyota et al. 2008; de Bruyn et al. 2011; Flatz et al. 2012), we are unaware of any assessment of breeding success at the level of each reproductive tactic in these taxa. In behavioral ecology, molecular paternity tests have become the standard tool for assessing reproductive tactics. Only the joint analyses of individual breeding success obtained with molecular techniques and detailed behavioral information during the breeding season would allow closer understanding of a species mating system. In this article, we first determine the mating system of the largest South American fur seal population, and second, we combine behavioral data and paternity assignment to evaluate the importance of male breeding tactics of South American fur seal through the quantification of the relative breeding success of each reproductive tactic.

MATERIALS AND METHODS

Study site

The South American fur seal breeds on rocky islands of the Uruguayan continental shelf that are the northernmost breeding sites in the Atlantic Ocean (Páez 2006). Their main rookery, Isla de Lobos (35°01′S, 54°50′W), is located at 9 km of the mainland and harbors approximately 60% of the South American fur seal Uruguayan population (Franco-Trecu V, unpublished data based on aerial surveys in 2013). The study area was located at Isla de Lobos and had approximately 500 m^2, where about 250–300 pups are born (Franco-Trecu et al. 2010) and about 36 territories were actively and simultaneously defend by males every year (Franco-Trecu 2005).

Behavioral data and biopsy samples collection

Behavioral observations were conducted between 24 November 2009 and 15 January 2010 in a breeding area that allowed us to observe animals from short distances in the study area for the entire breeding season. We observed animals using 10 × 50 binoculars in every day in 2 shifts (7:00–10:00 and 17:00–20:00 h) to match the times of the day with the highest proportion of females on land (Franco-Trecu 2005). We individually marked all possible reproductive males (n = 62) with semipermanent paint at the beginning of the breeding season and also after each territorial male was replaced by a new unmarked individual in the study area. In addition, we also recorded 28 females marked in previous years (Franco-Trecu 2010). We defined a grid on the study area with 2 × 2 m quadrants used to classified reproductive males in 2 breeding tactics, territorial and satellites, depending on their position in the grid and on the permanence of their stay in the breeding area. In the context of this work, territorial males were defined as those that permanently (i.e., were sighted every observation shift) defended a fixed area of the area used by females and pups. In contrast, satellite males stayed intermittently in a fraction of the study area farthest from the coastline that was not used by females and pups. However, whenever the tide level rose, territorial males remained in their fixed positions, but females with pups moved away from the coastline, partially using the areas frequented by satellite males. During the study period, no individual classified as territorial or satellite switched to the other reproductive tactic.

We conducted scan samplings (Martin and Bateson 1991) on an hourly basis in the study area to record the behavior (rest, male–male interaction, or male–female interaction—agonistic display or injury) of each marked male and the spatial positions of all marked individuals (males and females) in the grid overlaid in the study area. During each observation shift, we also recorded all copulations observed and the identity of the marked individuals involved. These observations allowed us to obtain for each male the reproductive tactics (territorial or satellite), the tenure time in the area, the number of copulations, and the frequencies of male–male and male–female interactions during the entire breeding season. We also estimated individuals' home ranges during the perinatal (estrous) period for females and for the entire breeding season for males using the set of their daily spatial positions. We obtained a tissue sample for paternity analysis from ~60% of the marked males in the study area using Dan-Inject darts and an air Rifle (Børkop, Denmark). Tissue samples were preserved in 95% alcohol for genetic analysis.

Based on counts of all pups born in our study area, we marked approximately 85% of them between 15 December 2010 and 27 February 2011. Each pup was marked with Allflex plastic tags, sexed, and weighed. A small skin flipper sample was obtained from each pup and conserved in 95% alcohol for genetic analysis. Given the strong adult South American fur seal female philopatry in the breeding area (Franco-Trecu V, unpublished data), we assumed that all pups born in the 2011 breeding season were conceived by territorial/satellite males of the preceding year.

DNA extraction and microsatellite typing

We extracted total DNA using a proteinase K digestion, extraction of proteins with sodium chloride, and alcohol precipitation following Miller et al. (1988) for 36 adult males and 220 pups. The 13 most polymorphic dinucleotide-repeat microsatellite loci previously used for this species and other pinnipeds were chosen for this study (Table 1). The amplified DNA was analyzed for length variation on an automated ABI Prism 310 genetic analyzer using the GeneScanTM 600 LIZ size standard (Applied Biosystems), and 10% of all samples were used as replicates to evaluate the reproducibility of the procedure and estimate the genotyping errors. We obtained the genotypes by processing the raw ABI files with GeneMarker 1.9 (SoftGenetics) and tested loci for null alleles with the Micro-Checker software (Van Oosterhout et al. 2004).

Data analysis

The median copulation date and the synchronization period whence 90% of copulations occurred were estimated using Trites' (1992) logistic approach. Based on the cumulative distribution of copulations, we divided the full reproductive period (between the first and last copulation recorded, see Results) into 3 phases of 15 days each (early, peak, and late).

We calculated the variance in males' breeding successes (V_{m}) for all potentially reproductive males in the study area and separately for both territorial and satellite males. The variance in breeding success was calculated as

$$V_m = \left[\sum_i k_i^2 m_i \Big/ \sum_i m_i \right] - \left[\sum_i k_i m_i \Big/ \sum_i m_i \right]^2$$

where k_i is the success category ($i = 1, 2, 3, \ldots$) that corresponded to the number of pups assigned by paternity of an individual, and m_i is the number of males in each breeding success category (Shuster and Wade 2003).

Home range analysis

We plotted the locations of all marked individuals over time in the grid over a georeferenced satellite photograph and used these spatial positions to estimate the individuals' home ranges during the study period. The individual home ranges were calculated using the 95% minimal convex polygon (MCP) estimated using the library adehabitat (Calenge 2006) in free software R (R Core Team 2013). The differences in the estimated MCPs between sexes were evaluated by the Mann–Whitney *U* test.

Heterozygosity, linkage disequilibrium, and Hardy–Weinberg equilibrium

The number of alleles per locus, and the observed (H_{O}) and the expected (H_{E}) heterozygosities were calculated using Arlequin 3.1

Table 1

PCR conditions and statistical results for each of the 10 loci used in the paternity analysis of South American fur seal males in Isla de Lobos, Uruguay

Locus	$MgCl_2$ (mM)	$AT_1/AT_2/AT_3/AT_4$ (°C)	Na	Size (pb)	Ho	He	PIC	Heterozygosity deficiency	PI	EP	Reference
Aa4	3	58°/56°/54°/50°	5	213–223	0.16	0.17	0.16	0.3343	0.70	0.01	Gemmell et al. (1997)
Pv 9	3	58°/56°/54°/50°	6	169–179	0.75	0.77	0.73	0.2273	0.10	0.37	Allen et al. (1995)
ZcwF07	3	58°/56°/54°/50°	9	137–159	0.83	0.82	0.79	0.7636	0.06	0.45	Hoffman et al. (2007)
PvcE	2	51°/50°	10	99–126	0.30	0.77	0.74	0.0001			Coltman et al. (1996)
Hg6.1	2	51°/50°	11	127–149	0.66	0.71	0.66	0.018	0.13	0.30	Allen et al. (1995)
Pv17	2	53°/52°/50°	12	154–181	0.29	0.71	0.68	0.0001			Hoelzel et al. (1999)
ZcwE04	2	53°/52°/50°	13	121–148	0.85	0.84	0.82	0.5076	0.04	0.54	Hoffman et al. (2007)
ZcwB07	2	51°/50°	13	158–187	0.68	0.72	0.68	0.2051	0.11	0.33	Hoffman et al. (2007)
Hg4.2	2	64°/63°/61°	14	140–172	0.83	0.88	0.87	0.05	0.02	0.62	Allen et al. (1995)
Pv11	3	60°	14	145–181	0.80	0.82	0.80	0.5684	0.05	0.57	Goodman (1997)
M11A	3	58°/56°/54°/50°	14	137–164	0.42	0.77	0.74	0.0001			Hoelzel et al. (1999)
ZcwE12	2	51°/50°	14	165–194	0.73	0.77	0.75	0.1285	0.07	0.77	Hoffman et al. (2007)
ZcwG04	2	53°/52°/50°	14	155–187	0.87	0.88	0.86	0.0256	0.03	0.59	Hoffman et al. (2007)
Mean					0.63	0.74	0.71		0.13	0.41	
SD					0.25	0.18	0.18		0.2	0.17	

AT_{1-4} are the annealing temperatures used in both single or touchdown PCR, Na is the allele number, size is the observed range in fragment size in base pairs (pb), Ho and He are the observed and expected heterozygosity per locus, PIC is the polymorphic informative content, and PI and EP are the probabilities of identity and exclusion per locus.

(Excoffier et al. 2005), and the average polymorphic information content (PIC) was calculated using CERVUS 3.0 (Kalinowiski et al. 2007). Linkage disequilibrium between loci and the deviations from the Hardy–Weinberg equilibrium for each locus and for all loci were calculated in Genepop 4.0 (Raymond and Rousset 1995) using the Monte Carlo Markov Chain method with 10 000 iterations and sequential Bonferroni adjustments (Rice 1989) to correct for multiple comparisons. Polymerase chain reaction conditions and statistics on the allelic variation of each locus are presented in Table 1. The loci PVCE, PV17, and M11A showed significant heterozygosity deficiency with respect to the Hardy–Weinberg equilibrium, and because there was evidence of null alleles at these loci, they were excluded from further analyses (Table 1). All remaining analyses were carried out with 10 loci. In order to assess the accuracy of the paternity assignments given that only one putative parent is known, we used GenAlEx 6.5 (Peakall and Smouse 2006) to estimate the probabilities of identity and exclusion for each locus and for increasing numbers of loci (Peakall and Smouse 2006).

Paternity

We used the maximum likelihood method implemented in CERVUS 3.0 (Kalinowiski et al. 2007) to assign paternity based on the difference between the likelihoods of the 2 most likely fathers of each offspring. We conducted simulations (10 000 cycles, a genotyping error rate of 0.010, allowing individuals to be missing data for up to 1 of the 10 loci) to estimate the critical values associated with assigning paternity using strict (95%) and relaxed (80%) levels of statistical confidence (Marshall et al. 1998). Each male was considered as candidate father if it was potentially resident in the study site during the breeding period. We estimated the number of potentially resident fathers in 2 ways as follows. First, given that the weighted tenure time of the 62 individually marked males in the area was exponentially distributed (Conover 1980) with a mean residence time of 13 days, the departures from the rookery occurred at random times and $1/13 = 0.077$ was the turnover rate (probability that a randomly chosen male leaves the breeding area) per day. Thus, most males were tenacious holders of a territory site acquired. We then counted the maximum number of reproductive males observed in each tercile of the residence times and, taking into account the turnover rate, we estimated that there were $79/(1 + 0.077) = 73$ potential fathers in the colony. Given that 36 males (including 10 satellites) had been individually marked and biopsied, we then had about 50% of the potential fathers in the study site. Second, we used the Microsoft Excel Macro, DADSHARE (www.zoo.cam.ac.uk/zoostaff/amos), to determine the minimum number of fathers necessary to produce the pool of genotypes of all sampled pups. We found that 79 males may be considered as close to the 100% of potential fathers and thus that the 36 males sampled would be 46% of them. We used both proportions (46% and 50%) of the potential fathers sampled in the paternity analyses carried out in CERVUS. To assess the sensitivity of paternity assignment by CERVUS, we estimated the most likely relationship (parent–offspring, full sibling, half sibling, and unrelated) between all possible pairs of pups and males using ML-Relate (Kalinowski et al. 2006) with $\alpha = 0.05$ significance level. While also based on maximum likelihood, ML-Relate does not require any previous estimation of the proportion of candidate fathers sampled (Kalinowski et al. 2006).

Behavioral models

We used generalized linear models (GLMs) (McCullagh and Nelder 1989) with a negative binomial distribution and a log link function to examine the effect of behavioral variables on the individual breeding success measured by paternity (here defined as the sum of the putative offsprings separately assigned at 95% and at 80% confidence levels). We had first considered GLM with a Poisson distribution, but the overdispersion in the data led us to use a negative binomial distribution instead (Bolker 2007). The explanatory variables of the model were the number of copulations, interaction frequencies (male–male and male–females), male reproductive tactics (territorial or satellites), and the weighted individual tenure (both as linear and quadratic effects). Because the abundance of females in estrus was normally distributed during the breeding season, individual tenure was weighted by the proportion of estrous females in each of 3 fortnights (early, peak, and late, see Results). All quantitative explanatory variables were standardized to have a zero mean and a unit standard deviation (SD) to facilitate the interpretation of their relative importance (Schielzeth 2010). The initial model contained all single effects and pairwise interactions of the explanatory variables. This initial model was simplified by the stepwise deletion of the least significant terms in a model and comparing successive steps of model simplification by the Akaike information criterion (deleting a term whenever there was a difference of more than 2 units between alternative models) until arriving to the most parsimonious model that could be fitted. All models were subjected to the customary residual analysis (McCullagh and Nelder 1989). All statistical analyses were carried out with library MASS (Venables and Ripley 2002) in free software R (R Core Team 2013).

We assessed the existence of differentiated categories in each male reproductive tactic using regression trees (Breiman et al. 1984). This method successively partitions the dimensional space of the response variable in exclusive groups defined by a single variable each time (while seeking to reduce the heterogeneity within each group) until arriving at a classification tree (Breiman et al. 1984). We used individual breeding success (as defined above) as the response variable and the male reproductive tactics, the number of copulations, the weighted tenure, the frequencies of male–male and male–female interactions as explanatory variables. We used bagging procedure (Breiman 1996) to train a collection of base classifiers on resampling (bootstrap replicates) of the set and combine the outputs of base classifiers with simple voting. We repeated the bagging procedure 20 times and used 5000 iterations. All analyses were carried out with libraries tree (Ripley 2012) and ipred in the free software R (R Core Team 2013).

RESULTS

There was a maximum of 36 territories established at the same time in the breeding area during the 2010 breeding season. Although territorial males had a high turnover rate and different tenure times, most satellite males had discontinuous tenures in the study area. We individually marked 62 potentially reproductive males (territorial and satellite reproductive tactics) that carried out 69% of the 118 observed copulations during the breeding season. The number of copulations per male did not significantly differ ($U = 143$, $P = 0.04$) between territorial (average ± SD = 1.6 ± 0.3) and satellites males (average ± SD = 0.6 ± 0.5). At least 260 pups were born in the study area during the 2011 breeding season. We obtained tissue samples for paternity analysis of 50% of the potentially reproductive males in the 2010 breeding season and for 85% of the pups born during the 2011 breeding season.

Copulations were recorded between 29 November 2010 and 13 January 2011 (i.e., 45 days) and their temporal distribution did not differ from normal (Kolmogorov–Smirnov test, $d = 0.12$, $P > 0.20$). We found that the female's synchronization period (90% of the copulations) lasted for 31 days (4 December 2010 to 3 January 2011) with the peak of copulations at 20 December 2010.

Home range analysis

We had a mean number of 39 individual locations (range: 18–55; SD = 12) for males and 44 (range: 13–91; SD = 18) for females. The average home range was significantly larger for females (105.8 ± 44 m^2) than for males (2.9 ± 2.3 m^2; Mann–Whitney $U = 0$, $P \ll 0.005$). Although the males' home ranges did not overlap with each other, those of females were typically overlapping with each other and with the home ranges of several males (Figure 1).

Paternity

We analyzed 256 (220 pups and 36 males) South American fur seal samples for 10 microsatellite loci. We obtained a 100% match in genotyping of the 10% of the replicates samples for the quality control, thus suggesting a very low genotyping error. No pair of loci were in linkage disequilibrium after Bonferroni adjustments (observed $P = 0.04$–0.9, Bonferroni $P = 0.001$, 45 tests). The average observed and expected heterozygosities were 0.63 and 0.73, respectively (Table 1). The average PIC taken across all loci was 0.71 (SD = 0.20). The average probability of identity for each locus was 0.13 (SD = 0.2) (Table 1) and for the combination of the 10 loci was less than 10^{-4} (see Supplementary Figure 1). The average probability of exclusion was 0.4 for each locus and 0.99 for the combination of the 10 loci (see Supplementary Material). Although we eliminated 3 loci because of heterozygosity deficiency, we deemed the remaining set of 10 loci to provide an informative analysis of paternity.

Using both 46% and 50% of potential parents, our analyses showed that paternity was established for 47% (103 out of 220) of the sampled pups among 80% (28 out of 36) of the candidate fathers (Figure 2). Most (~65%) paternities were assigned at 80% statistical confidence (i.e., 66 and 67 out of 103 pups with 46% and 50% of the candidate fathers, respectively) and the remaining 35% of pups were assigned at 95% statistical confidence. All paternities assigned with CERVUS for both percentages of potential fathers were identically assigned and thus confirmed in the analyses with ML-Relate (see Supplementary Table 1).

The overall average number of pups per putative father was 3.0 (SD = 2.9, range = 0–13), and the mean number did not significantly differ (Welch $t = -1.9201$, $P = 0.064$) between territorial (mean ± SD = 3.4 ± 3.1) and satellite (1.9 ± 1.53) males. The variance of male reproductive success (paternity) estimated according to Shuster and Wade (2003) was 1.86 for all males, 1.59 for satellites ($n = 10$), and 1.79 for territorial males ($n = 26$). The variance of individual breeding success was significantly (Fligner-Killeen chi-square test = 4.07, $P = 0.043$) higher for territorial than for satellite males.

Behavioral model

The breeding success (paternity assignment) varied between territorial and satellite males and was significantly related to the number of copulations, the weighted tenure time, and the male–female and male–male interaction frequencies forming complex interactions in the statistical model (Table 2). These complex interactions were interpreted with the aid of 3D surfaces for combinations of values of all explanatory variables (Figure 3). Although the frequency of male–male interactions was positively associated with increases in the paternity assignment for territorial males (Figure 3a,c), it had an opposite effect for the satellite males (Figure 3b,d). In contrast, the frequency of male–female interactions had a negative effect on paternity assignment for both territorial and satellite males (Figure 3a,b,e,f). The weighted tenure was important for territorial males because their paternity assignment increased with the duration of their stay in the study area (Figure 3e). However, satellite males achieved greater breeding success when their weighted tenures were lower than the average tenure (Figure 3f). The number of copulations was positively related to paternity assignment for both reproductive tactics (Figure 3c,d).

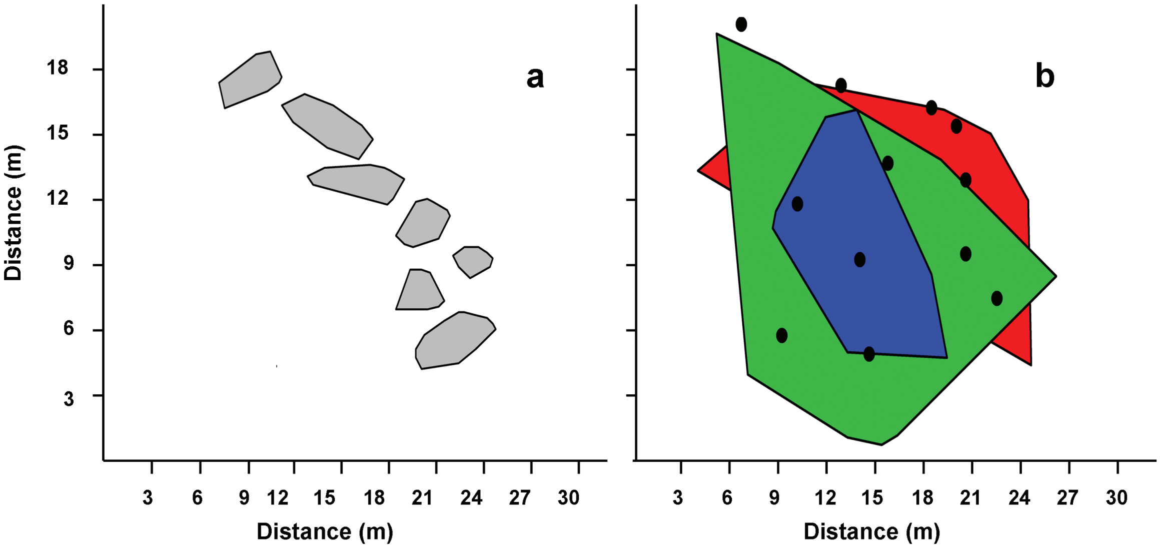

Figure 1

Home ranges (determined by the 95% MCP) of South American fur seal in Isla de Lobos, Uruguay, during the 2010 breeding season. Panel (a) illustrates pattern of the home ranges of 7 simultaneous randomly chosen territorial males in gray and panel (b) those of 3 random breeding females. The centroids of the male home ranges in the same periods are depicted as black dots.

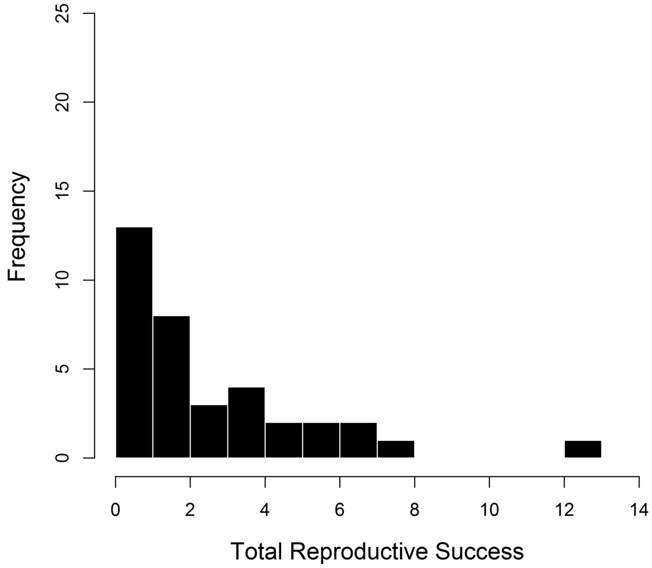

Figure 2
Frequency distributions of male breeding success of the South American fur seal in 2010 in Isla de Lobos, Uruguay, estimated through paternity analyses.

The regression tree for paternity assignment yielded 4 terminal nodes that may be interpreted as distinct behavioral reproductive categories of the South American fur seal males (Figure 4). Group 1, composed of territorial males, was on average the most successful reproductive category (paternity = 5.2 ± 3.9; *n* = 8). Although group 1 was further split according to the longest weighted tenure, individual males had the highest values of number of copulations and of the frequency of male–male interactions. Group 2 (paternity = 0.83 ± 0.75; *n* = 7) had the highest frequency of male–female interaction and was composed of 83% of the territorial males. Both group 3 (paternity = 3.4 ± 1.7, *n* = 12) and group 4 (paternity = 1.88 ± 1.6; *n* = 9) had low-weighted tenures, low frequency of copulations, and were only differentiated by the male reproductive tactics involved, territorial and satellite, respectively (Figure 4).

DISCUSSION

In this study, we have identified that the mating system of the largest population of *A. australis* in the South Atlantic Ocean is a lek. Further, combining behavioral and molecular approaches, we found that the territorial reproductive tactic was actually composed of 3 distinct categories and that a surprisingly high proportion of territorial males had a lower breeding success than the alternative satellite male reproductive tactics.

Lek mating system

Previous studies (Vaz-Ferreira 1982) had suggested that South American fur seal males defend groups of females, and therefore, its mating system was described as female-defense polygyny or harem. Nevertheless, our results clearly showed that the mating system is consistent with a lek. This is because males were clustered and displayed in areas where potentially receptive females gave birth and thereafter underwent postpartum estrus. In these reproductive areas, males defended small territories scarcely larger than the area occupied by their bodies, without any resources required for female reproduction. Females had extensive home ranges that overlapped

Table 2
Parameter estimates and *P* values (with significance shown in bold) of the set of behavioral variables used to explain the reproductive success of the South American fur seal in Isla de Lobos, Uruguay, using GLMs with a negative binomial distribution and a log link function

Model		Int	Ten	cat	cops	FIH	FIM	Ten^2	cops^2	Ten: cat	Ten:cops	cat:cops	Ten:FIH	cat:FrecIH	ten:FIM	cat:FIM	cat:Ten^2	AIC
1	Est.	0.332	−1.010	1.822	1.702	−0.223	−0.716	1.226	1.093	1.961	−1.917	−1.435	−0.188	−0.008	−1.851	1.452	−0.500	160.1
	P value	0.974	0.221	0.857	0.915	0.404	0.189	0.454	**0.009**	**0.042**	0.051	0.928	**0.050**	0.977	**0.017**	0.128	0.770	
2	Est.	−0.201	−1.224	2.367	0.418	−0.235	−0.825	0.864	1.171	2.154	−2.157		−0.212		−1.945	1.611		154.3
	P value	0.750	0.068	**0.002**	0.510	**0.002**	0.062	0.053	**0.002**	**0.010**	**0.009**		**0.004**		**0.007**	**0.054**		
3	Est.	−0.161	−1.024	2.238	0.217	−0.203	−0.022	0.626	0.923	1.951	−1.726		−0.184		−0.779			155.7
	P value	0.804	0.141	**0.004**	0.740	**0.005**	0.896	0.139	**0.004**	**0.023**	**0.026**		**0.013**		**0.005**			
4	Est.	0.182	−0.602	1.985	−0.236	−0.179	−0.717		0.742	2.005	−0.843		−0.164		−1.519	1.256		155.5
	P value	0.779	0.354	0.008	0.704	0.011	0.122		0.007	0.024	0.084		0.026		0.028	0.148		

The 4 models shown differed in the number of explanatory variables and of their interactions included and in the value of their AIC. Est.: parameter estimate, Int: model intercept, Ten: weight tenure (Ten^2: quadratic weight tenure), cat: reproductive tactic (territorial, satellite), cops: number of observed copulations (cops^2: quadratic number of observed copulations), FIH: frequency of male–female interactions, and FIM: frequency of male–male interactions. The weighted tenure and the number of copulations were centered and standardized prior to the statistical analyses. Model 2 was selected because of having the smallest AIC. The complex interactions among the explanatory variables are interpreted in Figure 3.

