TÁCTICAS ALTERNATIVAS DE APAREAMIENTO EN ARAÑAS CON REGALO NUPCIAL: SELECCIÓN SEXUAL Y AMBIENTE

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Resumen general:

La selección sexual es un proceso evolutivo que da forma a los rasgos sexuales actuando principalmente a través de la selección intersexual y la competencia intrasexual previo a la cópula, así como a través de sus análogos post cópula (elección críptica femenina y competencia espermática). Pero además, todos estos agentes de selección sexual pueden verse fuertemente afectados por las condiciones ambientales modelando interactivamente la evolución de los sistemas de apareamiento. En particular, los ambientes estresantes desafían la supervivencia de los individuos, lo que limita no sólo la inversión de los machos en la reproducción, sino también las preferencias y elección de las hembras. Los regalos nupciales son rasgos sexuales que están particularmente vinculados al medio ambiente y la reproducción. En principio, la producción del regalo es comúnmente condición dependiente, pero además en algunos casos los machos ofrecen presas disponibles por lo que el ambiente puede influir fuertemente en la posibilidad de adquirirlas. Por su parte, las hembras generalmente forrajean a través la obtención de cópulas con machos que ofrecen regalos nutritivos y mejoran su fecundidad aumentando el número de huevos. Por lo tanto, la poliandria intensifica la fuerza de la selección sexual post-copulatoria.

En la araña donadora de regalos *Paratrechalea ornata*, los machos envuelven en seda presas frescas como regalos nutritivos, pero también pueden envolver restos de presas o incluso partes vegetales como regalos simbólicos. Los regalos simbólicos son beneficiosos para los machos porque les permite un éxito de cópula similar que con los regalos nutritivos. Pero, para las hembras recibir este tipo de regalos carentes de nutrientes impacta de forma negativa sobre su fecundidad. Es por esto, que en los sistemas de apareamiento donde existen estos regalos engañosos, estos se mantienen en bajas frecuencias por selección negativa. Sin embargo, a diferencia de lo esperado, en la especie *P. ornata* los regalos simbólicos pueden alcanzar altas frecuencias en algunas poblaciones (incluso el 100%). Esta especie vive en hábitats ribereños, conocidos por ser altamente estresantes, lo que lleva a la hipótesis de que la variación en el rasgo sexual está íntimamente vinculada a las condiciones de estrés en ambientales locales en interacción con la intensidad de la selección sexual.

El primer capítulo de esta tesis se centró en estudiar desde una escala geográfica cómo la inversión reproductiva de los machos y la elección de las hembras en diferentes poblaciones responden a sus condiciones ambientales locales. Realizamos recolecciones de campo para evaluar las frecuencias de tipos de regalos (nutritivo, simbólico) en relación a variables climáticas, ecológicas e individuales. Encontramos que en los ambientes altamente estresantes (es decir con alta variabilidad en las precipitaciones) ocurren las mayores frecuencias de regalos simbólicos. Además, bajo condiciones de laboratorio, encontramos que en estas poblaciones con altas frecuencias de regalos simbólicos las hembras copulan durante tiempos similares con machos que ofrecen cualquier tipo de regalo. En contraste, en las poblaciones con frecuencias bajas de regalos simbólicos las hembras ejercen elección reduciendo el tiempo de cópula con machos que ofrecen regalos simbólicos. Tanto los resultados de campo como los de laboratorio son congruentes con la idea de que en ambientes altamente estresantes la elección femenina

se encuentra limitada y explica las altas frecuencias de regalos simbólicos en dichas poblaciones.

El segundo capítulo se centró en comprender la variación de la frecuencia de regalos simbólicos (0-80%) a lo largo de la estación reproductiva en una población con condiciones de estrés moderado. Mediante muestreos de campo y experimentos en condiciones de laboratorio, analizamos los efectos interactivos de la competencia pre- y post-copulatoria, la disponibilidad de presas y el tamaño de los machos. Encontramos que los machos pequeños y medianos producen regalos simbólicos cuando hay pocas presas y es alta la competencia post-copulatoria. Esto resulta en un acceso a más cópulas, pero con una duración reducida en comparación con los machos que ofrecen regalos nutritivos. En cambio, los machos grandes no se ven afectados por la disponibilidad de presas, y producen regalos simbólicos solo cuando la competencia post-copulatoria es baja. En conjunto estos resultados indican que cuando la competencia post-copulatoria es alta, el ofrecimiento de regalos simbólicos ayuda a los machos a maximizar su éxito reproductivo al aumentar el número de cópulas, pero no la transferencia de espermatozoides, lo que explica la alta variación en las frecuencias de los tipos de regalos y el mantenimiento de los regalos nutritivos en la población.