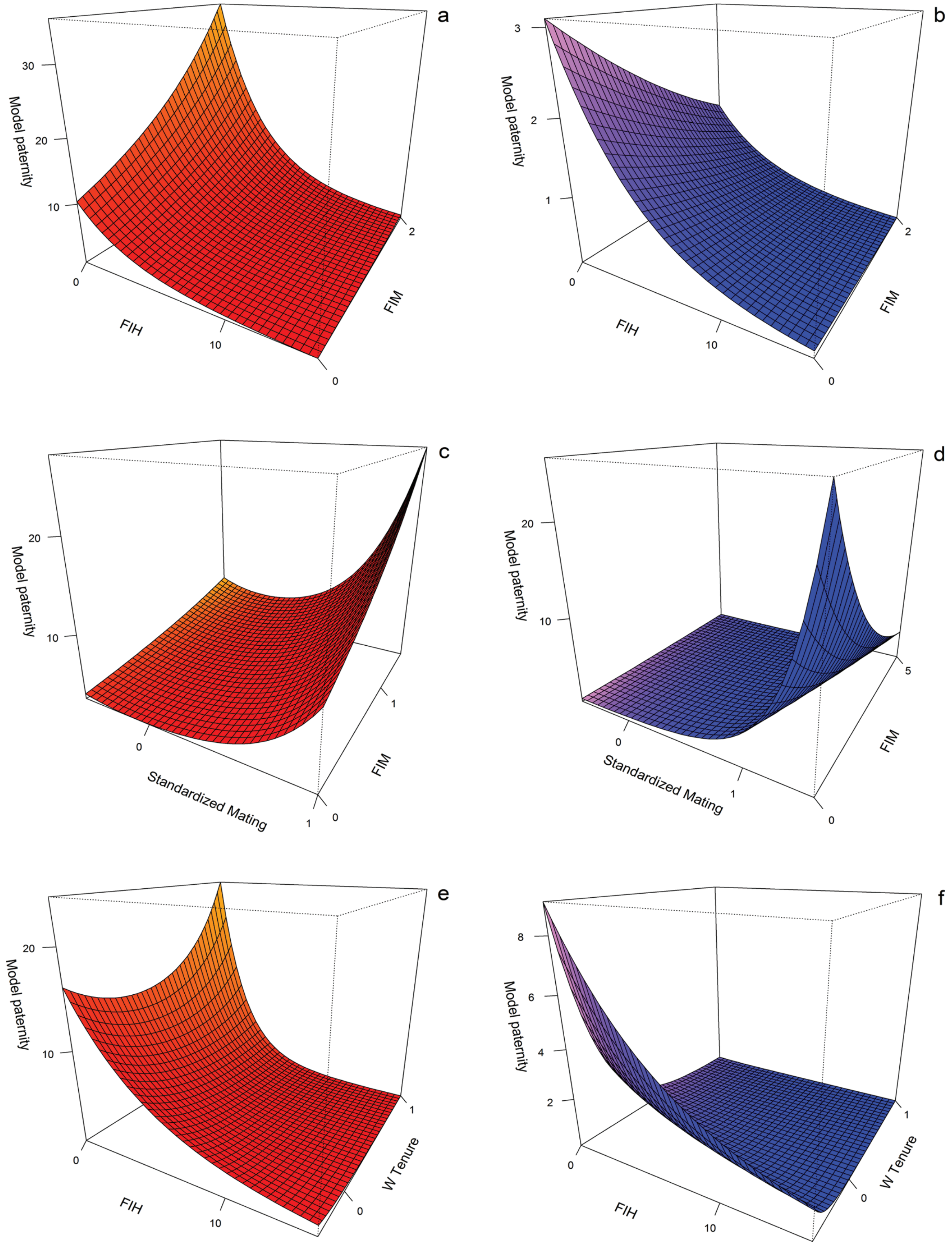

Figure 3

Three-dimensional surfaces showing the interactions among the explanatory variables in the GLM for the individual breeding success (Table 2) for territorial (a, c, and e) and satellite (b, d, and f) South American fur seal males in Isla de Lobos, Uruguay, during the 2010 breeding season. The explanatory variables are weighted tenure in the breeding area (WTenure), the number of observed copulations (standardized mating), the frequencies of male–female (FIH), and male–male (FIM) interactions. The weighted tenure and the number of copulations were centered and standardized prior to the statistical analyses.

with each other and with the territories of many males, indicating that they moved freely in the colony and that males did not monopolize access to females. Under these circumstances, females could assess potential mates and chose among them accordingly. These conditions meet the criteria for a mating system defined as lek where males aggregate, display, and defend stable territories

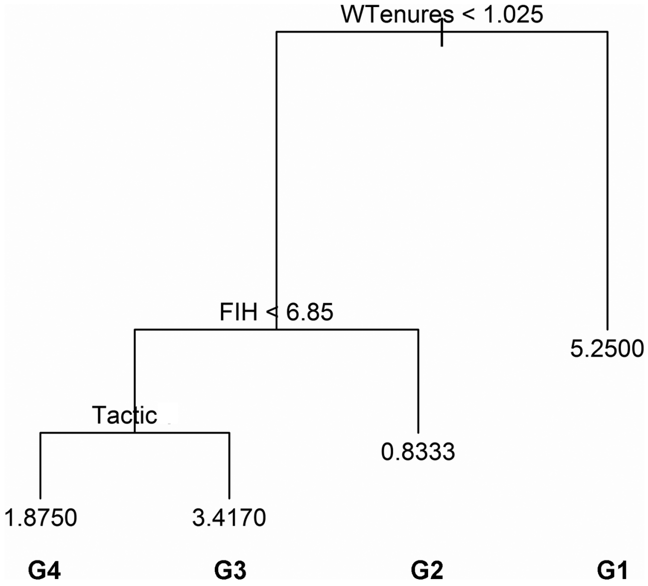

Figure 4
Results of the regression tree used to differentiate male reproductive categories of the South American fur seal in Isla de Lobos, Uruguay, for the 2010 breeding season. The regression tree used the individual breeding success (paternity) as the response variable and the male reproductive tactics (territorial, satellite), the number of copulations, the weighted tenure (WTenures), the frequencies of male–male, and male–female interactions (FIM, FIH) as explanatory variables. The results show 4 distinct groups (G1, G2, G3, and G4) whose average breeding successes are shown in each terminal node of the regression tree.

lacking of resources in areas of high concentration of females, with no pair bonding or parental care, and females have the opportunity to choose to mate with any male on the lek (Bradbury et al. 1986; Wiley 1991; Höglund and Alatalo 1995).

Early descriptions of classical lekking systems in birds usually reported extremely high levels of mating skew and high variance of individual breeding success (e.g., Wiley 1991; Höglund and Alatalo 1995). Although Shuster and Wade's (2003) variance has been proposed as the best characterization of the heterogeneity of breeding success (Shuster 2009; Krakauer et al. 2011), we cannot compare ours with others because of the scarcity of published estimates of Shuster and Wade's (2003) variance in pinnipeds. We then calculated the commonly used estimator of variance of individual breeding success and found it to be 8.17, being on the higher end of the estimated for several pinniped populations (Gonzalez-Suarez and Cassini 2014). Despite the high number of effective territorial males (due to the high turnover rate) and satellite males' access to females, our estimated variance in male breeding success should be considered high and in agreement with the levels generally expected for lek mating systems.

South American fur seal females aggregate in dense breeding colonies and have a high degree of synchrony in their sexual receptivity (31 days) compared with other otariid species (5 months in *Zalophus wollebaeki*; Pörschmann et al. 2010). Despite the high synchrony in sexual receptivity, we found that the variance of South American fur seal male breeding success was high and comparable with those found for other pinnipeds (Fabiani et al. 2004; Gonzalez-Suarez and Cassini 2014). The low breeding success of some territorial South American fur seal males (group 2 in Figure 4) may result from the relatively high female sexual synchrony and possible sperm limitation (see below) that prevents the monopolization of mating events by individual males. Besides fasting, territorial males incur the substantial energetic costs involved in defending small territories by the continuous interactions with other males, in addition to the high energy demand of thermoregulation during the austral summer. Accordingly, the average residence time of males was 13 days (range 1–40, SD = 10 days), and it is much shorter than the length of the females' breeding period (45 days), thus implying a high male turnover rate. In this scenario, South American fur seal males in good body condition would be able to face these costs and remain in the territory longer, whereas those having poorer body condition would avoid these energetic costs and adopt a subordinate social tactic such as satellite males (Isvaran 2005; Bro-Jorgensen et al. 2008; Taborsky et al. 2008; Noble et al. 2013; York et al. 2014).

Reproductive male tactics

Broadly speaking, male reproductive tactics fall into 2 main groups whereby dominant males have a higher reproductive success than other males adopting subordinate social tactics (Gross 1996; Oliveira et al. 2008; Wolff 2008). Although alternative male reproductive tactics have been described for a number of vertebrate taxa (Heckel and von Helversen 2002; Morris et al. 2008; Rezucha et al. 2012), differences in their breeding success have been measured only for a comparatively small number of species (Noble et al. 2013; York et al. 2014).

In pinnipeds, breeding success through paternity analyses had thus far only been assessed for territorial individuals (Hoffman et al. 2003; Kiyota et al. 2008; Pörschmann et al. 2010; Flatz et al. 2012). However, most of the aforementioned studies could only assign paternity to a small proportion of pups, a result that was generally explained away by invoking the existence of alternative reproductive tactics. Nevertheless, by having only sampled territorial males, these studies (Gemmell et al. 2001; Pörschmann et al. 2010; Flatz et al. 2012) were unable to quantify the breeding success of alternative reproductive tactics (such as satellite males in our context) and to assess their importance in the mating system. In spite of having assigned just 47% of paternity to reproductive males in the breeding area after sampling ~50% of reproductive males, we suggest that the weight of the evidence points to South American fur seal having a lek mating system. Studies of mating system in otariids have often assigned even lower levels (~15–30%) of paternity (Gemmell et al. 2001; Pörschmann et al. 2010; Flatz et al. 2012). The latter has been explained by the existence of alternative, nonexclusive reproductive tactics such as aquatic or nocturnal mating, or the incursion and mating of nonterritorial males (Gemmell et al. 2001; Pörschmann et al. 2010; Flatz et al. 2012).

Our results showed that explaining South American fur seal breeding success involved a complex interplay of several behavioral variables (Figure 3). In this study, molecular paternity assignment allowed us identifying different categories within the territorial reproductive tactic, indicating that breeding success of lekking males (or territorial) was actually very heterogenous (Figure 4 and Table 2). The latter can be illustrated by comparing the average breeding success of the 3 categories within the territorial male reproductive tactic (groups 1–3 in Figure 4). In some species with alternative male reproductive tactics, satellite or socially subordinate males typically have smaller testosterone levels than the dominant males (Oliveira et al. 2005; Knapp and Neff 2007) that generally incur in the greatest energy costs (Buchanan et al. 2001). These relationships between behavioral dominance and testosterone levels presumably occur because they involve increased agonistic interactions related to dominance (Vézina and Thomas 2000). A positive relationship between male aggression and breeding success has been found in other polygynous species such as lizards (Keogh et al. 2012) or primates (Lindenfors et al. 2007). Despite of the high costs of territoriality, given the heterogeneity in the breeding success of lekking male categories reported here, males with satellite reproductive tactics would have a higher average breeding success than one of these territorial categories (group 2 vs. group 4, Figure 4). Although the skewed distribution of male breeding success in lekking species has been a pattern widely recognized (e.g., Wiley 1991; Höglund and Alatalo 1995), there have been relatively few quantitative estimates of the net reproductive success as estimated by paternity analysis in mammals. Although a few males concentrate the highest proportion of mating events, most males defending territories in the lek incur in the costs of making displays but attain low reproductive benefits (Bro-Jorgensen 2003; Hamilton et al. 2006).

The behavioral traits in different lekking species that are associated with the differential reproductive success of individual males are attendance, display, and fighting frequencies (Fiske et al. 1998; Jiguet and Bretagnolle 2014). In South American fur seal, satellite males basically ensured their breeding success with a high number of copulations, whereas other behavioral variables (probably involving higher energetic costs) affected the breeding success of territorial males (Figure 3). An example of this was the male–male interaction frequency, which was only important in the breeding success of territorial males (Figure 3a,c). In contrast, the opposite was true for satellite males (Figure 3b,d), a result that was expected because the minimization of the energetic costs involved in frequent interactions with other males should be one of the benefits of this reproductive tactic.

It is likely that satellite males would incur in lower energetic costs involved in male–male interactions, thermoregulation, and site tenure than territorial males, thus being potentially able to invest in postcopulatory traits by augmenting both the quantity and quality of their sperm and seminal fluid (Simmons and Fitzpatrick 2012; Simpson et al. 2014). For instance, sperm quality covaries with social status in several fish species so that subordinate or parasitic males have higher sperm motility, velocity, and adenosine triphosphate concentration and attain twice the breeding success compared with the dominant tactic (e.g., Cornwallis and Birkhead 2007; Locatello et al. 2007). Furthermore, in some freshwater fish (*Rhodeus amarus*), male aggression was negatively correlated with the number of ejaculations, suggesting the existence of a trade-off between aggression and sperm production (Rezucha et al. 2012). It has also been shown that the existence of a trade-off whereby species with a high investment in body size or ornaments involved male–male competition (precopulatory traits) have reduced investment in postcopulatory traits such as testes mass (Fitzpatrick et al. 2012; Parker et al. 2013; Lüpold et al. 2014). In pinnipeds, the enhancement of the precopulatory traits may be sufficiently high so that dominant males could potentially suffer sperm limitation and hence attain a low individual fitness (Fitzpatrick et al. 2012). Therefore, the quantity and quality of sperm can be decisive for the fertilization success of satellite males and may explain why their breeding success could be higher than those of some territorial males. In the context of a lek mating system, female choice would typically involve mostly the territorial males, whereas the mating of satellite males would necessitate either force or repetitive harassment, thus hindering female mate choice and leading to shorter mating events.

Although possible, we believe that copulations outside the breeding area were unlikely. Although we have described satellites as an alternative reproductive tactic, we suggest that it is unlikely that other reproductive tactics would exist in this population for 2 reasons. First, we recorded 45% of the copulations (118 copulations/260 pups born) during the 2010 reproductive season in only 6h of daily observation. Second, multiple copulations in each female occur only rarely (3 events observed in 9 years of observation, Franco-Trecu V, unpublished data) in the breeding colony. The low frequency of multiple copulations observed in the study site is a good indicator that the observed copulations are a reliable characterization of the mating patterns in this South American fur seal population. We believe that 53% of fatherless offspring correspond to territorial males for whom we could not obtain tissue samples and satellite males that were not marked and sampled because of their short tenure times in the study site.

To our knowledge, this is the first study in pinnipeds that has assessed the breeding success of male alternative reproductive tactics. We found that the dominant reproductive tactic (territorial males) was composed of several categories, and surprisingly that an important proportion of the territorial males had a lower breeding success than males having the alternative reproductive tactic (satellite males). Understanding the evolutionary dynamics between alternative reproductive tactics requires data on each tactic's fitness (Gross 1996; Taborsky et al. 2008; Shuster 2009). We suggest that including alternative male reproductive tactics in the analyses and estimating their success is a substantial contribution to a better understanding of their true role and the ecological process involved in the maintenance of each reproductive tactic and the evolution of polygynous mating systems.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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TIDE LINE VS INTERNAL POOLS: MATING SYSTEM AND BREEDING SUCCESS OF SOUTH AMERICAN SEA LION MALES

Valentina Franco-Trecu[1,2*], Paula Costa-Urrutia[3], Yolanda Schramm[3], Bettina Tassino[4] and Pablo Inchausti[2]

[1]Proyecto Pinnípedos, Sección Etología, Facultad de Ciencias, Universidad de la República, Iguá 4225, Montevideo 11400, Uruguay.
[2]Departamento de Ecología y Evolución, Centro Universitario Regional Este (CURE) Universidad de la República, Tacuarembó S/N, Maldonado 20000, Uruguay
[3]Facultad de Ciencias Marinas, Universidad Autónoma de Baja California, Km 103 carretera Tijuana-Ensenada, 22860 Ensenada Baja California, México.
[4]Sección Etología, Facultad de Ciencias, Universidad de la República, Iguá 4225, Montevideo 11400, Uruguay.
* Corresponding author: pinnipedosuy@gmail.com
Tel: (598 2) 5258618, Fax: (598 2) 5258617

Abstract

The spatio-temporal distribution of breeding males can help understand the existence of alternative reproductive tactics and their breeding success in colonially breeding species. We quantified the breeding success of the South American sea lion (SASL) males in Uruguay according to their breeding location (tide line vs internal pool) in a rookery and assessed the dynamics of territory use and the fine-spatial kin structure during the breeding season. We sampled 73% of reproductive males and determined paternity for 80% of the pups born the following year. We found that male breeding success differed only between breeding locations, being higher at the tide line. We found that close kin males were only present at the tide line, suggesting a fine scale kin structure in the study area. Because of the shorter distances between territorial males at the tide line and the high energetic cost of agonistic interactions, kinship may be a mechanism for decreasing agonistic interaction at the tide line. Even though SASL has a polygynous mating system across its geographic range, each rookery has a single or homogeneous mating system. This is the first study showing the coexistence of two distinct mating systems in otariids rookery related to breeding location. While males of tide line have a female-defence polygyny into floating territories, males at the internal pools defended fixed territories establishing a resource-defence polygyny. We have shown the first evidence in otariids for the coexistence of two types of polygyny in a single breeding rookery.

Keywords: breeding success, mating system, *Otaria byronia*, paternity, reproductive tactics, thermoregulation

Introduction

Male mating behaviour in polygynous mating systems involves the monopolization of receptive females (female-defence polygyny), the control access of the resources that may indirectly attract receptive females (resource-defence polygyny) or the direct competition for dominant status or favourable positions within male aggregations (male dominance polygyny or leks) (Emlen and Oring 1977). Male reproductive success in polygynous systems is often determined by the number of mating events, which in turn often entail engaging in costly agonistic interactions toward other breeding males (Bateman 1948; Trivers 1972). In colonially breeding species, the spatial distribution of reproductive males may then provide important clues to understand the influence exerted by social interactions on the breeding success, and more generally on the mating system at the colony level (Emlen and Oring 1977; Davies and Hartley 1996).

Otariids (fur seals and sea lions) breed in dense colonies where territorial males compete for the access and monopolization of females with highly synchronous estrous (Cassini 1999). Males arriving at the colony settle at a specific location depending on the availability of space, priority of arrival, relative body sizes, or their rank or competitive abilities (Wolf and Trillmich 2007; Kiyota et al. 2008). Male breeding success often vary with the local density and spatial distribution of reproductive males, since the latter largely determine the strength and frequency of their agonistic interactions (Cassini and Vila 1990; Sutherland 1996; Cassini and Fernandez-Juricic 2003; Earley and Dugatkin 2010). These agonistic interactions among reproductive male otariids include ritualistic displays and/or physical aggression (Campagna and Le Boeuf 1988a; Bohorquez-Herrera et al. 2014) aimed at obtaining and maintaining territories in the colony and physically restraining female movement until the end of their estrous (Heath 1989). Male confrontations and agonistic interactions in otariids often entail high energetic costs and lead to increases in body temperature (Matsuura and Whittow 1974; Bohorquez-Herrera et al. 2014). Depending on the species-specific mechanisms involved in achieving physiological thermal equilibrium (Whittow et al. 1972; Wartzok 1991), agonistic interactions at high ambient temperature could constrain the occurrence or intensity of some male reproductive behaviours and lead to differences in breeding success (Campagna and Le Boeuf 1988b; Carey 1991; Bohorquez-Herrera et al. 2014). For instance, minimizing the risk of overheating strongly determines whether aggressive interactions among California sea lion (*Zalophus californicus*) males take place (Bohorquez-Herrera et al. 2014), since summer temperatures higher than 30ºC hinder their capacity to achieve physiological thermal equilibrium (Whittow et al. 1972).

Minimizing the energetic costs of the agonistic interactions involved in maximizing the number of mating events under the constraint imposed by high summer temperatures is bound to be the subject of natural selection (Krebs and Davies 1991; Sober 2006). If the frequency or intensity of these energetically costly agonistic interactions between kin were lower than between unrelated individuals (Waldman 1988), breeding individuals would be expected to exhibit a fine-scale kin structure in the colony (i.e. Kitchen et al. 2005; Nituch et al. 2008). Nevertheless, most studies involving kinship in pinnipeds to date have largely focused on females because of its interaction with philopatric (Schaeff et al. 1999; Pomeroy et al. 2000), allo-suckling and cross-fostering behaviours (Wolf and Trillmich 2008). The fine-scale spatial structure of reproductive individuals may also reveal the ecological mechanisms underpinning the maintenance of genetic diversity at the population level (Costa-Urrutia et al. 2012; Costa-Urrutia et al. 2013).

The South American sea lion (*Otaria byronia*; Blainville, 1820 - hereafter SASL) breed in dense colonies along the South American coast (Vaz-Ferreira 1982). In Uruguay, SASL breed in two colonies (Isla de Lobos and Cabo Polonio) separated by *ca*.70 km, and its overall population size of roughly 10,000 individuals in 2013 has declined at an average annual of rate 2.0% over the last 60 years (Franco-Trecu 2015). South American sea lion breeding season starts with the arrival of males to the colonies in mid-November (late austral spring), followed by the arrival of females that give birth to one pup in January (mid austral summer) and quickly undergo a short and highly synchronous estrous lasting one week. Thereafter, females begin alternate foraging trips at sea with nursing bouts ashore for almost a year (Campagna and Le Boeuf 1988a). Depending on the type of substrate in the rookery and its local density, SASL exhibit various types of polygynous mating systems across its geographic range, including female-defence (Punta Norte-Argentina), resource-defence (Puerto Pirámides-Argentina) (Campagna and Le Boeuf 1988a; Fernandez-Juricic and Cassini 2007) and lek-like (Ballestas Island-Perú) mating system (Soto and Trites 2011).

During our long-term (9 yr) study in Isla de Lobos (Uruguay), we have observed that reproductive SASL males consistently defend a small territories wherein mating take place in two distinct breeding locations of the rookery (either along a narrow tide line or at internal pools) during *ca.* three weeks. Because of the physiological limitations of otariids for heat dissipation, SASL males need to have access to water or shadow to minimize the risk of overheating during their long tenure of breeding territories when the average daily temperature on the rocks at Isla de Lobos is 33 ± 8 ºC (range: 19 – 49 ºC). While males at the tide line could easily minimize the risk of overheating, males at the small internal pools endure much higher temperatures. Because the potential energetic costs differ between breeding locations, SASL male breeding success would be expected to differ as well (i.e. Franco-Trecu et al. 2014). In this paper, we study the fine-scale mating behaviour of SASL in a small and declining population to assess whether male breeding success differed between the two breeding locations, depending on the length of individual tenure and on the pairwise kinship with territorial males. We also analyzed the dynamics of territory use in the two breeding locations in relation to breeding success and to the male's fine-spatial kin structure to assess whether male kinship leads to a spatial genetic heterogeneity within the rookery. Assuming that costly agonistic interactions would be weaker or less frequent among relatives (Waldman 1988), we hypothesized that reproductive SASL males should prefer to distribute close to their kin and hence the spatial distribution of reproductive males in the study site to be correlated with their degree of kinship. Despite of being unable to pinpoint to the mechanisms involved in SASL kin recognition, we think that they are likely to exist because weaned individuals of other sea lion species have shown long-term memory to respond to maternal calls (Gwilliam et al. 2008; Charrier et al. 2009; Pitcher et al. 2010; Pitcher et al. 2012), and SASL mother-pup gathering in dense breeding colonies relies on acoustic cues that differ among individuals (Trimble and Charrier 2011).

Methods

Study site

SASL breed on rocky islands of the Uruguayan continental shelf that constitute its northernmost breeding site in the Atlantic Ocean (Vaz-Ferreira 1982). Isla de Lobos

(35°01’S, 54°50’W) is a rookery located in the Rio de la Plata estuary at 9 km from the mainland. The Río de la Plata estuary has a large and highly dynamic mixing of seawater and freshwater due by the confluence of Brazil and Falkland currents with the Parana, Paraguay and Uruguay river discharges that generates one of the world’s most energetic and productive regions (Ortega and Martinez 2007). The astronomical tides in the Rio de la Plata have semi diurnal regime and are classified as micro tidal because their amplitude oscillates between 0.30 m and 1.0 m (Piedra-Cueva and Rodriguez-Borelli 2003). However, storm and winds may have strong effects in the Río de la Plata Estuary by changing the sea level by 3.0 – 4.0 m over a time period ranging from a few hours to a couple of days (Piedra-Cueva and Rodriguez-Borelli 2003). The study area (a rocky outcrop of approximately 1500 m^2) is located at the north-north-western of Isla de Lobos where *ca.* 80 pups are born per year, representing 20–25% of the total pupping at Isla de Lobos (Trimble and Insley 2010) and *ca.* 30 breeding territories have been actively and simultaneously defended by different males during the last nine years (Franco-Trecu, V. Obs. pers.).

Behavioural data and biopsy samples collection

Behavioural observations were conducted in January and February 2011 from a platform that allowed observe animals at short distances (between 5 and 10 m) in the study area during the entire breeding season. Starting on early January 2011, we individually marked all possible breeding males with semi-permanent paint upon arrival and the every newly arriving male thereafter as they started occupying territories, resulting in 23 (77%) males marked. Early in the morning and late afternoon we conducted two daily scan samplings (Martin and Bateson 1991) using 10 × 50 binoculars to count the number of males and to record their spatial positions in a grid with 2 x 2 m quadrants overlaid in the study area during the entire breeding season. The set of individual positions allowed classify all potential breeding males into two categories depending on their breeding location (tide line and internal pool territories). We also estimated the individual tenure length of a territory and calculated the distances between all pairs of marked males in the study area. We obtained a tissue sample for paternity analysis from ~91% of the males marked in 2011 in the study area using Dan-Inject darts and an air Rifle (Børkop, Denmark). These samples were preserved in 95% alcohol for genetic analyses. Based on the exhaustive counts in the study area, we marked 83% (*n* = 65) of the pups born in

January and February 2012 (i.e. the year after adult males were sampled). Each pup born in the study area in 2012 was marked with Allflex plastic tags, sexed and weighed and a small skin flipper sample was obtained and conserved in 95% alcohol for genetic analyses. Given the high SASL female philopatry in the breeding area (Feijoo et al. 2011), we assumed that all pups born in the 2012 breeding season were conceived by males of the preceding breeding season.

DNA extraction and microsatellite typing

We extracted total DNA for a total of 86 sea lions (21 adult males and 65 pups) using a proteinase K digestion, extraction of proteins with sodium chloride, and alcohol precipitation (Miller et al. 1988). All DNA extractions were quantified using a Nanodrop and run in a 2% agarose gel for quality control. We only carried out PCR reactions for samples having both at least of 30 ng of DNA template and a light band in the gel, thus making sure of DNA quantity and quality in each PCR reaction. We chose the 12 dinucleotide-repeat microsatellite loci with the highest polymorphism that had been previously used for SASL or for other pinnipeds (Table 1). We used the touchdown procedure for PCR conditions used by Franco-Trecu et al. (2014) for the South American fur seal (*Arctocephalus australis*). Details of PCR conditions and summary statistics are given in Table 1. The amplified DNA was analyzed for length variation with an automated ABI Prism 310 genetic analyzer using the GeneScanTM 600 LIZ size standard (Applied Biosystems). We replicated 10% of all samples to evaluate the genotyping reproducibility and to estimate the genotyping errors. All genotypes were obtained by processing the raw ABI files with GeneMarker 1.9 (SoftGenetics) by two researchers. All loci were tested for genotyping errors using Micro-Checker software (Van Oosterhout et al. 2004).

Heterozygosity, linkage disequilibrium and Hardy-Weinberg equilibrium

We calculated the number of alleles and the observed (H_O) and expected (H_E) heterozygosities for each locus using Arlequin 3.1 (Excoffier et al. 2005). The linkage disequilibrium between loci, the deviations from the Hardy-Weinberg equilibrium for each locus and the inbreeding coefficient (F_{IS}) were calculated with Genepop 4.0 (Raymond and Rousset 1995) using a Monte Carlo Markov Chain with 10,000 iterations and correcting the significance levels for multiple comparisons with Bonferroni adjustments (Rice 1989). The average polymorphic information contents (PIC) were calculated using CERVUS 3.0 (Kalinowiski et al. 2007).

Paternity

We estimated the probabilities of identity (PI) and of exclusion (PE) for each locus and for increasing numbers of loci to assess the accuracy of the paternity assignments when only one putative parent is known using GenAlEx 6.5 (Peakall and Smouse 2006). We assigned paternities based on the difference between the likelihoods of the two most likely fathers of each pup using Cervus 3.0 (Kalinowiski et al. 2007). We conducted simulations (10,000 cycles and a genotyping error rate of 0.010) allowing individuals to have missing data for up to one of the 10 loci to estimate the critical values associated with assigning paternity using strict (95%) and relaxed (80%) levels of statistical confidence (Marshall et al. 1998). Each male was considered a candidate father if it was potentially resident in the study site during the 2011 breeding season. The proportion of candidate fathers was calculated as the ratio between the number of marked and biopsied males and the number of potentially breeding males in the study site.

Kinship

We estimated the levels of kinship by the coefficient of relatedness between all pairs of breeding males using two likelihood- (dyadic and triadic, Milligan 2003; Wang et al. 2007) and five moment-based estimators (Queller and Goodnight 1989; Li et al. 1993; Lynch and Ritland 1999; Wang 2002) calculated by the Coancestry 1.0 program (Wang 2011). Since the performance of the kinship estimators may vary depending on allele frequencies, sample sizes, the number of polymorphic markers and the relatedness among dyads (Van de Casteele et al. 2001; Wang 2011), we evaluated their suitability with Monte Carlo simulations in the Coancestry 1.0 program (Wang 2011) that mimic the real data in terms of both the number of markers and sample sizes. We selected the optimal relatedness estimator for our data as the one having the highest correlation between the kinship estimators and the simulated relatedness values (see Weir et al. 2006; Wang 2011). Assuming random sampling, the values of the expected relatedness coefficients for alleles identity by descent in a outbreed population are: 0.5 for first-order relatives (parents–offspring and full siblings), 0.25 for second-order relatives (half siblings, grandsons and nephews), 0.125 for third-order relatives (cousins), and 0 for unrelated individuals (Hartl and Clark 1997). Although the TrioML and Queller and Goodnight (1989) estimators both had high and similar correlations between the actual and the simulated values ($r = 0.73$ and $r = 0.70$ respectively, both $P < 0.0001$), we used Queller and Goodnight's (1989) estimator because of its frequent use in the literature (Blouin 2003). The 95% confidence intervals of the relatedness estimators were calculated by bootstrapping using 1000 iterations.

Data analysis

The peak of birth dates and the synchronization period whence 90% of births occurred were estimated using Trites' (1992) logistic approach based on the cumulative distribution of pup daily counts and, given that estrous occurred just 3-5 days after parturition, we could then estimate the peak of copulations in the study site. We described the dynamics of space use by reproductive males during the breeding period by adjusting quadratic and logistic models to the number reproductive males at the tide line and internal pools every day, respectively. We examined whether individual breeding success (here defined as the sum of the putative offspring of each breeding male separately assigned at 95% and at 80% confidence levels) differed between breeding locations (tide line *vs.* internal pools) and according to the length of the tenure using generalized linear models (McCullagh and Nelder 1989) with a Poisson distribution and a log link function. We compared the average pairwise distances of reproductive males and the territories tenure between breeding locations (tide line and the internal pool) using *t-tests*.

We evaluated the relation between kinship and breeding success by calculating the Spearman correlation between the sum of the breeding successes (paternity) of every pair of reproductive males and their pairwise kinship coefficient. We studied the fine-scale male kin structure by assessing how the kinship coefficient (Queller and Goodnight 1989) varied with pairwise distances between reproductive males, and by comparing the proportion of kinship pairs between breeding locations. The first analysis involved estimating genetic correlograms for each week of the breeding season and for each breeding location using Genalex6 (Peakall and Smouse 2006) whose statistical significances were assessed by generating 95% confidence intervals for each distance class by bootstrap (Peakall and Smouse 2006). The second analysis involved comparing the proportion of breeding male pairs having total and only first order kinship ($r = 0.45$-0.60; i.e. parents–offspring and full siblings) between breeding locations for each week of the breeding season using a *G test* of homogeneity (Sokal and Rohlf 1995).

Results

The SASL males established up to 29 territories at any time in the study area during the 2011 breeding season. Territorial males had mean tenure of 12 days (SD = 7.0, range = 1 - 25 days) and most individuals were continuous residents. The overall variance of male reproductive success (paternity) was 2.6, and 1.4 for tide line and 1.1 for internal pool males (see Fig. 1, Table 2). We found that the birth synchronization period (90% of observed births) lasted for 19 days (12/1/2011 to 30/1/2011) with the peak of birth at 21/01/2011, and the peak of copulations to have occurred on 25/01/11.

Heterozigosity and linkage disequilibrium.

The mean observed (H_O) and expected (H_E) heterozygosity for all 12 loci were 0.62 and 0.68, respectively (Table 1). Two loci (PVCE and PV17) had significant heterozygosity deficiencies with respect to the Hardy-Weinberg equilibrium, and paternity assignments were based on the remaining ten loci (Table 1). The H_O and H_E after removing the later two loci were equal at 0.68. All pair of loci were in linkage equilibrium after Bonferroni adjustments of significance levels (observed $P = 0.1$- 0.001, Bonferroni $P = 0.0005$, 45 tests). The mean F_{IS} values for 12 and 10 loci were 0.08 (SD = 0.22) and -0.017 (SD = 0.06), indicating that the SASL was a non-inbreeding population. The mean Polymorphic Informative Content were almost identical for either 12 or 10 loci (mean = 0.6, SD = 0.16). The average probabilities of identity and of exclusion for each locus were 0.18 (SD = 0.13) and 0.29 (SD = 0.13), respectively (Table 1), and $< 10^{-4}$ and 0.98, respectively when considering all ten loci. After discarding the two loci having heterozygosity deficiency, we deemed the remaining set of ten loci to contain sufficient information to provide a reliable paternity and kinship analysis.

Paternity

Paternity was determined for 80% (52 out of 65) of the pups born in 2012, which were assigned to 90% (19 out 21) of the sampled candidate fathers in the study site. About one-half of the paternities were assigned with 95% statistical confidence (23 out of 52).

After adding together the paternities independently assigned with 95% and 80% confidence levels, the average number of pups per putative father was 2.5 (SD = 1.6, range = 0 - 5, see Fig. 1c and Table 2)

Male breeding success and kinship

Upon arrival at the rookery in early January, SASL males started occupying the breeding territories at the tide line and only two weeks later the territories at the internal pools began to be used (Fig. 2). Despite of the contrasting dynamics of territory occupancy between breeding locations (Fig. 2), the average length of territory tenure did not significantly differ between the tide line and the internal pools (t = -0.75, P = 0.46) whose means (± SD) were 13.1 (±8.2) and 10.8 (±5.6), respectively (Table 2). While males at the tide line moved depending on the random tidal variation of sea level (see Study site), those at internal pools remained in their fixed positions during the entire breeding season. During the peak of copulations (last week of January) when the highest number of reproductive males stayed at the colony, the average distance between males at the tide line (2.5 ± 1.6 m) was significantly lower than at the internal pools (5.1 ± 3.7 m) (t = -3.77, P < 0.001). The decline in territory occupancy after *ca.* 35 days (Fig. 2) corresponded to the decrease in the number of receptive females towards the end of the breeding season.

Breeding success was not significantly correlated with the kinship coefficient (Spearman *rho* = 0.029, P = 0.676). However, while the average breeding success significantly differed between breeding locations (tide line: 3.5 ± 1.2; internal pools: 1.3 ± 1.1; Fig. 1 a, b and Table 2), it was not significantly related to the length of individual tenure of a territory (Table 3). The average kinship coefficient between territorial males was 0.08 (SD=0.14) ranging between 0 and 0.54 (Table 2). It is noteworthy that 58% of male pairs had a kinship coefficient equal to zero (i.e. were genetically unrelated). Pairwise kinships and distances between territorial males were not significant correlated (all P > 0.05), neither overall nor for any week of the breeding season. In general, the correlations between pairwise kinship and distance for territorial males ranged from -0.2 to 0.16 for the distance class 2 - 4 m and were even lower for greater pairwise distances. Although these results suggest that SASL did not have an overall genetic structure over space at the scale of the study site, we did find that the proportion of male pairs having any degree of kinship significantly differed between breeding locations and varied over time (G_{test}= 10.361, *P*=0.016), being higher at the tide line for most of the breeding season (Fig. 3a). Males pairs having a 1st kinship order (i.e. father-offspring and full siblings) were almost exclusively present at the tide line (Fig. 3b), thus suggesting a fine-scale structure of kinship of males in the study site.

Discussion

Polygynous mating systems in mammals are classified according to the whether males defend an essential resource for females (resource-defence polygyny), controlling access to a group of receptive females without a resource being involved (female- defence polygyny) or, when the resources or females are not defendable, they aggregate, have communal displays and often defend dominance positions (male dominance polygyny or leks) (Emlen and Oring 1977; Davies 1991; Shuster and Wade 2003). In this study, combining behavioural and molecular approaches, we found that the SASL reproductive behaviour in Uruguay actually involves the coexistence of two types of polygyny associated at different locations in the same rookery (Isvaran 2005; Taborsky et al. 2008). On the one hand, males at the tide line monopolized relatively stable groups of females (female-defense polygyny) into floating territories (i.e. a territory that changes position from time to time) whose locations change with the random tidal variation at the study site (Wilson 1975; Alcock et al. 1978; Barrows 1983). On the other, males at the internal pools defended fixed territories (defined as territory having a stable location during the tenure of its holder) (Dewsbury 1978) and established a resource-defence polygyny (Emlen and Oring 1977).

Whenever different mating systems coexist in a single population (Thirgood et al. 1999; Santos and Nakagawa 2013) and insofar as they are expressed as distinct behavioural patterns with different breeding successes, they may be considered alternative reproductive tactics (Taborsky et al. 2008). Accordingly, we think that the two types of polygyny associated at different locations correspond to the coexistence of two distinct reproductive tactics at the same rookery where males at the tide line represent the dominant tactic with a higher average breeding success, and males at the internal pools represent the subordinate tactic with a lower average breeding success (Wolff 2008). We are confident that there are no other reproductive tactics (e.g. satellite, wandering or sneaking males) in our study site because we could assign paternities to a much higher percentage of pups (80%) than it has been commonly possible in otariids (~15-30%) (Gemmell et al. 2001; Pörschmann et al. 2010; Flatz et al. 2012; Franco-Trecu et al. 2014).

Alternative reproductive tactics often appear in vertebrate populations whenever there is strong competition for mating (Gross 1996; Shuster and Wade 2003; Oliveira et al. 2008), and appear as a "subordinate behaviours" often involving wandering, sneaking and/or harassing receptive females that escape the vigilance of dominant males that defend female groups or territories (Shuster and Wade 2003; Taborsky et al. 2008; Taborsky and Brockmann 2010). Examples include many vertebrate taxa ranging from fishes to mammals (Ryan and Causey 1989; Oliveira et al. 2005; Oliveira et al. 2008; Schütz et al. 2009; Young et al. 2013; York et al. 2014), including pinnipeds (e.g. de Bruyn et al. 2011; Franco-Trecu et al. 2014).

The coexistence of different types of polygyny in a single population has been observed in the fallow deer (Alvarez et al. 1990; Thirgood et al. 1999), the African antelope (Wirtz 1981), and the topi (Bro-Jorgensen and Durant 2003; Bro-Jorgensen 2008). Most instances of intra-population variation in vertebrate mating systems are thought to result from changes in the abundance or spatial distribution of resources and females and from demographic changes in population density or shifts in age structure (Dunbar 1982; Lott 1984; Wolff 2008). For example, despite of female defence polygyny is the most common mating system in male red deer (dominant tactic), has been reported to coexist with resource-defence (territoriality) as subordinate tactic (Carranza et al. 1995; Isvaran 2005). Accordingly, individual red deer males can switch between two or more reproductive tactics throughout lifetime or often within a single breeding season, whenever conditions change (Carranza et al. 1995; Taborsky et al. 2008). Also in *Damaliscus lunatus*, two types of polygyny coexist at the same population and central lek topi bulls are more successful than males that defend resource-based territories (Bro-Jorgensen and Durant 2003; Bro-Jorgensen 2008).

Ecological and demographic factors such as the magnitude of heat stress, the topography and type of substratum of the breeding site, the extent and frequency of female movements and rookery population density, are key to determine the extent of the spatial variation in the polygynous mating system of SASL populations (Campagna and Le Boeuf 1988a; Paves et al. 2005; Fernandez-Juricic and Cassini 2007; Soto and Trites 2011). Resource- and female-defence polygyny have been described for other SASL populations in the Atlantic (Campagna and Le Boeuf 1988a; Cassini and Vila 1990; Cappozzo and Perrin 2009) and in Chile (Paves et al. 2005), and further a lek-like mating system was reported in the tropical islands of Peru (Soto and Trites 2011). However, each population had a single or "pure" mating system, not the coexistence of types of polygyny that we found at Isla de Lobos. This coexistence of types of polygyny in Isla de Lobos generate one of the highest variances of reproductive success ever estimated in otariids (Franco-Trecu et al. 2014; Gonzalez-Suarez and Cassini 2014).

The high summer temperatures and the absence of suitable places inland to avoid overheating during territory tenure (Campagna and Le Boeuf 1988b) constrained the male spatial distribution and led to the coexistence of two mating systems in our study site. The dynamics of territory occupancy in our study area was such that the crowding at the tide line increased only after the finite number of internal pools were occupied (Fig. 2). Males at the tide line benefited from a low risk of overheating due to the continuously renewing seawater allowed them to thermoregulate during their entire territory tenure. These males also had a privileged location in relation to the female arrivals and hence a higher chance of successfully monopolize them than those at the internal pools. Nevertheless, the crowding at tide line leading to decreasing inter-male distances could have generated a high frequency of male-male interactions with associate energetic costs. On the other hand, while males at the internal pools would have difficulties to thermoregulate, they probably enjoyed the benefits of a lower frequency of male-male interactions and a lower risk of female stealing because inter-male distances were longer than those at the tide line. Given that territory occupancy did not change their quality, the dynamics of territory occupancy in our study site would resemble an ideal despotic distribution (Calsbeek and Sinervo 2002; Soutullo et al. 2006).

The high incidence of first order relatives (full sibling's males or parent-offspring) in the tide line suggests that parents and their offspring could breed in the same rookery. While we cannot discard it, we think that this is unlikely. Genetic analyses have shown that the SASL is geographically structured in the South Atlantic with high male dispersal and strong female philopatry (Feijoo et al 2010). In the case of full siblings, some males may re-copulate in the same rookery on different breeding seasons and thus generate sets of full sibs as it has been found for the Antarctic fur seal (*Arctocephalus gazelle* (Bonin et al. 2014).

Kinship and mating are probably the main factors that explain social interactions among mammals (Bergman 2010). Given the high energetic cost involved in territorial defence and in agonistic interactions towards neighbouring males, we hypothesized that SASL breeding males should prefer to distribute themselves close to their kin (Waldman 1988). Nevertheless, we found the latter is to be true only at the tide line where the average pairwise distance between males was shorter than at the internal pools. The high proportion of males with total and first-order kinship at the tide line suggests the existence of a fine scale kinship structure in the rookery. Although we think it likely, it remains to be shown that this fine scale kinship structure of SASL is related to a lower level of agonistic interactions between kin at the tide line that could explain the difference in male breeding success between the two locations. Males at the tide line might increase their inclusive fitness by lowering the energetic costs of territoriality of close kin and hence a kin selection process should not be ruled out, as it has been found in bottlenose dolphins (*Tursiops aduncus,* Moller 2012) and African elephant populations (*Loxodonta africana*, Chiyo et al. 2011). In addition, other species having similar dispersal tendencies as SASL such as swift foxes (*Vulpes velox*) also had a fine-scale kin structure and the tolerance to other breeding individuals was positively correlated with the degree of kinship (Karki 2003). These findings indicate that swift foxes (and presumably SASL too) could identify and maintain relationships with related individuals (Kitchen et al. 2005).

In sum, we suggest that constraints imposed by the rookery topography through the availability of sites to thermoregulate during the breeding season constrained SASL males' spatial use and the individual mating behaviour in Isla de Lobos. To our knowledge, we have shown the first evidence in otariids for the coexistence of two types of polygyny in a single breeding rookery. We also found higher level of kinship among dominant SASL males that were separated by shorter inter-individual distances than those at the internal pools. Because kinship has a major influence on patterns of aggression and affiliative behaviours (Smith 2014), we hypothesized that the kinship structure at the tide line could be a mechanism leading to a decrease in the aggression levels between neighbours, as it was reported for spiders (Walsh and Rayor 2008), amphibians (Markman et al. 2009), birds (Watson et al. 1994), rodents (Ensminger and Meikle 2005) and primates (Butovskaya 1993). Nevertheless, it remains to be tested whether kinship structure is related to lower aggression levels in SASL.

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Ethical standards

All procedures of animal manipulation were submitted and approved by the Ethics Committee in Animal Experimentation of the Universidad de la República, Uruguay as valid according to the national laws in animal welfare.

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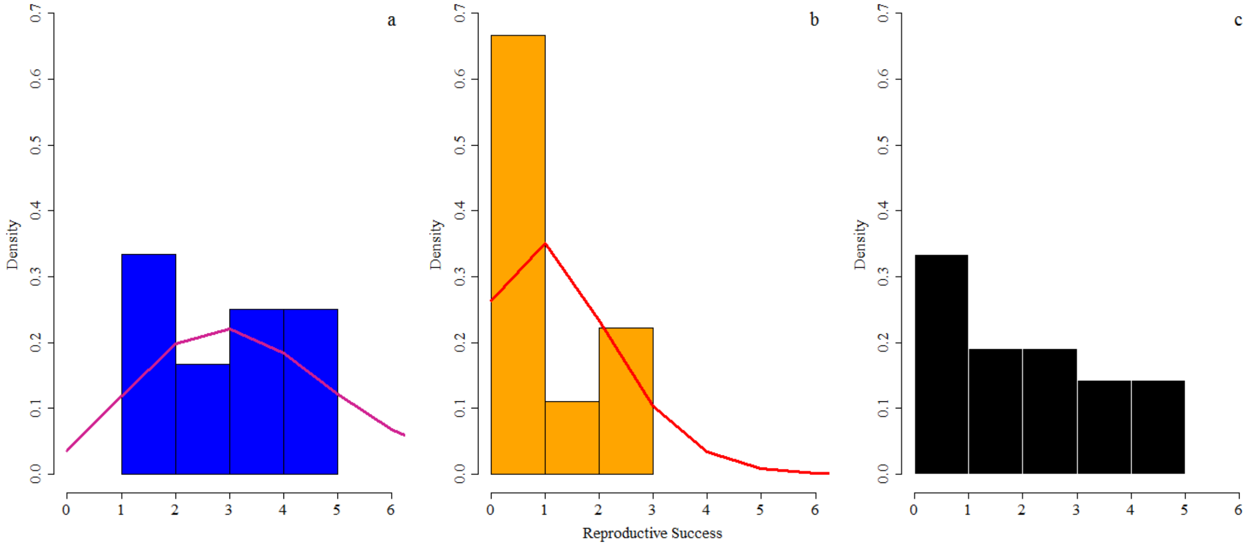

Figure 1. Frequency distributions of male breeding success of the South American sea lion in Isla de Lobos, Uruguay estimated by genetic paternity analyses for the a) tide line, b) internal pool and c) all males. Lines correspond to breeding success predicted for each reproductive tactic by the statistical model selected in Table 3.

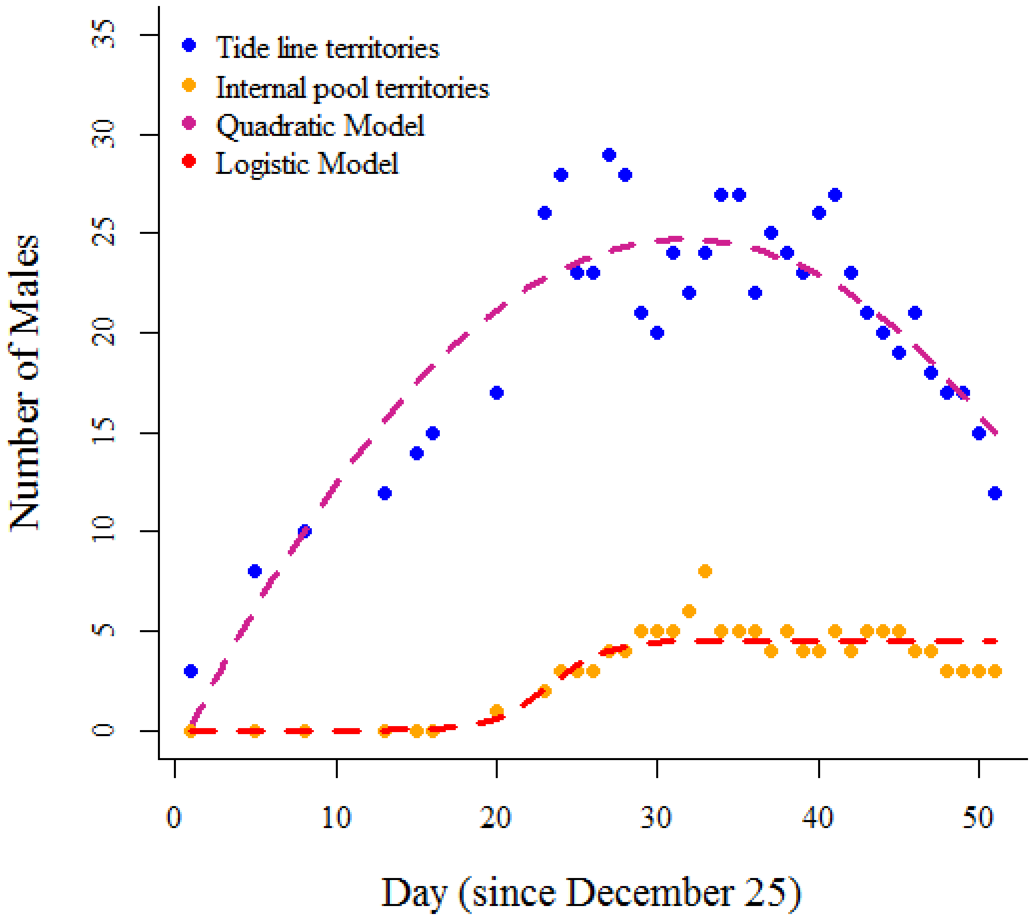

Figure 2. Temporal distribution of number male South American sea lions at tide line and internal pool in Isla de Lobos during the 2011 breeding season. Dotted lines represent a quadratic and logistic model to tide line and internal pool males, respectively.

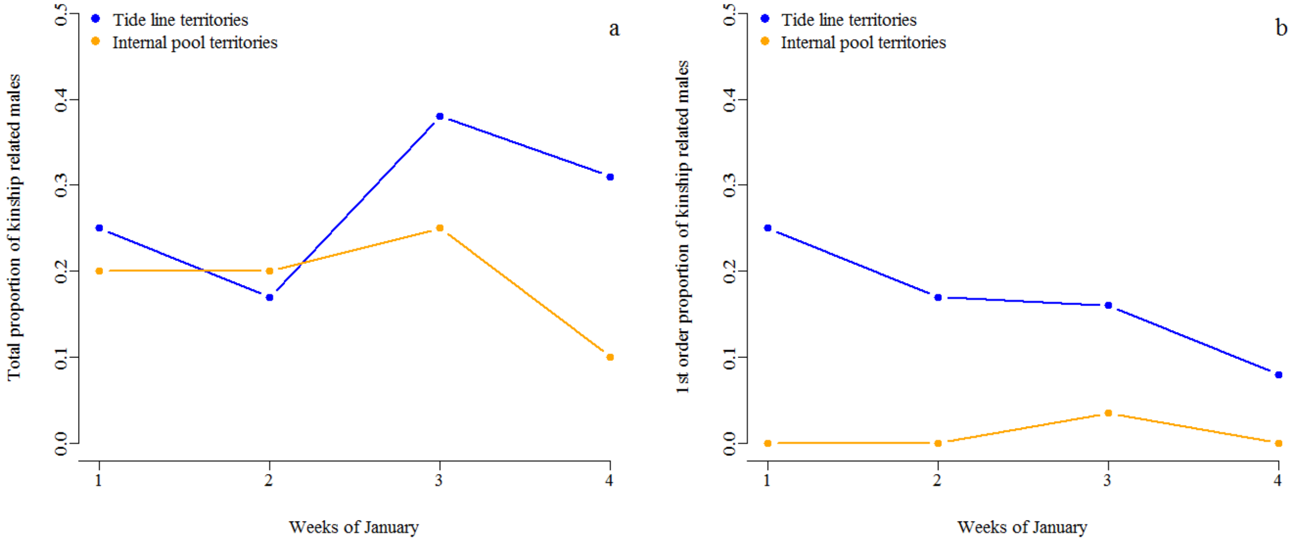

Figure 3. Proportion of South American sea lion males having any degree of kinship (a) and only first order: parents–offspring and full siblings (b) kinship for both reproductive tactics during the month of January 2011 in Isla de Lobos, Uruguay

Table 1. PCR conditions and statistical results for each of the loci used in the paternity analysis of South American Sea Lion males in Isla de Lobos, Uruguay. AT$_{1\text{-}4}$ are the annealing temperatures used in both single or touchdown PCR, Na is the allele number, size is the observed range in fragment size in base pairs (pb), Ho and He are the observed and expected heterozygosity per locus, F_{IS} is the inbreeding coefficient, p is the statistical significance of heterozygosity deficiency, PIC is the Polymorphic Informative content, and PI and EP are the probabilities of identity and of exclusion per locus, respectively. The two loci highlighted in bold were not included in the PI, PE and paternity analyses because of their significant heterozygosity deficiency.

Locus	MgCl$_2$ (mM)	AT$_1$…AT$_4$ (^{o}C)	Na	Range pb	H$_E$	H$_O$	FIS	p-v	PIC	PI	PE	References
Aa4	3	58°/56°/54°/50°	3	213-223	0.50	0.50	-0.01	0.58	0.38	0.11	0.33	Gemmell et al. 1997
Hg4.2	2	51°/50°	13	155-193	0.90	0.93	-0.04	0.85	0.88	0.39	0.11	Allen et al. 1995
M11A	3	58°/56°/54°/50°	9	149-173	0.80	0.77	0.04	0.10	0.77	0.06	0.45	Hoelzel et al. 1999
Pv11	3	60°	7	160-173	0.53	0.56	-0.07	0.83	0.48	0.37	0.12	Hoelzel et al. 1999
Pv17	2	53°/52°/50°	**8**	**154-179**	**0.78**	**0.38**	**0.51**	**0.001**	**0.74**			**Hoelzel et al. 1999**
Pv9	3	58°/56°/54°/50°	6	161-173	0.61	0.61	0.00	0.03	0.58	0.07	0.44	Allen et al. 1995
PvCE	2	51°/50°	**3**	**115-117**	**0.63**	**0.27**	**0.56**	**0.001**	**0.55**			**Coltman et al. 1996**
ZcwB07	2	51°/50°	8	173-190	0.72	0.75	-0.04	0.58	0.69	0.19	0.22	Hoffman et al. 2007
ZcwE04	2	53°/52°/50°	2	108-110	0.47	0.51	-0.10	0.87	0.36	0.28	0.14	Hoffman et al. 2007
ZcwE12	2	51°/50°	4	177-186	0.69	0.71	-0.03	0.83	0.63	0.17	0.25	Hoffman et al. 2007
ZcwF07	3	58°/56°/54°/50°	8	173-180	0.67	0.59	0.13	0.03	0.61	0.02	0.63	Hoffman et al. 2007
ZcwG04	2	53°/52°/50°	9	151-179	0.81	0.85	-0.05	0.96	0.78	0.16	0.26	Hoffman et al. 2007
Mean					**0.68**	**0.62**	**0.08**		**0.62**	**0.18**	**0.29**	
SD					**0.13**	**0.19**	**0.22**		**0.16**	**0.13**	**0.17**	

Table 2. Main descriptors of the mating behaviors of South American sea lion males reproducing at two different breeding location in the rookery of Isla de Lobos, Uruguay during the 2011 breeding season.

	Tide line (n= 13)	**Internal pool (n=8)**
Mating system	Female defense polygyny	Resource defense polygyny
Reproductive success (mean±SD)	3.5 ± 1.2	1.3 ± 1.1
Variance in reproductive success	1.4	1.1
Inter-male distances (m) (mean±SD)	2.5 ± 1.6	5.1 ± 3.7
Duration of individual territory tenure (days) (mean±SD)	13.1 ± 8.2	10.8 ± 5.6
Range in the proportion male kinships by week	0.17 to 0.38	0.10 to 0.25
Range in the proportion of first order kinship by week	0.08 to 0.25	0 to 0.04

Table 3. Parameter estimates and p-values (with significance shown in bold) for the set of behavioural variables used to explain the reproductive success of the South American sea lion in Isla de Lobos, Uruguay using generalized linear models with Poisson distributions and log link functions. The three models shown differed in the number of explanatory variables and their interactions included, in the value of their Akaike Information Criteria (AIC) and in residual deviance. The third model was selected based on having the smallest AIC, and the predicted values are used in Figure 2.

Model	**intercept (p-value)**	**Tactic -lm (p-value)**	**Tenure (p-value)**	**Tactic*Tenure (p-value)**	**AIC**	**Residual Deviance**	**df**
paternity ~ tactic * tenure	0.544 (0.363)	0.769 (0.254)	-0.013 (0.637)	0.009 (0.764)	76.069	15.407	17
paternity ~ tactic + tenure	0.393 (0.257)	0.949 (0.004)	-0.0052 (0.589)	-	74.16	15.498	18
paternity ~ tactic	0.288 (0.319)	**0.916** **(0.005)**	**-**	**-**	**72.45**	**15.789**	**19**

ABUNDANCIA Y DINÁMICA POBLACIONAL DEL LOBO FINO Y LEÓN MARINO EN COLONIAS REPRODUCTIVAS URUGUAYAS

Objetivos específicos:

4a. Estimar la abundancia poblacional actual por clase de edad del lobo fino y de león marino en las colonias de la costa del Uruguay.

4b. Estimar las tendencias poblacionales de ambas especies a partir de la información disponible sobre sus abundancias pasadas estimadas por métodos comparables

4c. En relación al león marino, dada la evidencia existente sobre tendencias poblacionales opuestas entre colonias reproductivas (Isla de Lobos y Cabo Polonio), se propone evaluar variables (tasa de supervivencia y de crecimiento de las crías, así como estrategia de alimentación de las hembras lactantes) que pudieran explicar las diferentes dinámicas observadas.

Hipótesis

A pesar de que los antecedentes indican que la tendencia poblacional del león marino en Uruguay es negativa, debido a que la población local de la principal colonia de Uruguay (Cabo Polonio) tiene una tasa de crecimiento poblacional positiva o estable (Pedraza et al. 2009), es probable que la misma compense el decrecimiento de la pequeña colonia de Isla de Lobos (Pedraza et al. 2009). Por lo tanto la primera hipótesis plantea que la tendencia de la población del león marino en Uruguay debería ser estable.

Las tendencias poblacionales del león marino difieren entre ambas colonias reproductivas, mientras en Cabo Polonio la tendencia poblacional es estable, en Isla de Lobos es decreciente. En este contexto la hipótesis plantea que en Cabo Polonio la masa al nacer, la tasa de crecimiento y la supervivencia de las crías son mayores que en Isla de Lobos (traduciéndose en su tendencia) y se relacionan con los hábitos alimenticios de las hembras.

RESUMEN

Estimar la abundancia poblacional a lo largo del tiempo es una herramienta útil para evaluar el efecto de procesos ecológicos y de variables de origen antrópico sobre la dinámica observada para poder predecir las respuestas poblacionales a futuro. Ésta última es información esencial para realizar una correcta gestión y conservación de los recursos naturales. Si bien la dinámica espacio-temporal de las poblaciones naturales es afectada por la variabilidad intrínseca de los hábitats, las interacciones bióticas y diversos efectos antrópicos como la extracción de recursos o la degradación de hábitats (Millenium-Ecosystem-Assessment 2005), en muchos casos, la complejidad de los efectos de las actividades humanas limitan la posibilidad de realizar predicciones fiables. Los pinnípedos (otaridos, fócidos y morsas) son mamíferos de gran tamaño corporal, longevos y con una baja tasa reproductiva (una cría por año). Estas características generan que sus poblaciones no sean particularmente resilientes (i.e. respondan y se recuperen rápidamente) frente a grandes extracciones de individuos como las realizadas en numerosas poblaciones (Gerber and Hilborn 2001). Las trayectorias poblacionales de la mayoría de las especies de pinnípedos han estado severamente influenciadas por la explotación comercial a gran escala. Esta actividad de explotación condujo a una severa disminución de los stocks de varias especies de pinnípedos hacia fines de siglo XIX y durante el siglo XX (Bonner 1982). Las respuestas a la extracción comercial de las poblaciones de pinnípedos han sido muy diversas entre especies y aún entre poblaciones locales de una misma especie (Dans et al. 2004; Páez 2006).

El lobo fino, *Arctocephalus australis*, se distribuye en Sudamérica, desde Torres (29,33º S; 49,71º O) Brasil, hasta Zorritos (4º S; 81º O) al norte de Perú (Riedman 1990; Rosas et al. 1994). El lobo fino presenta una distribución menos continua que la de su especie simpátrica, el león marino, localizándose en colonias donde se concentran grandes cantidades de individuos. La mayor concentración de individuos del lobo fino se encuentra en Uruguay y la misma fue estimada a partir de la estimaciones del número de crías y modelos matriciales en 300.000 (Páez 2000). Si bien existen para esta especie estimaciones de parámetros demográficos (Lima 1998; Lima and Páez 1997; Lima and Páez 1995), éstos fueron obtenidos durante la extracción comercial, por lo que es importante actualizarlos y evaluar si existen diferencias. El lobo fino ha sido explotado intensamente en toda su área de distribución geográfica desde el siglo XVIII. En

tiempos prehistóricos, los lobos finos fueron la base del sustento de poblaciones indígenas en zonas costeras de Sudamérica (Schiavini 1990). En Uruguay, el manejo y explotación estuvo a cargo del Estado pero la zafra dejó de practicarse en 1991 (DINARA 2008). En la actualidad, las poblaciones locales de lobo fino están recuperando sus abundancias y la población del Atlántico sur de esta especie se encontraría en fase de expansión (Crespo et al. 2015). No obstante, la tasa de crecimiento poblacional del lobo fino difiere fuertemente entre países ya que mientras que la población del Uruguay crecería a una tasa aproximada del 2% anual (Lima and Páez 1997; Páez 2006), en la Patagonia se ha estimado un incremento del 8% anual entre 1940 y 1990 (Crespo et al. 2015). Debido a que en las colonias del centro de la Patagonia no nacen más de 200 o 300 crías en una población de unos 15.000 individuos adultos, se supone que la fuerte tasa de crecimiento estimada estaría subsidiada por un fuerte componente de dispersión (Crespo et al. 2015).

El león marino sudamericano, *Otaria flavescens*, se distribuye en los Océanos Atlántico y Pacífico en simpatría con el lobo fino. La historia poblacional del león marino en Sudamérica ha estado estrechamente vinculada con las actividades humanas, ya que ha sido fuertemente afectada por la intensa caza comercial desde mediados del siglo XX en toda su área de distribución geográfica (Crespo and Pedraza 1991; DINARA 2008; Sielfeld 1999). En Argentina, la población global del león marino se encuentra en recuperación y se ha estimado una tasa de incremento poblacional del 5,7% anual, así como eventos de recolonización local y cambios en la estructura de edades (Dans et al. 2004; Grandi et al. 2012; Reyes et al. 1999; Schiavini et al. 2004). En Perú, la población del león marino parece recuperarse luego de la fuerte disminución asociada con el Evento del Niño en 1997 (Olivera & Majluf 2009). Las poblaciones del norte, centro y sur de Chile también han mostrado aumentos en sus tamaños poblacionales (Sepulveda et al. 2009, Sielfeld et al. 2009). Sin embargo, la población uruguaya del león marino es la única en su área de distribución que actualmente posee una tendencia decreciente en el número de nacimientos (Páez 2006; Pedraza et al. 2009). En Uruguay, el león marino principalmente se concentra en dos colonias reproductoras (Isla - Islote Lobos e Islas de Torres - Isla de Marco) y no se han observado áreas de expansión recientes de esta especie (loberías de juveniles y/o subadultos que puedan transformarse año tras año en loberías de cría). A pesar de tener una tendencia poblacional decreciente, no existen estimaciones directas del tamaño de la población uruguaya del león marino. La única estimación indirecta (12.000 individuos para el año 2005) fue realizada utilizando un modelo de dinámica de poblaciones matricial con valores de fecundidad y supervivencia provenientes de otras especies de lobos marinos (Páez 2006). A pesar de que en nuestro país el cese de la explotación ocurrió en 1986, el modelo empelado por Páez (2006) sugiere que la tendencia poblacional entre 1993-2005 sería decreciente, aunque diferentes según el sexo y edad de los individuos (Páez 2006).

La evidencia disponible sugiere que las abundancias y las tendencias poblacionales de ambas especies son heterogéneas y con una fuerte disparidad a lo largo de toda su distribución geográfica (Seal Conservation Society 2002, UNEP-WCMC 2002, IUCN 2008). Dada la singular situación de las poblaciones de Uruguay, resulta evidente la necesidad de realizar estimaciones de abundancias confiables para ambas poblaciones, utilizando métodos de estimación comparables con el resto del área de distribución. Durante el taller internacional "Estado de situación del Lobo Marino Común en su área de distribución" realizado en Valparaíso, Chile en 2009, se estableció el método de conteo por medio de censos aéreos como metodología estándar a emplear a fin de obtener estimaciones de abundancia fiables y comparables a lo largo del área de distribución de esta especie.

Se estimó la abundancia por clase de edad y sexo para ambas poblaciones por medio de censos aéreos realizados durante las temporadas reproductivas de 2011 y 2013 en Uruguay. Estos estimados de abundancia poblacional junto con datos previamente publicados (Ponce de León 2000; Vaz-Ferreira et al. 1984) fueron utilizados para estimar la tendencia poblacional de ambas especies en los últimos 60 años en Uruguay. Por otro lado, en relación al león marino, se compararon diversos parámetros entre ambas colonias de cría dadas sus tendencias contrastantes: Isla de Lobos con una disminución en el número de nacimientos *vs*. las islas de Cabo Polonio - Valizas, donde el número de crías aumenta (Pedraza et al. 2009). Se evaluaron diferencias en los hábitos alimenticios ($\delta^{15}N$ y $\delta^{13}C$) de las hembras lactantes, en la masa al nacer, la tasa de crecimiento individual y la supervivencia temprana de las crías, así como la estructura social entre las dos colonias para intentar explicar sus tendencias opuestas.

La abundancia total estimada para el lobo fino en febrero de 2013 fue aproximadamente de 70 mil individuos, mientras que la del león marino fue de 9 mil individuos aproximadamente. La tendencia poblacional del lobo fino pudo ser estimada únicamente para la Isla de Lobos, ya que no existen datos publicados sobre abundancia en la colonia de Cabo Polonio. Dicha tendencia fue significativa y positiva con una tasa de crecimiento anual del 1.5% (P = 0,037) para los últimos 60 años. La tendencia poblacional del león marino fue estimada para ambas colonias, así como para la población total. Mientras en Cabo Polonio la abundancia de la población se mantuvo constante (pendiente = - 0,005; P = 0.2), en la Isla de Lobos la población decreció a una tasa del 5% anual (P = 0,003) en los últimos 60 años. La tendencia de la población total disminuyó a una tasa del 2% anual. Estas tendencias poblacionales evidencian que la disminución poblacional observada en Uruguay podría ser consecuencia de la explotación comercial realizada en Isla de Lobos entre los años 1963 y 1986, sumada a la extracción de individuos para acuarios y zoológicos (hasta el año 2009), ambas realizadas únicamente en Isla de Lobos.

En relación a la comparación realizada entre colonias para el león marino, se encontró que los valores de δ^{13}C and δ^{15}N tanto de las células sanguíneas como del suero de las crías no variaron ni entre colonias ni sexos de los individuos. Únicamente los valores de δ^{15}N en suero fueron significativamente mayores para las crías hembra. Esto indicaría que las hembras del león marino en ambas colonias utilizan recursos similares. Las masas al nacer de las crías machos fueron significativamente mayores que las hembras, sin que se detectaran diferencias significativas entre las dos colonias. La tasa de crecimiento corporal fue significativamente mayor en Isla de Lobos, y marginalmente mayor en las cría macho. La masa inicial de las crías se relacionó de forma positiva con los valores de δ^{15}N en las células sanguíneas (preparto), mientras la tasa de crecimiento disminuyó con mayores valores de δ^{15}N en suero (postparto), de forma significativamente mayor en Isla de Lobos. El modelo seleccionado para estimar la sobrevivencia de las crías del león marino incorporó la variación temporal (meses) y las colonias. Durante el primer mes (febrero), la supervivencia fue prácticamente igual en ambas colonias, pero hubo importantes diferencias en la sobrevivencia en el segundo mes (marzo), siendo este último parámetro significativamente mayor en Cabo Polonio que en Isla de Lobos. Finalmente, la proporción de machos (adultos y subadultos) en cada colonia difirió significativamente entre colonias, siendo significativamente mayor en Isla de lobos. Esto último es importante porque los machos periféricos de león marino secuestran y matan a las crías, lo que podría explicar la menor supervivencia de las crías en la colonia más pequeña (Isla de Lobos). La tasa de crecimiento negativa encontrada en Isla de Lobos refleja el efecto acumulados de la extracción comercial así como la posterior venta de animales vivos para acuarios y zoológicos. Además de la disminución de abundancias, dichas extracciones han afectado la estructura social de los leones marinos en Isla de Lobos hasta un punto donde el efecto Allee ha llegado a ser importante, colaborando con la disminución de la población uruguaya del león marino.

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LONG-LASTING EFFECTS OF HARVESTING ON POPULATION TRENDS OF SYMPATRIC OTARIIDS IN URUGUAY

Valentina Franco-Trecu[1,2*], Massimiliano Drago[2], M. Florencia Grandi[3], Enrique A. Crespo[3,4] and Pablo Inchausti[2]

[1] Proyecto Pinnípedos, Sección Etología, Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay.

[2] Departamento de Ecología & Evolución, Centro Universitario Regional Este (CURE), Universidad de la República, Maldonado, Uruguay.

[3] Laboratorio de Mamíferos Marinos, Centro Nacional Patagónico (CONICET), Puerto Madryn, Chubut, Argentina

[4] Universidad Nacional de la Patagonia, Puerto Madryn, Chubut, Argentina

* e-mail: pinnipedosuy@gmail.com, Iguá 4225, Montevideo, Uruguay

Abstract

The abundances of marine mammal populations can be affected by a host a factors including natural environmental variation and anthropogenic impacts such as over-exploitation and habitat degradation. The South American fur seal (SAFS) and the South American sea lion (SASL) are two otariid species breed in sympatry in the Uruguayan coast. Given that these two species were intensively harvested and that they currently have dissimilar abundances, our overall aim was to update the estimates of abundance and trend for both species in Uruguay using the same methods employed elsewhere. We carried out aerial surveys in February 2011 and 2013 to estimate their current population abundance in all rookeries along the Uruguayan coast and, together historical data of pup abundance, we estimated population trends for these two otariid species in Uruguay for the last 60 years. Excluding juveniles, we estimated the total abundance in 9,188 (SD = 2,093) individuals of SASL and 72,653 (SD = 8,096) of SAFS in 2013. Using data count between 1956 and 2013, we estimated that the SASL pup production has declined at an annual rate of -2% (IC: -1.1 to -2.5) in Uruguayan population and that the SAFS has grown 1.5% over (IC: 0.2 to 2.8) the same period in the main rookery, Isla de Lobos. We discuss our result in a global, metapopulation and local scale.

Keywords: *Arctocephalus australis*, *Otaria flavescens,* abundances, aerial survey, population trend

Introduction

Understanding the determinants of the spatio-temporal dynamics of natural populations is the main goal of population ecology (Begon et al. 2006). Monitoring abundances/counts and estimating trends are important components for the management and conservation of animal populations (Anganuzzi 1993; Forney 2000). Population abundances can be affected by environmental variability in two main ways. First, natural variation in environmental conditions can generate changes in the abundance and/or spatial distribution of trophic resources that lead to changes in birth and mortality rates. Second, population abundances can change because the effect of anthropogenic processes such as over-exploitation and habitat degradation (Millenium-Ecosystem-Assessment 2005).

Pinnipeds (otariids, phocids and walrus) are large-bodied mammals with long generation times and low reproductive rates (one pup per year). These characteristics have often been associated with low resilience to exogenous perturbations and slow post-harvesting recoveries (Gerber and Hilborn 2001). Although population recoveries of previously impacted pinniped populations may have been hindered by low availability of food resources due to overfishing (Pauly et al. 1998; Alleway et al. 2014) and other human alterations of coastal ecosystems (Davenport and Davenport 2006; Bulleri and Chapman 2010), commercial sealing is believed to have been the main factor responsible for pinniped population declines during XIX and XX centuries (Bonner 1982). It is however noteworthy that post-harvesting responses have often differed among pinniped species and even among local populations of the same species (Trites and Larkin 1996; Gerber and Hilborn 2001; Dans et al. 2004; Grandi et al. 2014).

South American sea lion (*Otaria flavescens*, SASL) are distributed along the South American coast from southern Brazil in the Atlantic Ocean to northern Peru in the Pacific Ocean (Vaz-Ferreira 1976; Rosas et al. 1994). The population history of SASLs has been tightly linked to human activities since its abundance has been affected by intense commercial harvest from the 1950s until recently in its entire geographical range (i.e. Crovetto et al. 1979; Crespo and Pedraza 1991; Sielfeld 1999; Ponce de León 2000). The post harvesting dynamics of local SASL populations have shown a remarkable variation between sites. For instance, in Argentina, a range of local SASL populations are recovering with growth rates from 5 to 8% (Reyes et al. 1999; Dans et al. 2004; Schiavini et al. 2004; Grandi et al. 2014). In North Patagonia, the recovering of some SASL populations has been associated to colonization events of new areas and to changes in the local age structure (Grandi et al. 2008; Grandi et al. 2014). The Malvinas (Falkland) SASL population has been slowly recovering (Thompson et al. 2005) since 1995 and its current pup production is estimated in *c.a.* 4000 (A. Baylis Personal Communication). While the Peruvian population of SASL has slowly recovered since the large decline after the 1997 El Niño event (Olivera and Majluf 2012), those of Chile have showed different trends according to local environmental variation, ranging from slow recovery in the North (Bartheld et al. 2008) to stable in Central and Southern Chile (Sepulveda et al. 2011, Oliva et al. 2008). In Uruguay, SASL breeds in two rookeries (Isla - Islote de Lobos and Islas de Torres - del Marco) and no new breeding areas of this species has been observed for at least 60 years. We lack direct estimates of both the size and trends of SASL in Uruguay. The only indirect estimate available of population size (12.000 individuals in 2005) was obtained from a matrix population model with demographic parameters from other species of otariids (Páez 2006). Unlike the observed post-harvesting trend of the North Patagonian population (Dans et al. 2004), the aforementioned model predicted a decreasing trend between 1993 and 2005 (Páez 2006) almost 20 years after ending the SASL exploitation by Uruguayan State (~47,000 pups between 1963-1986; Ponce de León 2000).

The South American fur seal (*Arctocephalus australis* - SAFS), is distributed in the Atlantic and Pacific coasts of South America (Vaz-Ferreira 1982a) in sympatry with SASL in dense colonies. SAFS populations were the basis of livelihood for indigenous populations in Pre-Hispanic South American coastal areas (Schiavini 1985). Later, the species was intensively exploited from the 18th century until the end of the 20th century in most of its geographic range (Ponce de León 2000). Local SAFS populations seem to be recovering at varying rates after the end of harvesting (Crespo et al. 2015). For instance, while the pup of the Uruguayan population would be increasing at an approximate annual rate of 2% (Páez 2006), similar estimates range between 5% and 8% in Central and Southern Patagonia (Argentina), respectively (Crespo et al. 2015). Nevertheless, since only *c.a.* 200 pups are born per year in a population of 15.000 juvenile and adult individuals in the colonies of Central Patagonia, the high estimated population growth rate in this area is likely to have a strong dispersal component

(Crespo et al. 2015). In Uruguay, the State oversaw the management and exploitation of SAFS from the 1949 until 1991 that led to the overall culling of approximately 280,000 individuals (Ponce de León 2000). Private concessions had killed near 527,000 individuals in Uruguay during the previous 70 years (Ponce de León 2000). Although the most recent estimates of Uruguayan SASL population abundance (300,000 individuals in 2000) would suggest this population to be the largest in the Atlantic Ocean, these figures obtained based on extrapolations involving pup counts, mortality and recapture rates estimated over a short time period (Páez 2000), should be viewed with extreme caution.

Given that the two main pinniped species in South America were intensively harvested and that they currently have dissimilar trend throughout their geographic ranges, our overall aim was to update the estimates of abundance and trend for both pinniped species in Uruguay using the same methodology employed elsewhere for these pinniped species. We also carried out an extensive compilation of historical abundance data (including internal reports and news releases from the Uruguayan state agencies, congress abstracts and books published in Uruguay) of both species in Uruguay that allowed us to compare the current estimates of population abundance with those reported over the past 60 years. Finally, we discuss our results in the context of the population recovery of pinniped species in the South Western Atlantic.

Methods

Study area

The South American fur seal and sea lion rookeries on the Uruguayan continental shelf are the northernmost breeding sites of these species in the Atlantic Ocean. Rio de la Plata estuary have a highly dynamic mixing regime resulting from the mixing of freshwater and the convergence of the Brazil and Falkland/Malvinas currents that generate a frontal regime of high primary productivity (Ortega and Martinez 2007). Isla and Islote de Lobos (35º 01’ S; 54º 52’ W) are small (0.42 km^2 and 0.04 km^2, respectively) granite islands located at 9 km from mainland. The Islas de Torres group (34º 21' S, 53º 44' W) is comprised by three islands: Rasa (0.03 km^2), Encantada (0.02 km^2) and Islote (0.02 km^2) located *c.a.* 2 km from the mainland (and declared a Marine Protected Area in 2009). Isla del Marco (0.08 km^2) belongs to the Castillo Grande group (34º 25' S, 53º 46' W) is located North-east of the Isla de Torres (Fig. 1).

Aerial survey and counting methodology

The whole coast of the study area was surveyed by flying a low-wing, single-engine aircraft (Cessna 182) at constant average speed and altitude of 300 m to detect the presence of pinniped individuals ashore. The surveys were performed at the beginning of February in 2011 and 2013, when most of the individuals of both species were still present at the rookeries and the 100% of the pups of both species had been born (Franco-Trecu et al. 2010; Trimble and Insley 2010). During each aerial survey, we took more than 600 photographs for all islands using a Nikon D80 digital camera of 10.2 MP equipped with a 80 - 200 mm telephoto lens, using a configuration of shutter speed and diaphragm opening adequate for the conditions of light and sensibility at the moment of the surveys (ISO 200 o higher). We used the set of photos of each island to form a mosaic by editing and mounting a selection of the best shots in each survey.

Three experienced observers (VFT, MD and MFG) carried out independent countings of each mosaic using the OTARIIDAE software (Bartheld et al. 2008). Individuals of each species were counted separately by age-class and sex: adult males (AM, territorial and peripheral), sub-adult males (SAM), pups (P, born during the season of the census), and indeterminate (females + juveniles, both sexes pooled together) individuals. These categories were based on body shape and colour, location in the rookery and other behavioural cues of each species (Vaz-Ferreira and Sierra de Soriano 1963; Vaz-Ferreira 1973; Vaz-Ferreira 1982a; Vaz-Ferreira 1982b; Crespo and

Pedraza 1991). In established breeding rookeries, the indeterminate individuals of each species were mainly composed of juvenile and adult females, their high similarity hindered assigning age and sex to individuals.

Data analysis

We estimated the average number of individuals and the standard deviation (SD) across observers of each age class of both species in each photo for each island/colony in 2013. Because this censusing methodology (aerial surveys) underestimates the pup number and non-pups individuals due to an unknown proportion of individuals at sea at the time of counting (Reyes et al. 1999; Sepulveda et al. 2011), we applied different correction factors for each age class to estimate the total population size of each species. However, because the substrate type and the breeding period differ along the geographic range, the correction factors should ideally be obtained for each location. The correction factors for each species were estimated as follows. First, the pup counts of each species were corrected by using simultaneous pup counts on land for each species carried out in two reproductive areas from Isla de Lobos at the same day of the aerial surveys (see Results). Second, although the number of adult males is not usually underestimated in aerial surveys due to their large body size (Reyes et al. 1999), those counts need be corrected since the surveys were carried towards the end of the reproductive period when an unknown proportion of breeding males were no longer in the rookeries. We estimated the correction factor for males (adults and subadults) of each species using the distribution of the number of territorial males over time (daily land counts for at least 40 days) in four breeding seasons (2009-2012). We divided the maximum number of males at the reproductive peak by the number of males counted the day of the flight. Finally, even though females of both species could not be distinguished from juveniles in the photos, the number of indeterminate individuals of each species counted on photos would be an underestimation because of the unknonwn fraction of individuals foraging away from the rookery. Because juveniles of both species are known to move freely away from the rookeries and their abundances change seasonally at the colonies (Crespo et al. 2015), it is very difficult to estimate a correction factor for the indeterminate individuals of both species. However, given that the number of adult females present at the rookery can be estimated from the estimated number of pups and the fertility rates (see below), we calculated the number of sexually mature females of each species as the estimated number of pups (corresponding to the minimum number of breeding females) * 100/fertility.

We averaged the corrected counts for each age group to obtain the best estimates population abundance for each photo in 2013. The overall abundance of each species in each island, colony and Uruguay for 2013 were obtained by sum the previous averages. Because the standard deviations of the counts across observers differed among photos in 2013, we used the average coefficient of variation among photos from each islands/colonies as an estimate of the relative precision of the overall abundances among observers. We then multiplied the average coefficient of variation of each species by its average abundance to obtain the standard deviation of the overall abundance of each species. Given that reproductive colonies of SASL typically have a constant male-pup ratio at a given time (Crespo 1988), we also estimated the males/pup ratio for both species in each rookery in 2013. We estimated each species' fertility as the ratio between the maximum numbers of pups to females in 2013 breeding season. The pup abundances of both species in 2011 were estimated in the same way just explained above and were used to estimate the population trends (see Fig. 2).

We estimated the long-term population trends of both pinniped species in Uruguay based on compiled information of pup counts and current pup estimates. We used pup counts because these were the only available long-term (1956 – 2000) data of pinniped abundance in Uruguay (Ximenes 1973, Vaz-Ferreira et al. 1976, 1981, Ponce de León 2000). Our estimation of population trends only used abundance data obtained by direct pups count and we discarded estimates obtained from models and extrapolations (e.g. Páez 2000; Páez 2006).

Results

South American sea lion

For the six islands surveyed along the Uruguayan coast (Fig. 1), only one (Islote from Cabo Polonio) was not an evident breeding area (i.e. without pup production) because the newborn pups were less than 0.5% of total count while this proportion is ranges between 20 and 40% in other islands (see Table 1). The correction factors for SASL in 2013 were 2.2 for males, 1.6 for pups and female fertility rate was estimated at 0.60. Excluding juvenile individuals, we estimated the total SASL abundance in Uruguay in 2013 to be 9,181 (SD = 1062) individuals, of which 1,610 adult males (SD = 101), 437 sub-adult males (SD = 94), 4,459 females sexually mature (SD = 541) and 2,675 pups (SD = 324), representing ~30% of the population (see values without corrections in Table 1). Both the SASL pup corrected count and the total abundance were higher in Cabo Polonio than in Isla de Lobos. The SASL pup abundance was 2315 (593) for Cabo Polonio and 360 (56) for Isla de Lobos. Considering only breeding areas, male/pup ratio were 0.66 in Cabo Polonio and 1.44 in Isla de Lobos in 2013. SASL had a negative population trend in Uruguay between 1956 and 2013 and a yearly decline rate of -2% (Fig. 2). However, the population trend in Cabo Polonio colony did not significantly differ from zero and thus this local population may be considered stable.

South American fur seal

The Islote - Cabo Polonio was not a reproductive area for *A. australis* either since the proportion of newborn pups was also very low (< 2% of the total abundance) compared with the other reproductive colonies (see Table 2). The correction factors for SAFS in 2013 were 2.0 and 3.9 for males and pups respectively, whereas fertility for females was estimated at 0.83. Excluding again juveniles individuals, the overall SAFS population size in Uruguay in 2013 was 71,757 (SD = 5,008) individuals, of which 1,864 adult males (SD = 462), 636 sub-adult males (SD = 26), 37,846 sexually reproductive females (SD = 2470) and 31,412 pups (SD = 2050) that constituted 44% of the overall SAFS population (see values without corrections in Table 2). We found that 60% of the Uruguayan SAFS population was found in Isla de Lobos. Mean pup abundance estimated was 12,656 for Cabo Polonio and 18,756 for Isla de Lobos in 2013. Male/pup ratio was 0.06 in Isla de Lobos and Cabo Polonio. We estimated the long-term population trend for SAFS only for Isla de Lobos for which there were pup counts available. SAFS showed a positive trend between 1956 and 2013 with a 1.5% annual growth rate in Isla de Lobos (Fig. 3).

Discussion

The estimates of Uruguayan pinniped abundances obtained in this study have implications at different scales. First, at a global scale, our findings help understand the differential impact that commercial exploitation had on the long-term, post-harvesting recovery of pinniped populations. Second, at a meta-population scale in the South Atlantic Ocean, this study addresses the needs to assess the variation of local population abundances of each species over time so as to understand the importance of dispersal movement in the recent repopulation of SAFS rookeries in Central Patagonia, Argentina Finally, at a local scale, information reported herein are the first direct estimates of population abundance of the two Uruguayan otariids species ever obtained that should help guide the appropriate population management and conservation of these species in our country.

Methodological considerations

Our SASL pup correction factor (1.6 or 37% of underestimation) was quite comparable with those estimated in Patagonia, Argentina (~32%; Reyes et al. 1999) and in northern Chile (~30%; Sepulveda et al. 2011). As expected, the SAFS pup correction factor was higher (correction factor = 4) that SASL's, not only because SAFS smaller body size but also because SAFS pups tendency to form dense bunched pods at the shade of high rocks where they are not visible from the air.

Global scale

Environmental variation and anthropogenic impacts can all change population parameters and have the potential to cause declines in population size (Menges 1990; Mangel and Tier 1994; Gerber and Hilborn 2001). There are several examples of local fur seal populations that were exploited to near extinction that have showed a steady recovery several years after of the end of harvesting (i.e. *A. gazella*: Bengtson et al., 1990, *A. tropicalis*: Guinet et al., 1994; *A. forsteri*: Harcourt & Lalas, 1995). Even though SASL and SAFS were both commercially exploited in Isla de Lobos, SAFS has shown a positive population trend in the last 60 years despite of the intense exploitation (~ 800,000 individuals culled between 1893 and 1991) it had suffered. In contrast, SASL has not shown any signs of recovering at Isla de Lobos after the end of its exploitation in 1986. This study constitutes a clear example of differential impact of commercial exploitation on two sympatric species with similar life histories (breeding phenology, generation times, reproduction rates, etc). However, the situation of SASL in Uruguay is not unique since populations of other sea lion species have shown negative post-harvesting trends elsewhere (Trites and Donnelly 2003; Bando et al. 2005; Trites et al. 2007). The lack of recovery of sea lion populations has been attributed to the reduction in food availability by overfishing in the coastal-benthic habitats where they preferentially forage (Pauly et al. 1998; Trites and Donnelly 2003; Milessi et al. 2005; Alleway et al. 2014). However, the post-harvesting decline of the Uruguayan SASL population that seems unique in its geographic range probably resulted from the cumulative impact of pup harvesting (~47,000 between 1963 and 1978, Ponce de León 2000) and known adult extractions to zoos and aquaria between 1996 and 2008 (DINARA 2010). Both extractions only carried out in Isla de Lobos probably generated changes in social structure to the point that Allee-like effects through pup infanticide by peripheral males prevented the population recovery at this site (Drago et al. 2011; Franco-Trecu et al. in press). For instance, the different male-pup ratios between rookeries (0.66 *vs.* 1.44 in Cabo Polonio and Isla de Lobos, respectively) highlight the contrasting population structures in these two sites. This two-fold difference between the Uruguayan SASL rookeries stand in contrast with the estimates in Patagonia, Argentina where this ratio has been found to remain constant among traditional breeding rookeries (Crespo 1988).

Metapopulation scale

Genetic analyses have shown that local SAFS and SASL populations are connected by dispersal at the scale of the South Atlantic Ocean (Feijoo et al. 2011; Crespo et al. 2015). Thus, changes in population abundance of Uruguayan colonies can have a significant impact on the dynamics of other local pinniped populations. Several sources of evidence indicate that, after weaning, juvenile SAFS from Uruguay disperse to different rookeries within the South Atlantic Ocean, often travelling more than 1,000 km from their birthplace (Crespo et al. 2015). The rapid population expansion of the Uruguayan SAFS population suggests that it may be acting as a source of individuals to other local populations in southern Argentina (Crespo et al. 2015), where the important increase of pup production in recent years may only be explained by the income of individuals from elsewhere. Regarding the SASL, and despite of the negative population trend here reported, the number of pups estimated for the Uruguayan population (2,675 ± 324) is c.a. 10% of the estimated abundance in Patagonia (Southern: 8,469 pups, Central: 9,382 pups and Northern: 11,859 pups) (Reyes et al. 1999; Grandi et al. 2010; Grandi et al. 2012; Grandi et al. 2014), thus it is an important proportion of the South Atlantic SASL population. In South and North Patagonia colonies, as well as in Islas Malvinas, local SASL populations have shown a positive trends and new breeding areas have been observed (Reyes et al. 1999, Dans et al. 2004, Schiavini et al. 2004, Grandi et al. 2008, 2014, Baylis A. com pers). Hence, a relation between an overall decrease of SASL abundance in Uruguay and an increase in Malvinas and Patagonia, Argentina should not be discarded.

Local scale

This study reports, for the first time, direct estimates of population abundances of two Uruguayan otariid species obtained using methods comparable to those employed elsewhere in their geographic ranges. These estimates and trends are highly relevant since both species are valuable natural resources from an environmental-ecosystemic standpoint, as well as from a touristic and scenic one. Moreover, SASL lie at the heart of frequent conflicts of interest with artisanal fishermen along the Uruguay coast because this species sometimes feed on the fish caught in gillnets and long-lines and damage the fishing gears (Szteren and Páez 2002) and also because it sometimes is incidentally bycaught during fishing operations (Franco-Trecu et al. 2009). Even when this conflict has recently started to be approached in a participatory research with fishers, the latter demand solutions to the authorities in charge of resource management (Trimble and Berkes 2013; Trimble and Lazaro 2014). In this context, knowing the abundance, trend and foraging behaviour of the local SASL populations is essential to make adequate management decisions and settle or ameliorate conflicts with fishers in Uruguay.

The spatial segregation of trophic niches between sympatric species is well known to minimise interspecific competition (Begon et al. 2006). The trophic segregation between SASL and SAFS (Franco-Trecu et al. 2012; Franco-Trecu et al. 2013; Franco-Trecu et al. 2014) implies either the absence or the release from competition of these species in the Uruguayan coast. Therefore, the contrasting trends and population abundances between SAFS and SASL would be unrelated to interspecific trophic interactions. We believe that the population decrease of SASL in Uruguay is more likely to be explained by the inappropriate management decisions taken over the last decades. The cumulative effects of population extractions: pup harvesting (~47,000) and zoo and aquaria sales (144 and 285 young males and females, respectively) not only reduced the local population size, but also could have disrupted its social structure to the point where Allee effects could have become important (Franco-Trecu et al. 2015) obstructing the post-harvesting population recovery of SASL in Isla de Lobos. In addition, coastal ecosystems also suffer other environmental impacts associated with high human population densities such as overfishing (Milessi et al. 2005; Defeo et al. 2009), pollution (Clausen and York 2008; Bulleri and Chapman 2010), and perturbation due to recreational activities and ports (Davenport and Davenport 2006). We think that these activities may have also further affected the resource abundance and the quality in foraging areas used by SASL in Uruguay and contributed to the lack of recovery after the end of its commercial harvesting (Riet Sapriza et al. 2013).

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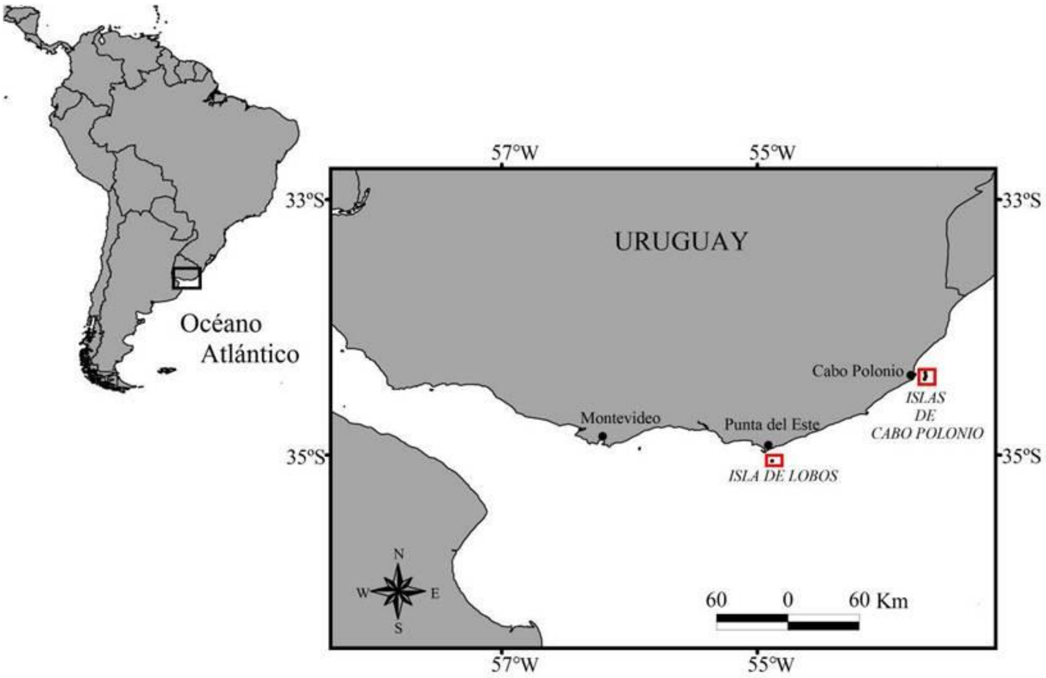

Figure 1. Breeding colonies of the South American sea lion and fur seal (*Otaria flavescens and Arctocephalus australis*) in Uruguay at Isla de Lobos and Cabo Polonio.

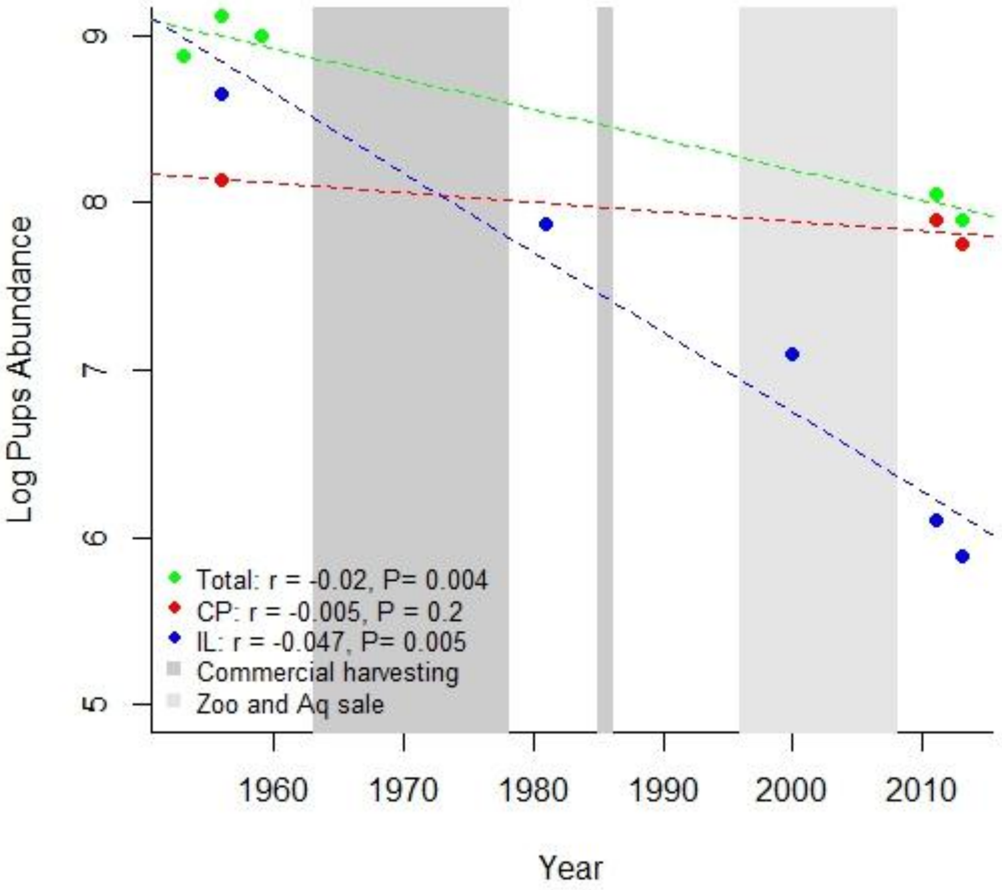

Figure 2. Population abundances and trends of South American sea lions pups from the Uruguayan population (green), and in each colony, Cabo Polonio in red and Isla de Lobos en blue, between 1956 and 2013. Grey bars refer to the periods of extraction: commercial (dark) and Zoos and Aquariums sale (clear).

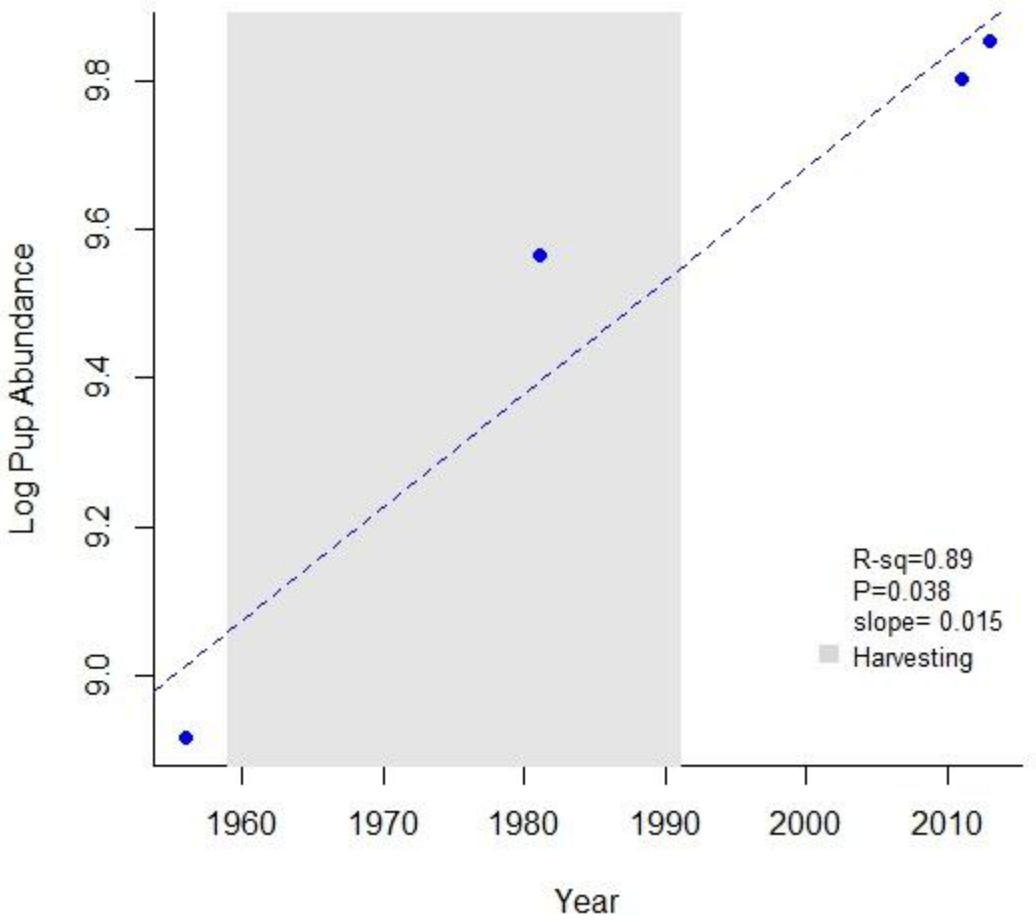

Figure 3. Population abundances and trends of South American fur seals pups from Isla de Lobos (Uruguay) between 1956 and 2013. Grey bar refers to the periods of commercial extraction.

Table 1. Uncorrected counts of South American sea lion of each age class (MAD: Adult males, SAM: subadult males, H+J: females + juveniles, P: pups) in each island in Uruguay in 2013. Values correspond to the mean and SD of counts of the photographs of each site by three independent observers (VFT, MD and FG)

Island/colony	**MAD**	**SAM**	**H+J**	**P**
Encantada	178 ± 18	32 ± 25	1241 ± 75	524 ± 212
Islote Cabo Polonio	19 ± 2	25 ± 18	524 ± 16	1.5 ± 1
Isla del Marco	241 ± 39	61 ± 43	1546 ± 76	587 ± 88
Isla Rasa	118 ± 0	22 ± 0	847 ± 0	335 ± 0
Cabo Polonio	***557 ± 52***	***140 ± 78***	***4157 ± 144***	***1447 ± 371***
Isla de Lobos	124 ± 15	47 ± 9	353 ± 70	118 ± 18
Islote Lobos	51 ± 17	12 ± 1	299 ± 64	107 ± 17
Isla Lobos	***175 ± 40***	***59 ± 8***	***652 ± 135***	***225 ± 35***

Table 2. Uncorrected counts of South American fur seal of each age class (MAD: Adult males, SAM: subadult males, H+J: females + juveniles, P: pups) in each island in Uruguay in 2013. Values correspond to the mean and SD of counts of the photographs of each site by three independent observers (VFT, MD and FG)

Island / Colony	MAD	SAM	H+J	P
Encantada	62 ± 13	12 ± 0	2961 ± 255	1083 ± 206
Islote Cabo Polonio	45 ± 63	1 ± 1	938 ± 233	20 ± 8
Isla del Marco	177 ± 170	2 ± 2	3766 ± 325	895 ± 157
Isla Rasa	51 ± 0	0	4080 ± 0	1166 ± 0
Cabo Polonio	***335 ± 215***	***15 ± 3***	***11745 ± 675***	***3164 ± 386***
Isla de lobos	511 ± 211	300 ± 23	22852 ± 1167	4511 ± 444
Islote de lobos	86 ± 77	3 ± 1	1852 ± 155	178 ± 31
Isla Lobos	***597 ± 247***	***303 ± 23***	***24704 ± 1665***	***4689 ± 639***

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Postharvesting population dynamics of the South American sea lion (*Otaria byronia*) in the southwestern Atlantic

VALENTINA FRANCO-TRECU,[1] Proyecto Pinnípedos, Sección Etología, Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay; **MASSIMILIANO DRAGO**, Departamento de Ecología & Evolución, Centro Universitario Regional Este (CURE), Universidad de la República, Maldonado, Uruguay; **CLAUDIA BALADÁN**, Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay; **MATEO D. GARCÍA-OLAZÁBAL**, Departamento de Ecología & Evolución, Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay; **ENRIQUE A. CRESPO**, Laboratorio de Mamíferos Marinos, Centro Nacional Patagónico (CONICET), Puerto Madryn, Chubut, Argentina and Universidad Nacional de la Patagonia, Puerto Madryn, Chubut, Argentina; **LUIS CARDONA**, Department of Animal Biology and Irbio, Faculty of Biology, University of Barcelona, Barcelona, Spain; and **PABLO INCHAUSTI**, Departamento de Ecología & Evolución, Centro Universitario Regional Este (CURE), Universidad de la República, Maldonado, Uruguay.

ABSTRACT

Many pinniped populations precipitously declined during the 19th and 20th centuries due to overharvesting. In Uruguay, the South American sea lion (SASL) was harvested until 1986. Birth rates in two nearby breeding colonies have had opposite trends for at least 20 yr. We assessed different mechanisms that could explain opposite trends in birth rates in the two SASL colonies. We compared feeding habits (δ^{15}N and δ^{13}C) of breeding females, birth mass, individual growth rate and early survival of pups and the social structure between colonies. Breeding females from the two colonies did not differ in their feeding habits. However, male and female pups grew faster but had a lower survival in the second month in the smallest colony. We found differences in the social structures, with a higher proportion of males in the smallest colony. The latter is important because peripheral SASL males may abduct and kill pups, which may explain the lower survival of pups in smaller colonies. We believe that the cumulative effects of population extractions have lowered the local SASL population size and disrupted its social structure to the point where Allee-like effects could become important and hamper the recovery of the Uruguayan SASL population.

Key words: population dynamics, harvesting, behavior, population recovery, Allee effect.

Overfishing and commercial exploitation have caused the decline of many populations and even the extinction of tens of marine species (Dulvy *et al.* 2003, Davidson *et al.* 2012). Marine top predators have been strongly affected by several global

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[1] Corresponding author (e-mail: pinnipedosuy@gmail.com).

anthropogenic drivers and approximately 25% of marine mammal species are currently classified as threatened (IUCN 2013). The relatively high level of threat of marine mammal species has been associated with their commercial exploitation in the past which, combined with their low population growth rates and relatively small population sizes, brought many marine mammal species to the brink of extinction (Costa *et al.* 2006). Once commercial exploitation finished or became regulated, populations were to recover to preharvesting levels or at least to levels of abundance consistent with available food resources and suitable breeding habitats. The recovery of a population released from harvesting pressure requires it to attain a high birth rate (which depends on both the breeding success and pup survival) and high adult survival rates. However, the capacity of impacted marine mammal populations to recover from low, postharvesting abundances has been jeopardized by the joint impact of habitat degradation and overfishing on the functioning of marine food webs and ecosystems in many coastal areas used by these species (Springer *et al.* 2003, Millenium-Ecosystem-Assessment 2005, Bulleri and Chapman 2010, Williamson *et al.* 2014)

Populations of many pinniped species declined precipitously during the 19th and 20th centuries due to overharvesting (Bonner 1982, Gerber and Hilborn 2001), including the South American sea lion (*Otaria byronia*) because many of its local populations suffered great reductions in their sizes (Crespo and Pedraza 1991, Sielfeld 1999). Since the end of commercial harvesting, South American sea lion populations in the South Atlantic Ocean have shown different responses. The population from northern Patagonia remained stable for almost 30 yr until it started to grow in 1990 (Dans *et al.* 2004). A similar trajectory was observed in the Falkland Islands (Islas Malvinas) population, where *ca.* 44,000 South American sea lions were killed between 1935 and 1962, and the local South American sea lion population has increased at a rate of ~3.8% per year between 1995 and 2003 (Thompson *et al.* 2005). In contrast, despite the end of the commercial exploitation of the South American sea lion in 1986 at Isla de Lobos, the number of pups born each year has continued to decline, reaching approximately 1,200 pups born in 2000 (Ponce de León 2000), a figure that is roughly 25% of those born in 1956 before the start of the harvest (Vaz-Ferreira *et al.* 1984). More than 47,000 pups were harvested between 1963 and 1984 at Isla de Lobos (Ponce de León 2000), and even though harvesting prior to 1963 was unknown, 400 pups were harvested from this rookery between 1985 and 1986 (Ponce de León 2000). Regardless of the observed decline in the birth rate at Isla de Lobos between 1956 and 2000, 429 juveniles (285 females, $\bar{x}$ = 20, SD = 17/yr) were further captured and sold to zoos and aquariums between 1996 and 2008 (DINARA 2008, 2010). Nevertheless, it remains unclear why the Isla de Lobos South American sea lion population has failed to recover after the end of the intense harvesting in 1986.

South American sea lions breed in two colonies separated by *ca.* 70 km along the Uruguayan coast (Fig.1): Isla de Lobos (currently the smaller rockery), where birth rates have steadily declined between 1995 and 2004, and Cabo Polonio/Valizas, where birth rates have steadily increased since 1995 (Páez 2006). Despite these contrasting trends, the overall South American sea lion population in Uruguay supposedly has declined at an average annual rate of 1.73% in 1995–2007 (Páez 2006, DINARA 2012). Genetic analyses for the southwest Atlantic have showed that the South American sea lion functions as a single population with relatively high female philopatry (Feijoo *et al.* 2011). However, at a more local level, further genetic analyses suggest that the two Uruguayan colonies are part of a single breeding population (Feijoo 2009). Assuming that South American sea lion females could potentially recruit indistinctly to either colony in Uruguay when first breeding, it is still unclear why the postharvesting birth rates have differed between Cabo Polonio and Isla de Lobos.

Here, we assess different mechanisms that could explain the contrasting trends in birth rates in two South American sea lion colonies in Uruguay. Given that females are highly dependent on local food resources (Riet-Sapriza *et al.* 2013), we hypothesize that differences in food availability to females of each colony lead to differences in mass at birth, early growth rates and early survival rates of pups. Our second hypothesis is that differences in the population structure between colonies could lead to a different early survival of pups between the two colonies. Although the South American sea lion does not have terrestrial predators, harassment by conspecifics peripheral males (adults and subadults) may lead to high pup mortality (Campagna *et al.* 1992, Drago *et al.* 2011). We tested these hypotheses using data on the feeding habits of females, birth mass, individual growth rate and first month survival of pups, and the social structures in the two sea lion breeding colonies in Uruguay. From these hypotheses, we predict (1) that differences in the female prepartum feeding habits could lead to differences in the mass at birth and individual growth rates between colonies, (2) that higher mass at birth and individual growth rates should be associated with higher pup survival rates, and (3) that higher proportion of peripheral males (adults and subadults) in smaller colonies would be associated with higher pup mortality (McMahon *et al.* 2000, Baker and Fowler 2009).

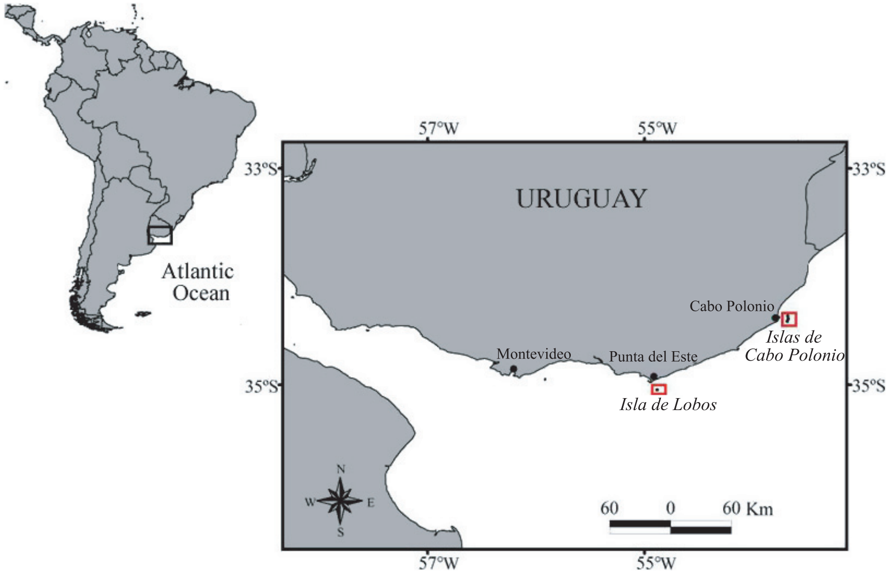

Figure 1. Breeding colonies of the South American sea lion (*Otaria byronia*) in Uruguay in Isla de Lobos and Cabo Polonio.

MATERIALS AND METHODS

Study Area

The South American sea lion rookeries on the Uruguayan continental shelf are the northernmost breeding sites of this species in the Atlantic Ocean. Isla de Lobos and Cabo Polonio (declared a Marine Protected Area by decree 337/2009), are located in the easternmost part of the Río de la Plata estuary and in the Atlantic Ocean, respectively (Fig. 1). These zones have a highly dynamic mixing regime resulting from the mixing of freshwater and the convergence of the Brazil and Falkland/Malvinas currents that generate a frontal regime of high primary productivity (Ortega and Martinez 2007). We worked in a breeding area located in the northwest part of Isla de Lobos, where *ca*. 90 pups are born each year (Trimble and Insley 2010) and in Isla Rasa, Cabo Polonio, where *ca*. 600 pups are born each summer (VF-T, unpublished data).

Data and Sample Collection

At the beginning of the 2013 breeding season (January), we captured 88 and 151 randomly chosen newborn pups with a hoop net in Isla de Lobos and Cabo Polonio, respectively. All pups were identified with Allflex tags applied to both fore flippers, their standard length and weight (±0.10 kg) were measured, and their sex was registered. Whenever possible, we obtained 5 mL blood samples (n = 20 in Isla de Lobos and n = 17 in Cabo Polonio) from the caudal digital vein. Blood samples were preserved in sterile tubes and centrifuged in the field site and blood cells were stocked at −20°C until further analyses. On the second week of January, we conducted four exhaustive counts in each colony, differentiating individuals by age class (adult males, subadult males, pups, juveniles and females). Breeding females were also counted, but their numbers were discarded because they could not be distinguished visually from juveniles of either sex. All terrestrial counts were conducted from short distances from reproductive areas using 10 × 50 binoculars. Marked pups were recaptured, weighted and further blood samples were obtained in the third week of February using the method described above, except that only serum samples were retained for further analyses. During February and March, we carried out fortnightly scan samplings (Martin and Bateson 1991) in each colony to visually recapture the marked pups. Because during the first months of their lives South American sea lion pups exclusively feed on maternal milk, their isotope values can be used to investigate the adult females' foraging ecology (Drago *et al*. 2010*b*, Franco-Trecu *et al*. 2012). Furthermore, given that serum half-life in endotherms is 3–4 d and that of blood cells is 28–30 d (Hobson and Clark 1993, Hilderbrand *et al*. 1996), the isotopic value of blood cells collected just after birth and that of the serum collected 5–6 wk later can be used as proxies of the South American sea lion female diet in the prepartum and early lactation periods, respectively. All procedures of animal manipulation were submitted and approved by the Ethics Committee in Animal Experimentation of the Universidad de la República, Uruguay as valid according to the national laws in animal welfare.

Sample Treatment: Stable Isotope Analysis

Feeding habits of the females with marked pups were studied using stable isotope (δ^{15}N and δ^{13}C) analyses based on the fact that prey-to-consumers isotopic enrichment to change in a predictable manner according to the specific dietary fractionation of marine food chains (Hobson *et al.* 1994, Post 2002, Newsome *et al.* 2007). δ^{15}N and δ^{13}C denote the trophic position (Post 2002) and the feeding sources used by predators (DeNiro and Epstein 1978, Bearhop *et al.* 2004) at different temporal scales depending on the moment of production and the turnover rate of the tissue analyzed (Dalerum and Angerbjörn 2005).

Once thawed, blood cell and serum samples were dried at 60°C and grounded to a fine powder with mortar and pestle. Lipids were extracted with a chloroform/methanol (2:1) solution (Bligh and Dyer 1959) because they are depleted in ^{13}C in comparison with other molecules, thus they could confound the results by decreasing the δ^{13}C value (DeNiro and Epstein 1978). Nevertheless, since chemical extraction of lipids may lead to unpredictable changes in δ^{15}N values due to the unintended removal of amino acids (Sotiropoulos *et al.* 2004, Ryan *et al.* 2012), we extracted them for carbon isotope analysis and used a nonextracted subsample for nitrogen determination.

Stable isotope analyses were carried out at the Scientific-Technical Services of the University of Barcelona, Spain. Stable isotope ratios are expressed in delta (δ) notation as parts per thousand (‰), and are reported and defined as: $\delta\, {}^{j}X = [({}^{j}X/{}^{i}X)_{\text{sample}}/({}^{j}X/{}^{i}X)_{\text{standard}}] - 1$, where ${}^{j}X$ is the heavier isotope (^{13}C or ^{15}N), and ${}^{i}X$ is the lighter isotope (^{12}C or ^{14}N) in the analytical sample and international measurement standard (Bond and Hobson 2012); reference standards were the Vienna Pee Dee Belemnite (VPDB) calcium carbonate for δ^{13}C and atmospheric nitrogen (air) for δ^{15}N. Secondary isotopic reference materials of known ^{13}C/^{12}C ratios, as given by the International Atomic Energy Agency (IAEA, Vienna, Austria), namely polyethylene (IAEA CH_7, $\delta^{13}C = -31.8$‰), graphite (IAEA $USGS_{24}$, $\delta^{13}C = -16.1$‰) and sucrose (IAEA CH_6, $\delta^{13}C = -10.4$‰), were used for calibration to a precision of 0.2‰. For nitrogen, secondary isotopic reference materials of known ^{15}N/^{14}N ratios, namely $(NH_4)_2SO_4$ (IAEA N_1, $\delta^{15}N = +0.4$‰ and IAEA N_2, $\delta^{15}N = +20.3$‰) and KNO_3 (IAEA NO_3, $\delta^{15}N = +4.7$‰) were used to a precision of 0.3‰.

Data Analysis

The specific growth rate (*SGR*), expressed as percentage of body weight gained or lost per day (%/d), was calculated according to the following expression: $SGR = [\ln (W_{t+d}/W_{t0})*d^{-1}] \times 100$, where W_{t0} is the initial body weight (kg) of the pup, W_{t+d} is the final body weight (kg) after d days. We compared differences in the W_{t0}, *SGR*, and blood cells and serum stable isotope values (δ^{13}C and δ^{15}N) between colonies using two way ANOVAs that included colony and sex (because the South American sea lion is a sexually dimorphic species) as categorical explanatory variables and their interaction. When possible, we simplified the initial statistical models by the stepwise removal of terms without any significant effects. We used the Akaike Information Criterion (AIC) to select the most parsimonious model from a priori set of plausible statistical models. Models with AIC > 2 in relation to the AIC of the model with lowest AIC tend to have little empirical support (Bolker 2007). We used separate analyses of covariance to evaluate whether pups' W_{t0} was related with δ^{13}C and δ^{15}N female's blood cell isotopic values and whether these relations varied depending on pup sex and colony. These analyses allowed corroborating whether a female's diet during prepartum affected her newborn pup's mass. The same procedure was used to determine whether pup's *SGR* was related with serum δ^{13}C and δ^{15}N values (as early lactation diet) and the extent to which these relationships varied depending on the pup sex and colony. Finally, we compared the population structure between colonies by comparing the proportions of adult and subadult males using the chi-squared test for multiple proportions. All statistical analyses were carried out in free software R 3.0.2 (R Development Core Team 2013).

We estimated the monthly pup survival rate for each sex and breeding colony using the standard Capture, Mark and Recapture method (Cormack-Jolly-Seber model; Williams *et al*. 2002) for the fortnightly scans that yielded a presence-absence matrix for 239 pups over three months. We performed the standard goodness of fit test of Cormak-Jolly-Seber model using the software UCARE 2.2 (Choquet *et al.* 2009) and assessed overdispersion using the bootstrap method according to Cook and White (2006). We formulated 19 *a priori* statistical models (Table 3) involving whether monthly survival and the recapture probability varied between colonies, time, and/or sexes and with none of them. Model selection based on the Akaike Information Criterion was performed as described before after correcting for overdispersion as needed. All models of monthly survival were fitted using the program MARK 6.0 (White and Burnham 1999).

RESULTS

The average δ^{13}C and δ^{15}N values in blood cells from newborn pups (Fig. 2) did not significantly differ between either colonies or sexes (models 9 and 11, Table 1). The mean ± SD values of δ^{13}C and δ^{15}N in blood cells for Cabo Polonio were −16.3 ± 0.3 and 19.9 ± 0.3, while for Isla de Lobos were −16.1 ± 0.3 and 19.9 ± 0.5, respectively (Fig. 2). The same was true for the δ^{13}C value in serum

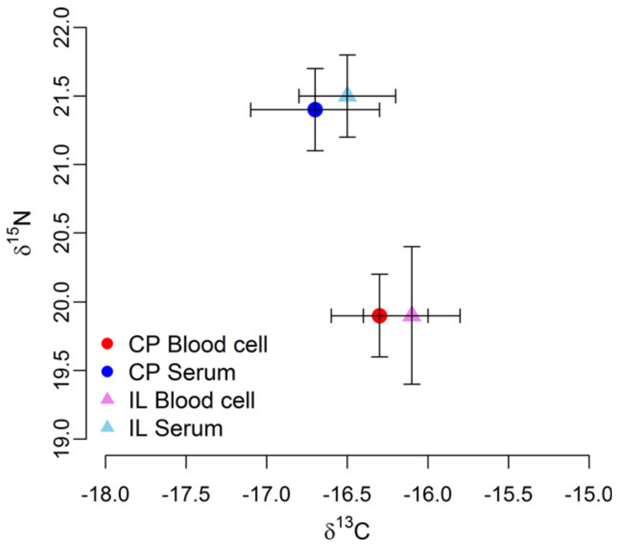

Figure 2. Biplot of the isotopic contents of δ^{13}C and δ^{15}N of blood cells (red and pink) and serum (blue and skyblue) of the South American sea lion pups (*Otaria byronia*), from Cabo Polonio (CP, circles) and Isla de Lobos (IL, triangles). Error bars correspond to standard deviations of each variable.

Table 1. Two way ANOVA for the initial mass (W_{t0}), the specific growth rate (SGR), and the isotopic value (δ^{13}C and δ^{15}N) in serum (s) and red blood cells (rc) of South American sea lion (*Otaria byronia*) pups, with sex and breeding colony as explanatory variables. The table shows the set of models formulated for each analysis that were simplified on the basis of the ΔAIC < 2. The selected models (lowest AIC) for each analysis is highlighted in gray. Reference levels are Isla de Lobos (IL) for colony and male for sex.

	Model	Intercept	Colony (IL)	Sex (male)	Colony*Sex	AIC
1	W_{t0} ~ Colony*Sex	14.30 (<<0.01)	-0.97 (0.08)	1.68 (0.002)	0.92 (0.26)	403.86
2	W_{t0} ~ Colony+Sex	14.20 (<<0.01)	-0.56 (0.17)	2.05 (<<0.01)	–	403.15
3	W_{t0} ~ Sex	13.90 (<<0.01)	–	2.10 (<<0.01)	–	403.06
4	SGR ~ Colony*Sex	0.75 (<<0.01)	0.44 (0.027)	0.28 (0.15)	-0.08 (0.75)	39.67
5	SGR ~ Colony+Sex	0.77 (<<0.01)	0.39 (<<0.01)	0.23 (0.08)	–	37.78
6	SGR ~ Colony	0.91 (<<0.01)	0.37 (<<0.01)	–	–	39.23
7	δ^{13}Crc ~ Colony*Sex	−16.40 (<<0.01)	0.21 (0.16)	0.14 (0.37)	−0.07 (0.73)	20.03
8	δ^{13}Crc ~ Colony+Sex	−16.40 (<<0.01)	0.18 (0.08)	0.10 (0.32)	–	18.16
9	δ^{13}Crc ~ Colony	−16.30 (<<0.01)	0.15 (0.12)	–	–	17.23
10	δ^{15}Nrc ~ Colony*Sex	19.90 (<<0.01)	0.03 (0.90)	−0.08 (0.71)	−0.009 (0.98)	48.84
11	δ^{15}Nrc ~ Colony+Sex	19.90 (<<0.01)	0.02 (0.88)	−0.09 (0.55)	–	46.84
12	δ^{13}Cs ~ Colony*Sex	−16.70 (<<0.01)	0.18 (0.33)	0.09 (0.60)	−0.13 (0.58)	36.53
13	δ^{13}Cs ~ Colony+Sex	−16.60 (<<0.01)	0.11 (0.39)	0.01 (0.89)	–	34.87
14	δ^{15}Ns ~ Colony*Sex	21.54 (<<0.01)	0.05 (0.7)	−0.22 (0.14)	0.02 (0.91)	20.64
15	δ^{15}Ns ~ Colony+Sex	21.53 (<<0.01)	0.07 (0.49)	−0.21 (0.04)	–	18.66
16	δ^{15}Ns ~ Sex	21.57 (<<0.01)	–	−0.22 (0.03)	–	17.19

(early lactation) (model 13, Table 1), but the δ^{15}N values were significantly higher in female pups (model 16, Table 1). The mean values of δ^{13}C and δ^{15}N serum in Cabo Polonio were −16.7 ± 0.4 and 21.4 ± 0.3, while in Isla de Lobos they were −16.5 ± 0.3 and 21.5 ± 0.3, respectively (Fig. 2). Although the birth mass of male pups (*0* ± SD: 16.0 ± 2.1) was significantly higher than female pups (13.9 ± 1.8) in both colonies, there was no significant difference between colonies (Cabo Polonio = 15.2 ± 2.07, Isla de Lobos = 14.5 ± 2.4) (model 3, Table 1). The mean ± SD pup specific growth rate was significantly higher in Isla de Lobos (1.28 ± 0.4) than in Cabo Polonio (0.91 ± 0.4), being marginally higher for male pups (model 5, Table 1, Fig. 3). None of the statistical models selected (Table 1) had significant interactions between sex and colony. Pup's initial mass was marginally related to the red blood cell δ^{13}C (prepartum), and it increased for higher values of red blood cell δ^{15}N (Table 2, Fig. 4b). In turn, pup *SGR* was not related to the serum δ^{13}C (postpartum period). However, *SGR* decreased for higher values of δ^{15}N, being significantly higher in Isla de Lobos (Table 2, Fig. 4a).

The most parsimonious model of pup monthly survival included temporal variation (months) and colony (Table 3, Fig. 5) and received 68% of the empirical support from the data. Prior to comparing these models, we had assessed the goodness of fit of the data to the saturated model and found it acceptable (P = 0.748), according

Table 2. Analyses of covariance of the initial mass (W_{t0}) and specific growth rate (*SGR*) as a function of the isotopic value of δ^{13}C and δ^{15}N in serum and red blood cells of South American sea lion pups (*Otaria byronia*), with sex and breeding colony and their interaction as categorical variables. The F-values (and its associated P-value) for each explanatory variable and interaction (columns) are shown for the entire set of statistical models for each response variable (rows). The initial statistical models and the criteria for model simplification are explained in the main text.

	δ^{13}C red blood	Colony	Sex	Colony*Sex
W_{t0}	4.12 (0.05)	1.4 (0.25)	2.95 (0.09)	1.86 (0.18)
	4.00 (0.05)	1.36 (0.25)	2.87 (0.10)	–
	3.84 (0.06)	–	1.80 (0.19)	–
	3.78 (0.06)	1.28 (0.26)	–	–
	3.76 (0.06)	–	–	–
	δ^{15}N red blood	Colony	Sex	Colony*Sex
W_{t0}	7.81 (0.01)	4.75 (0.04)	4.34 (0.05)	2.03 (0.16)
	7.56 (0.01)	4.59 (0.04)	4.20 (0.05)	–
	δ^{13}C serum	Colony	Sex	Colony*Sex
SGR	0.29 (0.59)	10.1 (0.003)	2.14 (0.15)	0.18 (0.68)
	0.31 (0.58)	10.3 (0.003)	2.20 (0.15)	–
	0.29 (0.60)	8.50 (0.006)	–	–
	δ^{15}N serum	Colony	Sex	Colony*Sex
SGR	11.8 (0.001)	15.5 (0.0004)	0.24 (0.63)	0.09 (0.77)
	12.2 (0.001)	15.9 (0.0003)	0.24 (0.63)	–
	12.3 (0.001)	15.9 (0.0003)	–	–

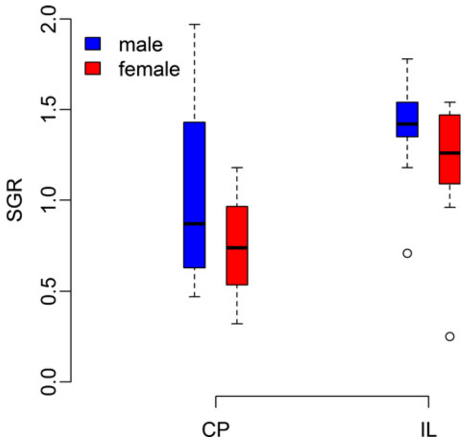

Figure 3. Boxplots for the specific growth rate (*SGR*) of pups of each sex of the South American sea lion in the breeding colonies of Cabo Polonio (CP) and Isla de Lobos (IL).

to the criteria of Choquet *et al.* (2009). In the selected model (Table 3, Fig. 5), while the first month survival rate of pups was practically the same in both colonies (Cabo Polonio: 0.82, CI = 0.58–0.99; Isla de Lobos: 0.86, CI = 0.62–0.99), there are important differences in the pup monthly survival between colonies during the second month (Cabo Polonio: 0.70, CI = 0.48–0.99; Isla de Lobos: 0.32, CI = 0.19–0.51).

Finally, the percentages of males (adults + subadults) obtained from the terrestrial counts in each colony differed significantly between colonies ($\chi^2 = 26.045$, df = 4, $P = 3.0 \times 10^{-5}$), being 17% ± 2.3% and 36% ± 5.5% in Cabo Polonio and Isla de Lobos, respectively.

DISCUSSION

We found that breeding females from the two South American sea lion colonies in Uruguay did not differ in their feeding habits and that pups grew faster and had a lower survival in March in the smallest colony that also had the highest proportion of males.

In otariids, the pup growth rate is strongly influenced by their mothers' feeding habits through the energetic quality of the resources consumed and the frequency and duration of maternal attendances on land (Trillmich and Weissing 2006, Drago *et al.* 2010*a*). Among the prey consumed by SASL, Franco-Trecu *et al.* (2012) found that pelagic species in the Uruguayan continental shelf had lower values of δ^{13}C and δ^{15}N than benthic ones. Although potential pelagic prey of South American sea lion often contain a higher energy input than benthic ones due to their higher lipid content (Drago *et al.* 2009), gathering pelagic prey typically requires longer foraging trips and higher search effort for lactating South American sea lion mothers. Therefore, the negative relation between the *SGR* and the δ^{15}N suggests that higher pup *SGR* were attained whenever pelagic prey predominated female diet (Drago *et al.* 2010*a*). However, the feeding habits of breeding South American sea lion females did not differ between colonies, thus suggesting that they fed on prey at similar trophic levels in food webs sustained by the same primary producers (Fig. 2). The latter is expected

Table 3. Models of monthly (February, March) survival and recapture (*p*) probabilities for the South American sea lion pups (*Otaria byronia*) in Uruguay, where both parameters could vary between sexes, breeding colonies (Cabo Polonio and Isla de Lobos), over time (*t*; February, March) or being constant (.) (or combinations thereof). The Akaike Information Criterion (AIC), the difference between each model AIC and the smallest AICc of all models considered (ΔAICc), the AICc weight, and the number of parameter estimated are shown for each model.

	Model	AICc	ΔAICc	AICc weights	Parameters
1	survival (colony,*t*), *p*(.)	455.99	0	0.68	5
2	survival (colony,*t*), *p*(sex,colony)	458.45	2.45	0.2	8
3	survival (colony,sex,*t*), *p*(.)	460.05	4.06	0.09	9
4	survival (sex,colony,*t*), *p*(sex,colony,*t*)	465.67	9.68	0.01	12
5	survival (sex,colony), *p*(.)	465.91	9.92	0	5
6	survival (colony), *p*(.)	465.97	9.98	0	3
7	survival (.), *p*(.)	466.81	10.82	0	2
8	survival (sex,colony), *p*(colony)	466.96	10.97	0	6
9	survival (colony), *p*(colony)	467.07	11.08	0	4
10	survival (sex,colony), *p*(sex)	467.15	11.15	0	6
11	survival (colony), *p*(sex)	467.48	11.49	0	4
12	survival (.), *p*(colony)	467.92	11.93	0	3
13	survival (colony), *p*(sex,colony)	468.1	12.11	0	6
14	survival (.), *p*(sex)	468.3	12.31	0	3
15	survival (.), *p*(sex,colony)	468.69	12.69	0	5
16	survival (sex), *p*(.)	468.73	12.74	0	3
17	survival (sex), *p*(colony)	469.86	13.86	0	4
18	survival (sex), *p*(sex)	470.04	14.04	0	4
19	survival (sex,colony), *p*(sex,colony)	470.7	14.71	0	8

since the two South American sea lion breeding colonies are separated by only 70 km, a distance well within the range of female's foraging trips (39–136 Km, Riet-Sapriza *et al.* 2013). Had differences in South American sea lion females' feeding habits affected pup success, we would have expected to find significant relationships between the δ^{13}C and δ^{15}N values in blood cell and serum and the pup's body mass at birth and *SGR*, respectively. Thus, while differences in the foraging strategies of lactating females may explain differences in the pup growth rate, they could not account for differences between colonies in Uruguay. Thus, SASL females from Isla de Lobos may have lower costs to resources than those of Cabo Polonio, which may increase their efficiency of energy transfer and lead to higher pup growth rates (Trillmich and Weissing 2006). Even though the availability of trophic resources in areas surrounding each colony could differ, such differences might not necessarily be reflected in the isotopic values of pup serum and blood cells.

Drago *et al.* (2011) found that South American sea lion pups grew faster and had a lower survival in smaller colonies in northern Patagonia, even though the diet composition of females was unrelated to local population size. That is, pups both in Uruguay and northern Patagonia grew faster but had a lower survival where females had a higher per capita resource share due to lower local abundance. In both cases, the negative correlation between individual growth and pup early survival seems unrelated to the availability of trophic resources and changes in feeding habits and its causes must lie elsewhere. Drago *et al.* (2011) also found that the survival rate of pups increased with colony size and with the ratio pups to subadult males, and attributed

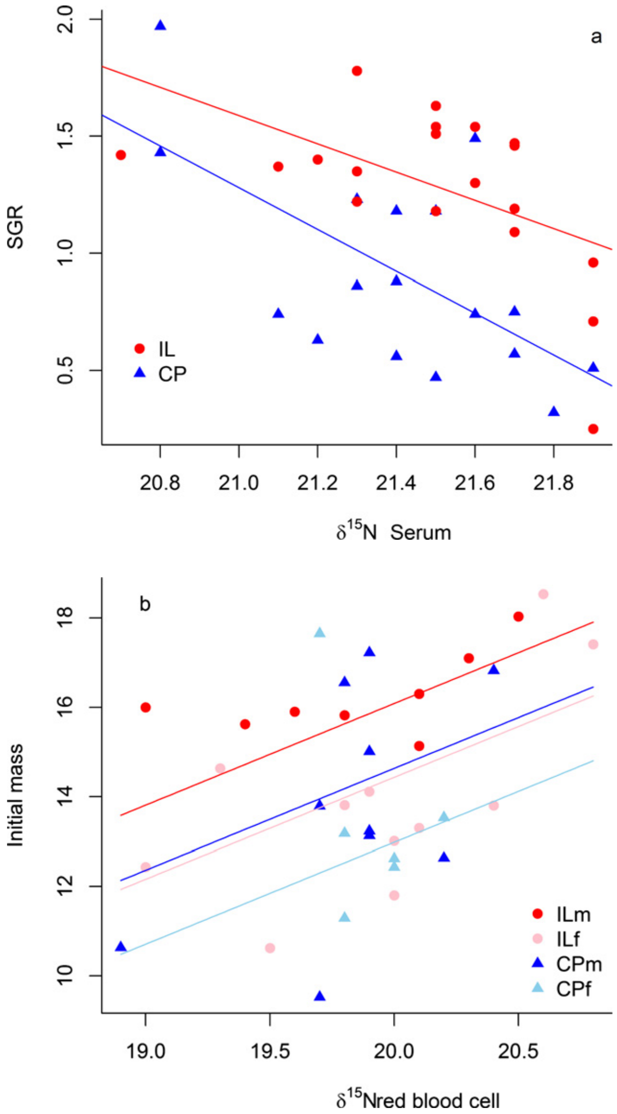

Figure 4. Relations between the (a) specific growth rate (*SGR*) and (b) the initial mass with the δ^{15}N contents in serum and blood of the South American sea lion (*Otaria byronia*) pups (m: male; f: female) born in the two breeding colonies (CP: Cabo Polonio; IL: Isla de Lobos) in Uruguay. The straight lines correspond to the best fit lines of the selected models shown in Table 1.

the finding to Allee-like effects that could help explain the kinetics of recovery of local South American sea lion populations since the end of harvesting.

The differences in pup survival rates between the Uruguayan colonies can be explained by differences in neither female dietary habits nor the initial mass of the newborn pups. The higher pup survival and lower growth rates found in the largest

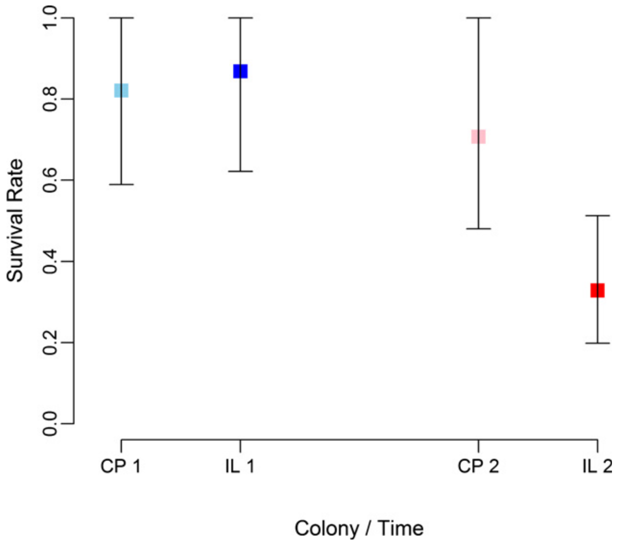

Figure 5. Monthly (February = 1 and March = 2) survival rates (and their 95% confidence interval) of South American sea lion (*Otaria byronia*) pups born in the two breeding colonies (CP: Cabo Polonio; IL: Isla de Lobos) in Uruguay.

Uruguayan colony could be explained if pups were born larger in Cabo Polonio, allowing them to withstand longer fasts between consecutive attendances of their mothers. Nevertheless, we did not find significant differences in the pup′s masses at birth between colonies. Conversely, we did find differences in the social structure between the colonies, with a higher proportion of subadult and adult males in the smaller colony. An antisocial behavior (abduction and eventual killing of pups) of peripheral South American sea lion males has been reported (adults and subadults) in both Uruguayan (Vaz-Ferreira 1965, 1976) and Argentine colonies (Campagna *et al.* 1988). Given the differences in the social structures found between colonies, the antisocial behavior could point to infanticide as a likely cause for the higher pup mortality rates found in the smaller colony. Our results are then in agreement with those found in colonies of northern Patagonia and would imply that colony size is related to both *SGR* and early South American sea lion pup survival (Drago *et al.* 2011). Although *SGR* values were almost the same as in small and large colonies in Argentina (smaller colony: 1.3% ± 0.7%/d and larger colony: 0.6% ± 0.6%/d) and Uruguay, pup survival rates reported by Drago *et al.* (2011) for Argentina were higher (0.91–0.97) than those estimated in Uruguay (lower and upper mean 0.32–0.86). However, these pup survival estimates cannot be directly compared because they were based on very different approaches (proportion of death animals in Argentina and capture-mark-recapture in Uruguay) and methods that do not jointly estimate survival and recapture probabilities generally yield biased survival rates (Williams *et al.* 2002).

The birth rate of the smallest South American sea lion colony (Isla de Lobos) in Uruguay has shown a historical decline since 1956 (Ponce de León 2000, Páez 2006). While the low birth rates until the 1980s probably resulted from the impact of pup harvesting, the recovery of the Isla de Lobos population would have been expected

30 yr after the end of harvesting. However, the Isla de Lobos colony had a lower early pup survival and a higher proportion of males than Cabo Polonio. We believe that the cumulative effects of population extractions (pup harvesting and zoo and aquaria sales) could have not only lowered the local population size, but also disrupted its social structure to the point where Allee-like effects could have become important and have hampered the postharvesting recovery of South American sea lion in the southwest Atlantic.

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DISCUSION GENERAL

La Ecología de poblaciones como disciplina, principalmente pretende comprender cómo y por qué las abundancias de las poblaciones cambian en tiempo y espacio. Esto la convierte en una disciplina principalmente descriptiva ya que los patrones observables de dinámica poblacional obtenidos a través del análisis de series temporales y de modelos, son raramente evaluables en forma experimental. Por otro lado, la Ecología del comportamiento, basada en la teoría sintética de la evolución, pretende comprender las implicancias ecológicas y evolutivas de las diferentes estrategias comportamentales desarrolladas por los individuos que eventualmente conducen a la maximización de su fitness individual. En este contexto, esta tesis pretendió generar una conexión entre ambas disciplinas. Por un lado, se aportó conocimiento detallado sobre diversos aspectos comportamentales en relación a la presencia de tácticas alimenticias y reproductivas. Por otro, se estimó la abundancia poblacional por métodos directos, la tendencia en ambas colonias reproductivas, la fertilidad, y se pretendió estimar la sobrevivencia por clase de edad (ver Anexo). El modelo de estudio fueron dos poblaciones de otáridos simpátricas que habitan islas de la costa uruguaya y que presentan tendencias poblacionales opuestas, a pesar de poseer ecologías e historias de vida similares, pero que estuvieron expuestas a diferentes niveles de explotación comercial en el pasado reciente. Por tratarse de especies longevas, con una cría por año, es necesario tener una larga serie temporal, tanto de datos comportamentales como de abundancia y parámetros demográficos, para poder acoplar estos resultados y establecer los mecanismos que determinan los patrones observados. Esta tesis pretende constituir una punto de partida en la exploración de esta conexión, evidenciando la diversidad de tácticas comportamentales que se desarrollan en estas poblaciones, iniciando además una serie temporal sobre datos de abundancias y parámetros poblacionales.

La obtención de recursos alimenticios afecta el fitness individual a través de su impacto directo sobre las tasas demográficas (supervivencia y fertilidad) que determinan la dinámica poblacional (Krebs and Davies 1991). En este contexto, estudiar la ecología trófica por medio de diferentes aproximaciones o herramientas, ayuda a comprender cómo cambios en el hábitat se pueden reflejar de una u otra manera en la dinámica de las poblaciones. Sin embargo, los valores resultantes de las tasas demográficas pueden ser afectados por una diversidad de factores además de las fluctuaciones ambientales o del impacto en la abundancia de los recursos. Por ejemplo, las variaciones en la proporción sexual operacional, cambios en el sistema de apareamiento (grado de poliginia), alteraciones en la sincronía reproductiva de las hembras y las interacciones competitivas para la obtención de parejas, también afectan los parámetros reproductivos y finalmente la dinámica de una población local (Bessa-Gomes et al. 2004; Lee et al. 2011). En este contexto, se hizo especial hincapié, por un lado en el estudio de los hábitos alimenticios del lobo fino y león marino por medio del análisis de fecas y de isótopos estables, así como por medio de los perfiles de buceo y telemetría. Por otro lado, en relación a la biología reproductiva, se estudió la varianza en el éxito reproductivo (paternidad) de los machos de ambas especies, característica esencial para definir el sistema de apareamiento, además del grado de sincronía reproductiva de las hembras y la diversidad de tácticas desarrolladas por los machos para maximizar su éxito.

Ecología Trófica

Algunos años atrás, comenzó un auge en el desarrollo de los modelos de mezcla (*Mixing models*) (Moore and Semmens 2008; Parnell et al. 2010; Phillips and Gregg 2003; Phillips 2012) para estimar la composición de la dieta por medio de los valores isotópicos de las presas, del depredador y el factor de discriminación del tejido empleado en el análisis. En este marco, se ha remarcado la importancia del uso de técnicas complementarias para obtener información más precisa que la aportada por los modelos de mezcla originales (Ward et al. 2011; Yeakel et al. 2011). En esta tesis, se trabajó en esta dirección, complementando los métodos tradicionales (análisis de fecas) con la técnica de isótopos estables para estimar la composición de la dieta. Al incorporar información previa (obtenida por medio de las fecas) a los modelos de mezcla (Parnell et al. 2010), se encontraron diferentes efectos que la ecología de las especies pueden tener a la hora de interpretar los resultados, y deben ser tenidos en cuenta.

En relación a los hábitos alimenticios, a nivel poblacional, las hembras del lobo fino presentaron una dieta compuesta por varias especies presa, aunque una importante proporción de la misma fue ocupada por unas pocas especies de presas con hábitos pelágicos. La dieta del león marino fue más diversa que la del lobo fino ya que la importancia de las especies presas consumidas fue más equitativa, sin presas dominantes. A pesar de ello, la amplitud del área de nicho isotópico del lobo fino fue mucho mayor que la del león marino. Probablemente esto último se deba a que todos los individuos del lobo fino presentan dietas similares (alto solapamiento en el espacio isotópico entre individuos), consumiendo en altas proporciones pocas especies presas, pero muchas en bajas cantidades, comportamiento que se refleja en el nicho isotópico a nivel poblacional e individual. Este resultado es respaldado por la gran extensión de las áreas de alimentación que poseen los individuos de lobo fino. Dichas áreas presentan amplia variación relacionada con la latitud (abarcando entre 5 y 6 grados) y la diversidad de ambientes (evidenciados en los patrones de buceo) que se reflejan en la firma del $\delta^{13}C$, además de la variación relacionada con el nivel trófico de las presas que se refleja en los valores de $\delta^{15}N$. Esto se basa en el hecho de que comparaciones entre presas costero - bentónicas vs pelágicas en el ambiente uruguayo han mostrado que tanto los valores del $\delta^{13}C$ como los del $\delta^{15}N$ disminuyen a medida que nos alejamos de la costa (Franco-Trecu et al. 2012). Por otro lado, la menor área de nicho isotópico del león marino estaría reflejando la baja diversidad de ambientes utilizados, ya que las hembras lactantes típicamente se alimentan en áreas restringidas, cercanas a la colonia reproductiva, realizando principalmente buceos bentónicos a 20m. A pesar de que el león marino tiene una mayor diversidad de especies presa que el lobo fino en su dieta, esto no se refleja en la amplitud de nicho isotópico a nivel poblacional, en comparación con la amplitud que presenta el lobo fino. Probablemente sea debido a que casi todas las especies presa del león marino presentan un nivel trófico similar y una variación en $\delta^{13}C$ muy acotada (ver Fig. 2 en Franco-Trecu et al. 2013). Sin embargo, cuando se estudiaron las firmas isotópicas en un tejido que integra una ventana temporal de varios años, incluso incluyendo machos adultos, se reportó un mayor nivel de especialización individual a largo plazo en el león marino, lo que podría asociarse a un uso diferencial de las especies presa por parte de los individuos, y/o al uso de áreas exclusivas, tal y como se observó en las trayectorias individuales de las hembras de león marino por medio del seguimiento satelital (Fig. 4 en Riet-Sapriza et al. 2013). Este es un resultado interesante, considerando que si bien la especialización trófica a nivel individual ha sido reportada en muchas especies de vertebrados (Bolnick et al. 2011; Bolnick et al. 2007; Bolnick et al. 2003), generalmente ha sido documentada sólo para cortos periodos de tiempo (Woo et al. 2008).

Respecto a la segregación sexual, aquí se reporta evidencia de segregación en relación al origen de la productividad primara ($\delta^{13}C$) y al nivel trófico explotado ($\delta^{15}N$) entre ambos sexos. Estos resultados eran de esperar dado que en especies dimórficas la segregación sexual ha sido ampliamente documentada (Forero et al. 2002; Beck et al. 2007; Cherel et al. 2007; Kernaléguen et al. 2012). Sin embargo, es interesante comprender cuáles podrían ser los mecanismos que expliquen estas diferencias entre sexos. Al tener un mayor tamaño corporal, los machos poseen la capacidad de realizar buceos más largos y más profundos debido a su mayor capacidad aeróbica (Kooyman 2009). Además, existen aspectos comportamentales relacionadas al cuidado de la progenie que también influyen el comportamiento trófico. Los machos al no estar involucrados en el cuidado de las crías, no poseen limitantes en cuanto a las distancias que pueden alejarse de las colonias de cría, pudiendo realizar viajes a zonas más distantes (Campagna et al. 2001). Haciendo uso de estas capacidades, los machos explotan zonas de forrajeo más amplias que las hembras (Bearhop et al. 2004) obteniendo beneficios relacionados con la exclusividad en el uso de ciertas áreas, disminuyendo la posible competencia intra-específica (Drago et al. 2015).

El comportamiento trófico puede ser influenciado por conductores internos de los individuos, como la edad o el tamaño corporal, así como por controladores externos, como variaciones ambientales o la presencia de otras especies en el sistema (Forchhammer et al. 2001; Morales et al. 2010; Stephens et al. 2007; Tiedemann et al. 2014). En los mamíferos, la gestación y lactancia tienen importantes consecuencias en el estado fisiológico de las hembras imponiendo elevadas demandas energéticas (Martin et al. 2013; Nathan et al. 2008), donde la calidad y cantidad de recursos utilizados puede determinar el éxito individual (Bardsen et al. 2008; Speakman 2008; Thompson et al. 2012). Aquí se reporta evidencia sobre cómo el estatus reproductivo de las hembras del lobo fino y su condición corporal influyeron sobre su comportamiento trófico, acotando las distancias recorridas en los viajes de alimentación y la superficie de las áreas utilizadas. Las hembras que tuvieron mayor peso utilizaron *home range* más amplios durante el primer viaje de alimentación, pudiendo explotar mayor diversidad de ambientes y presas. Sin embargo, se encontró una correlación negativa entre el área del *home range* durante el primer y segundo viaje efectuados luego del nacimiento de la cría. Las hembras que tuvieron mayores áreas durante el primer viaje, estuvieron ausentes de la colonia por un mayor período de tiempo, lo que condujo a un incremento de la mortalidad de sus crías como costo asociado. Además el comportamiento de buceo también fue diferente entre estos dos viajes, con mayor cantidad de buceos durante el día y perfiles más bentónicos durante el primer viaje. Estas modificaciones en el comportamiento alimenticio, no solo reflejan características del áreas de alimentación que están utilizando, sino que también probablemente determinan el tipo de recursos consumidos, su aporte energético y la calidad de la leche producida (Beauplet et al. 2005; Beauplet and Guinet 2007; Beauplet et al. 2003). Estos hallazgos representan evidencia empírica sobre cómo los controladores internos influyen en el comportamiento de forrajeo individual y su éxito reproductivo.

Mientras las hembras de lobo fino realizan viajes de hasta 15 días y sus cachorros soportaron estos períodos de ayuno (Franco-Trecu 2010), las hembras de león marino únicamente realizan viajes de alimentación de corta duración. ¿Por qué el león marino no amplia su área de alimentación? A nivel general, entre los factores internos que afectan el comportamiento se destacan el estatus reproductivo, el tamaño corporal o condición física así como la evitación del infanticidio (Martin et al. 2013). El infanticidio ha sido ampliamente reportado (Campagna et al. 1988; Drago et al. 2011) en poblaciones de león marino del Atlántico Sur, teniendo incluso un efecto particularmente importante en las colonias de baja densidad (Drago et al. 2011, ver capítulo 4). La combinación de estos dos factores internos (baja tolerancia al ayuno y evitación del infanticidio de las crías) podría limitar las hembras de león marino a realizar viajes de alimentación cortos, con frecuentes retornos a la colonia, generando así áreas de alimentación en las cercanías de la colonia reproductiva. De la misma manera que factores internos (estatus reproductivo y tamaño corporal) afectaron las áreas de alimentación utilizadas durante el primer viaje por las hembras de lobo fino, en el león marino (donde variables morfológicas no tuvieron efecto) factores externos como el infanticidio durante el período reproductivo parecería tener un rol importante en los hábitos alimenticios de sus madres.

Se observó una segregación trófica entre ambas especies de pinnipedos en aguas uruguayas que se refleja por medio de la diversidad de metodologías y técnicas utilizadas. Estos resultados, sin embargo no pueden descartar la posibilidad de que exista algún grado de competencia entre ellas, ya que por ejemplo podrían estar explotando las mismas especies presas, pero de diferentes tamaños (reflejado por medio del $\delta^{15}N$) o en diferentes áreas (reflejado por medio del $\delta^{13}C$). Otra opción es que las dos especies dependan de una misma especie presa basal, una de ellas de forma directa y la otra indirecta.

Ecología Reproductiva

Si bien las tácticas reproductivas desarrolladas por los machos se clasifican en función del fitness obtenido (Taborsky et al. 2008), aquí se reportó que la táctica reproductiva caracterizada como “dominante” en el lobo fino presentó una amplia heterogeneidad en el éxito reproductivo individual alcanzado (paternidad). De hecho, la táctica comportamentalmente dominante (machos territoriales) se dividió en tres categorías de acuerdo al éxito reproductivo alcanzado, donde una de estas categorías tuvo incluso menor éxito que la táctica alternativa (machos satelitales, cuarta categoría). Las características que determinaron la pertenencia de estas 4 categorías se relacionaron, además de con la táctica adoptada (territorial o periférico), con otros aspectos comportamentales como la frecuencia de interacción con otros machos, con hembras, el periodo de permanencia y la duración del mismo. De esta forma estos resultados indican que por más que los individuos desarrollen comportamientos generales (ej. ubicación en la colonia) que los definen dentro de la táctica dominante, otros comportamientos a menor escala pueden determinar el éxito reproductivo alcanzado por los machos. Estos hallazgos cuestionan la forma de definir las tácticas reproductivas y hacen evidente la necesidad de incrementar las investigaciones que utilizan la combinación de herramientas moleculares junto a detalladas observaciones comportamentales.

La coexistencia de dos sistemas de apareamiento en una misma población ha sido reportada en pocas especies de ungulados (Alvarez et al. 1990; Thirgood et al. 1999), por lo que otro hallazgo interesante de esta tesis refiere al primer registro de dicha coexistencia dentro de los pinnípedos, aquí reportada para el león marino. Los dos tipo de poliginia reportados (defensa de hembras y de recursos) difirieron en el éxito alcanzado por lo que podrían ser asimilados a diferentes táctica de comportamiento reproductivo (Isvaran 2005; Taborsky et al. 2008). Por un lado, un grupo de machos realizó una poliginia de defensa de hembras en territorios flotantes que cambian de posición en el tiempo (Alcock et al. 1978; Barrows 1983; Wilson 1975), con el mayor éxito reproductivo representaría a la táctica dominante. Por otro lado, otros machos establecieron un sistema de defensa de recursos y de hembras, defendiendo territorios fijos (en un mismo lugar durante la residencia) (Dewsbury 1978), siendo la táctica subordinada, con menor éxito reproductivo. Se concluyó que factores fisiológicos (ej. estrés térmico) y demográficos sumados a la topografía y el tipo de sustrato del sitio de reproducción son claves para determinar el sistema de apareamiento, al menos, en poblaciones de otáridos (Arnold and Duvall 1994; Carranza 2000; Davies 1991).

Ecología de Poblaciones

En esta tesis se reportan por primera vez las abundancias poblacionales de las dos especies de otáridos que habitan en Uruguay, estimadas por medio de métodos directos y comparables con los utilizados a lo largo de su distribución geográfica. Esta información es relevante ya que ambas especies representan un valioso recurso natural desde el punto de vista ecológico - ecosistémico, así como turístico y escénico. Además se muestra evidencia que sugiere que la extracción de individuos conllevó a la desestructuración social en la colonia de Isla de Lobos del león marino, hasta el punto donde la acción de un efecto tipo Allee podría obstaculizar la recuperación poblacional de esta especie en Uruguay, por medio de la disminución en la sobrevivencia de las crías causada por comportamientos antisociales de los machos. Estos resultados ayudan a comprender las diferentes tendencias poblacionales que se encontraron entre ambas colonias para el león marino.

Se plantea que las tendencias poblacionales contrastantes de estas dos especies simpátricas probablemente sean el resultado de la sinergia de conductores individuales internos (ej. condición corporal, evitación del infanticidio) y de limitaciones o impactos externos (ej. efectos antropogénicos, batimetría) que afectan diferencialmente el comportamiento de forrajeo individual en ambas poblaciones e indirectamente sus tasas demográficas. En el caso del lobo fino, aunque su explotación en Uruguay se realizó después de la colonización española desde el 1500, se conoce el número de individuos cosechados solo para diversos períodos entre 1873 y 1991 cuando se sacrificaron más de 800 mil ejemplares en un total de 104 años. A pesar de ello, a dos décadas del cese de la explotación comercial, la población de lobo fino muestra signos de recuperación con una tendencia positiva, al menos en la principal colonia reproductiva del Atlántico (Isla de Lobos) sin aparentes problemas de conservación. Esto probablemente se relacione con que una importante cantidad de los individuos extraídos fueron machos (Ponce de León 2000), teniendo un bajo impacto en la población por tratarse de una especie poligínica. Además, el lobo fino explota principalmente recursos pelágicos, ricos energéticamente (Drago et al. 2010; Eder and Lewis 2005), en un ambiente menos afectado por actividades antrópicas como las pesquerías y la contaminación. La gran amplitud de nicho isotópico, la diversidad de áreas de alimentación utilizadas y de patrones de buceo que presentan los individuos de esta especie indican, que éstos tienen el potencial de explotar una amplia diversidad de recursos y ambientes, siendo por tanto flexibles a cambios en la abundancia de sus presas. En relación a la abundancia estimada, los resultados aquí reportados (~70mil) presentan diferencias importantes con los previamente estimados por medio de simulaciones y extrapolaciones (~300mil, Páez 2000). Si bien la abundancia estimada del lobo fino en Uruguay aquí presentada no incluye los individuos juveniles, las diferencias ambos estimados probablemente se deban a los diferentes métodos utilizados. Sin embargo, la tasa de incremento poblacional del lobo fino aquí estimada coincide con la reportada previamente por Lima y Páez (1997) y por Páez (2006).

En relación al león marino, la población uruguaya presenta una tendencia negativa, probablemente debida, como se planteó anteriormente, a la sinergia de diversos factores. Por un lado, la actual degradación del ambiente costero, área en donde se concentra la zona de alimentación de esta especie, relacionada a la contaminación (Bulleri and Chapman 2010; Clausen and York 2008; Davenport and Davenport 2006) y al impacto creciente de las pesquerías (Alleway et al. 2014; Milessi et al. 2005; Pauly et al. 1998), probablemente afecte la disponibilidad y calidad de los recursos tróficos disponibles para los individuos de esta especie. Además, otros factores internos como la evitación del infanticidio o la baja tolerancia al ayuno de las crías del león marino, limitarían las áreas de alimentación que las hembras pueden usar o el tiempo que éstas pueden estar ausentes. De esta manera las hembras de león marino se verían obligadas a utilizar únicamente recursos bentónicos, con bajo aporte energético, en una zona costera donde además ocurre la interacción negativa con pesquerías, ya sea indirecta por competencia de recursos o directa por captura incidental (Franco-Trecu et al. 2009; Riet Sapriza et al. 2013; Szteren and Páez 2002). Por otro lado, la explotación comercial de león marino efectuada en el pasado reciente en la Isla de Lobos implicó la cosecha de un total de ~47mil cachorros menores a un año de edad durante al menos 15 años (Ponce de León 2000). Una vez que la principal explotación comercial cesó en 1978, la abundancia de las crías de león marino continuó disminuyendo, hecho que fue documentado tanto en 1984 (Vaz-Ferreira et al. 1984) como en el 2000 (Ponce de León 2000). Esta disminución estaría reflejando el bajo número de hembras reproductivas en la Isla de Lobos. A pesar de ello, el Estado uruguayo extrajo 144 machos y 285 hembras juveniles de esta especie entre 1996 y 2008 para comercializar en pie a zoológicos y acuarios de diversas partes del mundo (DINARA 2010). Si bien esta última extracción fue de menor magnitud que la realizada entre años de 1960 y 1970, es probable que ambas, en conjunto, hayan generado la desestructuración social de población de león marino en Isla de Lobos. Este hecho se refleja en la mayor proporción de machos por cría en comparación con las colonias reproductivas de Cabo Polonio (1.44 vs. 0.51 respectivamente). Este cambio de la estructura social probablemente haya colaborado con la ausencia de recuperación poblacional en Isla de Lobos luego del fin de la cosecha comercial, ya que un efecto tipo Allee (del infanticidio realizado por los machos satélites) habría incrementado la mortalidad de las crías. Resultados similares se han reportado para colonias de Patagonia Norte, donde el proceso de expansión del león marino ha generado nuevas áreas de cría con estructuras sociales diferentes a las encontradas en las colonias tradicionales (Drago et al. 2011; Grandi et al. 2008; Grandi et al. 2014). Finalmente, el león marino en Uruguay, al igual que su área de distribución, constituye el centro de un conflicto con las pesquerías artesanales costeras (Szteren and Páez 2002). Si bien esta problemática está siendo recientemente abordada de forma participativa, los pescadores reclaman soluciones a las autoridades encargadas de la gestión del recurso (Trimble and Berkes 2013; Trimble and Lazaro 2014). En este contexto conocer la abundancia, los valores de los parámetros demográficos, las características de sus hábitos alimenticios así como los mecanismos que pueden estar implicados en la dinámica de su población, son sumamente relevantes para llevar adelante un correcto manejo del recurso, y descontinuar el mal manejo realizado hasta el momento, principal responsable de la disminución poblacional que enfrenta esta especie en Uruguay.

Si bien uno de los objetivos de esta tesis era estimar los parámetros poblacionales, generar un modelo demográfico matricial y modelar la dinámica futura de ambas poblaciones, esto no fue posible debido a limitaciones relacionadas con la biología de las especies (ver Anexo). Sin embargo, se pretendió aportar en esa línea estimando la fertilidad, las abundancias poblacionales actuales por clase de edad, las tendencias poblacionales y los posibles mecanismos que podrían explicarla. Generalmente los modelos demográficos son los más utilizados en el manejo de poblaciones y hábitats, donde raramente se tiene en cuenta la existencia de diferentes tácticas inter-individuales en la contribución final al fitness. A pesar de que en algunos casos se conoce el efecto de cambios ambientales en el comportamiento de los individuos (ej. rendimiento de forrajeo, comportamiento territorial, uso de hábitat y las consecuencias resultantes de fitness), muy pocos estudios han incorporado dichas relaciones en los modelos de dinámica poblacional debido en parte a la gran cantidad de información a nivel individual necesaria para formular y resolver los modelos basados en individuos (Sergio 2003; Sutherland 1996). Por este motivo, considero que los aportes realizados en esta tesis pretenden fundar parte importante de la base de datos necesaria para poder modelar la dinámica de las poblaciones de estas especies de pinnípedos teniendo en cuenta la diversidad de tácticas comportamentales en relación a la ecología trófica y reproductiva y los efectos de estás ultimas sobre el fitness individual.

Hipótesis sometidas a prueba

La hipótesis propuesta en el **Capítulo 1** fue apoyada en términos generales. Los diversos métodos empleados indicaron que los leones marinos utilizaron áreas costeras, presas demersales, realizando buceo bentónicos. El lobo fino, por otro lado, si bien utilizó principalmente áreas alejadas de la costa, realizando un comportamiento de buceo pelágico, mostró variación entre viajes de alimentación. Durante el primer viaje de alimentación utilizó áreas más costeras realizando tanto buceo bentónicos como pelágicos durante el día y la noche. Si bien esta diferenciación ocurre solamente por un período de tiempo muy acotado (pocos días al año), es importante tenerlo en cuenta. Además a partir de estos resultados surge una nueva hipótesis donde se propone que el estatus reproductivo y la condición corporal de las hembras (la presencia de la cría y su biomasa) estaría determinando la capacidad de alejarse de la colonia de cría en el lobo fino, mientras en el león marino estas condicionantes estarían relacionadas con la capacidad de ayuno de sus crías y la batimetría de la zona.

La hipótesis puesta a prueba en el **Capítulo 2** fue apoyada en relación al nivel inter-específico ya que se encontró que el león marino (población con tasa decreciente) presentó un mayor grado de especialización individual. Sin embargo, a nivel intra-específico se reportaron diferencias entre sexos únicamente para los valores del $\delta^{13}C$, con valores de $\delta^{15}N$ similares entre hembras y machos. Debido al dimorfismo sexual que presentan estas especies, era de esperar que los machos consumieran presas de mayor nivel trófico. Por otro lado, en el león marino el área de nicho isotópico fue mayor en las hembras que en los machos, este resultado no era el esperado, ya que los machos al no realizar cuidado parental tienen mayor independencia para explotar mayor diversidad de ambientes y presas, ampliando de esta forma la diversidad de valores isotópicos y su área de nicho.

En el **Capítulo 3**, la hipótesis proponía una mayor varianza en el éxito reproductivo de los machos del lobo fino tal como fue encontrado, y esto se relacionó con que el sistema de apareamiento de esta especie fue reclasificado, con un sistema de lek. En los sistemas de lek, a diferencia de los sistemas de defensa de hembras y de defensa de recursos (reportados para el león marino), las hembras seleccionan el macho con que copular, de manera que no existen limitaciones relacionadas a la capacidad de monopolización de recursos por parte del macho. La descripción de los sistemas de apareamiento de ambas poblaciones coincide con lo esperado, donde una mayor heterogeneidad en el acceso a las cópulas de los machos del lobo fino, generó una mayor varianza en el éxito reproductivo. Por otro lado, en ambas especies se reportaron tácticas reproductivas alternativas dado los diferentes éxitos que alcanzaron. Sin embargo sería interesante poner a prueba, si estas tácticas individuales se mantienen a largo plazo o si dependen de ciertas condiciones (ej. orden de llegada, tamaño corporal, edad, éxito del año anterior, etc.), ya que en el lobo fino, dentro de la táctica dominante, se reportaron categorías con diferentes éxitos reproductivos, que podrían implicar que la táctica subordina sea más redituable en ciertas ocasiones.

La primer hipótesis planteada en el **Capítulo 4** fue rechazada ya que la tendencia poblacional de la colonia reproductiva de Cabo Polonio fue estable y no compensó la disminución en el número de crías en la colonia de Isla de Lobos, determinando una tendencia poblacional total negativa. La segunda hipótesis fue parcialmente rechazada ya que no aunque no hubo diferencias en la masa al nacer entre colonias, e incluso la tasa de crecimiento fue mayor en Isla de Lobos, la supervivencia fue mayor en Cabo Polonio, colonia que presenta la tendencia poblacional estable. Sin embargo, contrario a lo planteado estas diferencias no se relacionaron con los hábitos alimenticios de las hembras, que no fueron diferentes, sino con distintas estructuras sociales entre colonias. Planteamos como hipótesis para explicar estas diferencias en la sobrevivencia de los cachorros que el infanticidio sería el principal responsable. Además planteamos que la desestructuración social (bajo número de hembras en Isla de Lobos, que determina una relación de crías/ macho mayor) es producto de la extracción comercial realizada en esta colonia. Sería interesante modelar el efecto de las extracciones pasadas en las dinámicas y abundancias poblacionales actuales.

Perspectivas y/o proposiciones

Se plantea que sería importante:

- continuar con los monitoreos de abundancia de ambas especies por medio de censos aéreos en ambas colonias reproductivas
- continuar con la veda de extracción de individuos de león marino, al menos en Isla de Lobos, y monitorear variaciones en la estructura poblacional de ambas colonias en relación a la tasa de sobrevivencia de las crías
- mejorar los modelos poblacionales de captura-marcaje y recaptura, incrementando las recapturas visuales de individuos previamente marcados y continuando con el marcaje de crías de ambas especies en cada año
- evaluar relaciones entre el fitness de las hembras y las tácticas alimenticias desarrolladas
- evaluar a largo plazo las tácticas reproductivas a nivel individual de los machos de ambas especies y sus implicancias sobre el fitness individual
- formular modelos basados en individuos para comprender las causas proximales que expliquen las variaciones en las tasas demográficas de cada una de las dos poblaciones estudiadas.

Anexo

Uno de los objetivos específicos del capítulo 4, pretendía "*Estimar la sobrevivencia por clase de edad para ambas especies en Isla de Lobos y modelar la dinámica poblacional*". En relación al mismo me interesa recalcar que se hicieron todos los intentos posibles para cumplirlo. A continuación se detallan los modelos ajustados y los problemas encontrados en relación a los resultados.

Para estimar la sobrevivencia anual en cada clase de edad y sexo se utilizaron los procedimientos estándares de captura-marcaje-recaptura (Williams et al., 2002). Inicialmente se ajustaron modelos Cormack-Jolly-Seber (CJS) en el programa Mark 6.0 (White and Burnham, 1999) a partir de una matriz de marcaje y recaptura incorporando, para el lobo fino, información de 796 crías marcadas en el año de su nacimiento entre 2006 y 2012, con recapturas visuales hasta el año 2013 (8 años, 7 transiciones interanuales), repartidas en dos grupos según el sexo. Para el león marino se utilizaron registros de 385 crías entre 2006 y 2013 (9 años). Se evaluaron diferentes modelos incorporando el efecto del sexo y la edad en la sobrevivencia y del sexo en la probabilidad de recaptura (Tabla 1 y 2).

Tabla 1. Modelos de sobrevivencia (phi) y probabilidad de recaptura (p) ajustados para las crías de lobo fino (*A. australis*) en Uruguay. La sobrevivencia varió entre sexos, edades, o fue constante (.) o combinaciones de estos casos. La probabilidad de recaptura fue constante o varió entre sexos. Para cada modelo se muestra el valor de AICc (criterio de información Akaike), ΔAICc representa la diferencia entre el AIC de cada modelo y el menor AIC de todos los modelos considerados, AICc W es el peso de Akaike de cada modelo. Se muestra además el número de parámetros estimado y la devianza para cada modelo.

Modelo	AICc	ΔAICc	AICc W	Nº Par	Deviance
{phi(sex 2ed),p(.)}	721.04	0.00	0.33	5	132.61
{phi(m(.), f(2ed)),p(.)}	721.40	0.37	0.28	4	135.00
{phi(sex 2ed),p(sex)}	722.40	1.36	0.17	6	131.94
{phi(f(.) m(2ed)),p(.)}	722.86	1.82	0.13	4	136.45
{phi(.),p(.)}	725.31	4.28	0.04	2	142.94
{phi(sex),p(.)}	726.50	5.46	0.02	3	142.11
{phi(2ed),p(sex)}	726.63	5.59	0.02	4	140.22

Los estimados de sobrevivencia adulta y juvenil de ninguno de estos modelos estadísticos fue consistente con los valores esperados y reportados para especies longevas como el lobo fino y el león marino. En un segundo set de modelos, se sumaron

109 hembras marcadas de lobo fino de edad desconocida y también se incorporó un tercer grupo (hembras adultas) a la matriz general de datos. Dado que el marcaje de hembras en Isla de Lobos se inició en 2004, la nueva matriz incorporó (9 años). En este caso se generaron modelos (Tabla 3) donde la sobrevivencia incorporó el efecto del sexo y de 3 clases de edades. La tercer clase de edad las hembras (>4 años) marcadas en el año de su nacimiento, fueron consideradas adultas y se agruparon con el grupo de hembras marcadas en edad desconocida.

Tabla 2. Modelos de sobrevivencia (phi) y probabilidad de recaptura (p) ajustados para las crías del león marino (*O. flavescens*) en Uruguay. La sobrevivencia varió entre sexos, edades, o fue constante (.) o combinaciones de estos casos. La probabilidad de recaptura fue constante o varió entre sexos. Para cada modelo se muestra el valor de AICc (criterio de información Akaike), ΔAICc representa la diferencia entre el AIC de cada modelo y el menor AIC de todos los modelos considerados, AICc W es el peso del AIC en cada modelo. Se muestra además el número de parámetros estimado y la devianza para cada modelo.

Model	AICc	ΔQAICc	AICc W	Nº Par	Deviance
{phi(edad3) p(.)}	437.7	0.0	0.6	4	111.4
{phi(edad) p(.)}	441.4	3.7	0.1	8	106.6
{phi(edad3,sex) p(.)}	441.9	4.2	0.1	7	109.3
{phi(.) p(.)}	443.0	5.2	0.0	2	120.7
{phi(edad2) p(.)}	443.0	5.3	0.0	3	118.7
{phi(año1,edad3) p(.)}	443.5	5.8	0.0	9	106.7
{phi(sex) p(.)}	445.0	7.3	0.0	3	120.7
{phi(año1,edad3,sex) p(.)}	445.2	7.5	0.0	17	90.7
{phi(sex) p(sex)}	445.7	8.0	0.0	4	119.3
{phi(edad2*sex) p(.)}	446.5	8.8	0.0	5	118.1
{phi(edad,sex) p(.)}	448.8	11.1	0.0	13	103.2
{phi(cohorte) p(.)}	448.9	11.2	0.0	7	116.3
{phi(t) p(.)}	452.0	14.3	0.0	8	117.2
{phi(cohorte,sex) p(.)}	452.3	14.6	0.0	13	106.8
{phi(sex,t) p(.)}	456.3	18.6	0.0	15	106.3
{phi(t) p(t)}	456.5	18.7	0.0	13	110.9

Nuevamente, los estimados de sobrevivencia fueron inconsistentes y mucho menores de los valores esperados para una especie longeva. Finalmente, se ajustó un tercer set de modelos multiestado (Williams et al. 2002) para tratar de incorporar información adicional para mejorar los estimados insatisfactorios previamente obtenidos. Este último set de modelos incorporó información conocida sobre individuos muertos, considerando 4 categorías: crías, juveniles, adultos y muertos (ver Fig. 1). A ciertas transiciones se les seleccionó una probabilidad de ocurrencia de cero, ya que eran imposibles de ocurrir como es el caso de pasar de juvenil a cría o salir del estado absorbente "Muerto". También se estableció que ciertas probabilidades deberían sumar 1, como por ejemplo la sobrevivencia adulta + la transición de "Adulto" a "Muerto". Los modelos ajustados estimaron las probabilidades de transición entre estados que posteriormente fueron utilizadas para estimar la sobrevivencia de cada clase de edad. Para el caso del lobo fino se utilizó la matriz de 905 individuos (crías y hembras adultas), mientras para el león marino se utilizó la matriz 385 crías.

Tabla 3. Modelos de sobrevivencia (phi) y probabilidad de recaptura (p) para crías y hembras adultas de lobo fino (*A. australis*) en Uruguay. Los parámetros variaron entre sexos, edades, o fueron constante (.) o combinaciones de estos casos. Para cada modelo se muestra el valor de AICc (criterio de información Akaike), ΔAICc representa la la diferencia entre el AIC de cada modelo y el más pequeño de todos los modelos considerados, AICc W es el peso del AIC en cada modelo. Se muestra además el número de parámetros estimado y la devianza para cada modelo.

Model	**AICc**	**ΔAICc**	**AICc W**	**Nº Par**	**Deviance**
{phi(male(.) fem 3ed),p(cat)}	1493.4	0.0	0.8	7	445.6
{phi(sex 3ed),p(cat)}	1497.4	4.0	0.1	9	445.6
{phi(sex 3ed),p(cr vs ad)}	1498.9	5.5	0.1	8	449.1
{phi(3ed),p(cr vs ad)}	1504.2	10.8	0.0	5	460.5
{phi(3ed, sex juv y ad),p(cr vs ad)}	1506.6	13.2	0.0	7	458.8
{phi(sex),p(cat)}	1522.0	28.6	0.0	5	478.3
{phi(sex 3ed),p(.)}	1540.6	47.3	0.0	7	492.9

La estimación de parámetros en todos los casos fue realizada empleando métodos de máximo de verosimilitud así como métodos bayesianos con el software Mark 6.0 (White and Burnham 1999). Los modelos bayesianos utilizaron Cadenas de Markov Monte Carlo (MCMC) con 5000 y 1000 muestras de “tunning” y “burning” y con hiper-distribuciones normales vagas y no informativas para todos los parámetros de sobrevivencia y recaptura . Todas las estimaciones se basaron en 10.000 remuestreos de las cadenas de Markov cuya convergencia a una distribución estacionara fue evaluado usando el criterio de Geweke (1992).

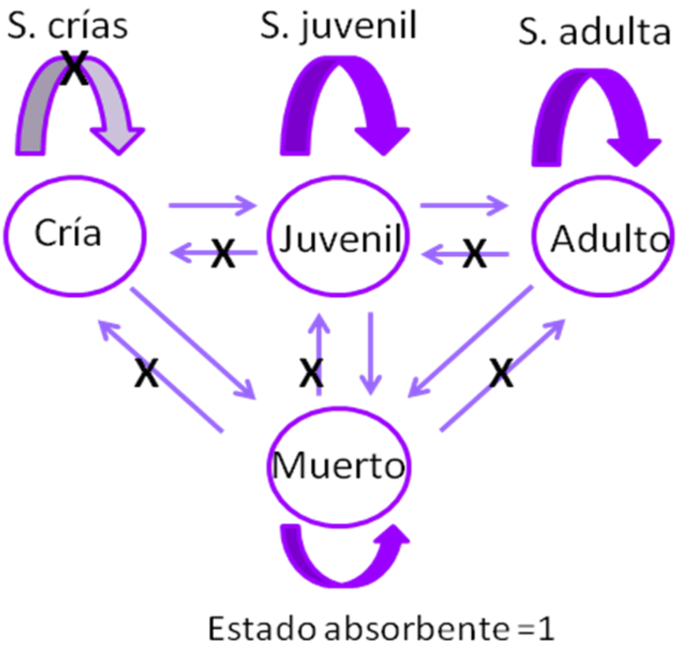

Figura 1. Esquema representativo de las categorías utilizadas en los modelos multiestado. Las cruces negras indican las transiciones improbables, a las que se les colocó una probabilidad de cero. La categoría "Muerto" fue el único estado absorbente, donde la probabilidad de permanecer en él es igual a 1.

A pesar de todos los esfuerzos realizados para obtener estimados razonables de la sobrevivencia juvenil y adulta de ambas especies, los resultados no fueron acordes con lo esperado para especies longevas, ya que la sobrevivencia adulta estimada tuvo, en todos los casos, valores muy bajos. Probablemente esto último se deba, no solo a la baja tasa de recaptura, sino a que las recapturas visuales de animales vivos que llegaron a la edad adulta fue muy baja, a pesar de la cantidad de individuos marcados (Fig. 2 y 3). Además de estas recapturas, se tuvieron registros de animales muertos varados en la costa de Uruguay, Argentina y Brasil.

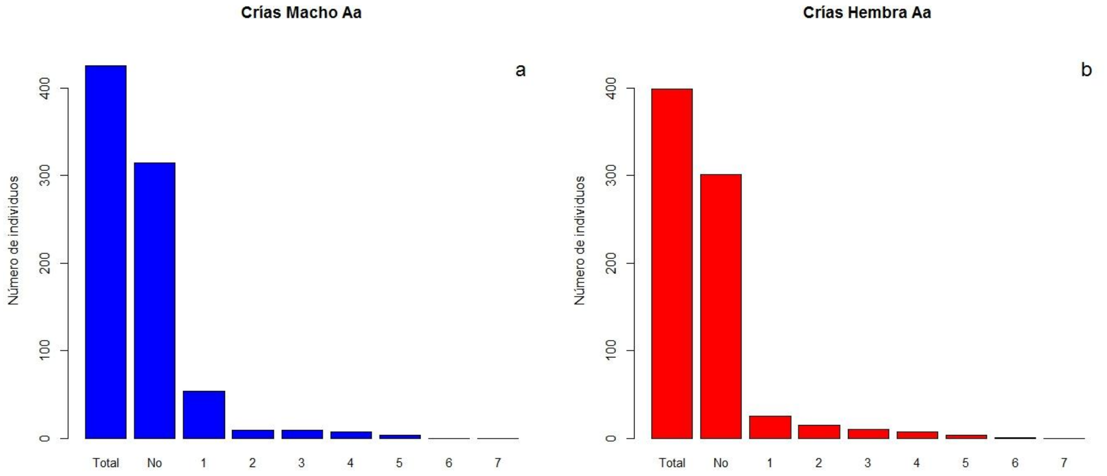

Figura 2. Histograma de crías a) macho y b) hembra, marcados y recapturados del lobo fino sudamericano. Total: refiere a la cantidad de individuos marcados, No: a los individuos que nunca fueron recapturados. 1 al 7 son las edades de recaptura.

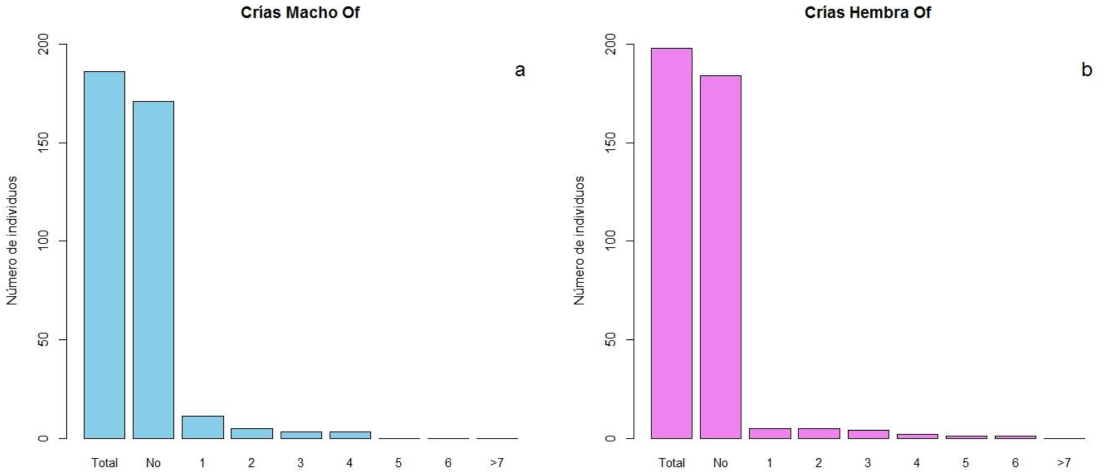

Figura 3. Histograma de crías a) macho y b) hembra, marcados y recapturados del león marino sudamericano. Total: refiere a la cantidad de individuos marcados, No: a los individuos que nunca fueron recapturados. 1 a >7 son las edades de recaptura.

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