En conclusión, los resultados de esta tesis ejemplifican cómo las presiones ambientales y sexuales, como lo son la variabilidad climática, la elección femenina o la competencia por cópulas, modelan la inversión de los machos en los regalos nupciales. Particularmente, cuando los ambientes son demasiado estresantes e impredecibles el costo de depender de las condiciones ambientales es demasiado alto. Por ende, las hembras pueden beneficiarse de independizar su éxito reproductivo del tipo de regalo, relajando sus preferencias. Al mismo tiempo, los machos pueden beneficiarse de producir siempre regalos simbólicos independizándose de la inestable disponibilidad de presas. Estas presiones selectivas pueden resultar en una disminución de la plasticidad de los individuos relacionada a la producción de regalos, es decir que en poblaciones altamente estresadas los machos mayoritariamente producen regalos simbólicos. De esta manera, los diferentes grados de variabilidad ambiental experimentados por las distintas poblaciones pueden favorecer que éstas presenten diferentes niveles de plasticidad en la inversión reproductiva de sus individuos. Estos resultados señalan la importancia de estudiar el efecto de las condiciones ambientales y más precisamente de la variabilidad climática y su interacción con la selección sexual al estudiar la evolución de los rasgos sexuales.

General summary:

Sexual selection is an evolutionary process that shapes sexual traits by acting primarily through intersexual selection and intrasexual competition prior to copulation, as well as through their post-copulatory analogues (cryptic female choice and sperm competition). In addition, all these agents of sexual selection can be strongly affected by environmental conditions, interactively modelling the evolution of mating systems. In particular, stressful environments challenge individuals' survival, limiting not only male investment in reproduction, but also female preferences and choice. Nuptial gifts are sexual traits particularly linked to the environment and reproduction. On the one hand, the production of the gift is commonly condition dependent, but also in some cases males offer available prey, so the environment can strongly influence the possibility of acquiring it. On the other hand, females generally forage by obtaining matings with males that offer nutritive gifts and improve their fecundity by increasing the number of eggs. Therefore, polyandry intensifies the force of post-copulatory sexual selection.

In the gift-giving spider *Paratrechalea ornata*, males wrap in silk fresh prey as nutritive gifts, but they can also wrap prey leftovers or even plant parts as worthless gifts. Worthless gifts are beneficial for males because these allow males to acquire similar mating success as when offering nutritive gifts. But, for females, receiving this type of nutrient-deficient gifts has a negative impact on their fecundity. Thus, in mating systems where these deceptive gifts exist, these are maintained at low proportions by female choice. Opposite to the expectations, in the species *P. ornata* worthless gifts can reach high proportions in some populations (even 100%). This species lives in riparian habitats, known to be highly stressful, leading to the hypothesis that sexual trait variation is closely linked to local environmental stress conditions in interaction with the intensity of sexual selection.

The first chapter of this thesis focused on studying from a geographical scale how males' reproductive investment and female choice in different populations respond to their local environmental conditions. We carried out field collections to evaluate the proportions of mating tactics (nutritive gift, worthless gift) in relation to climatic, ecological and individual variables. We found that in highly stressful environments, with high variability in rainfall, occur the highest proportions of worthless gifts. In addition, under laboratory conditions, we found that in these populations with high worthless gifts proportions, females mate with similar durations with males that perform either mating tactic. In contrast, in populations with low worthless gifts proportions, females exercise choice by reducing mating duration with males offering worthless gifts. Both the field and laboratory findings are consistent with the hypothesis that in highly stressful environments female choosiness is limited and explains the high proportions of worthless gifts in these populations.

The second chapter focused on understanding the variation in the proportions of worthless gifts (0-80%) throughout the mating season in a population under moderate stressful conditions. Through field collections and experiments under laboratory conditions, we analysed the interactive effects of pre- and post-copulatory competition, prey availability, and male size. We found that small and medium-sized males produce

worthless gifts when prey availability is low and post-copulatory competition is high. This results in access to more matings but with reduced duration compared to males offering nutritive gifts. In contrast, large males are not affected by prey availability, producing worthless gifts only when post-copulatory competition is low. Taken together, these results indicate that when post-copulatory competition is high, offering worthless gifts helps males to maximize their reproductive success by increasing the number of matings but not sperm transfer, which explains the high variation in the mating tactic proportions and the maintenance of nutritive gifts in the population.

In conclusion, the results from this thesis exemplify how environmental and sexual pressures such as climatic variability, female choice or mating competition shape the males' investment in nuptial gifts. Particularly, when environments are highly stressful and unpredictable the cost of depending on environmental conditions is too high. Therefore, females can benefit by becoming independent of the mating tactic for their reproductive success, relaxing their preferences. At the same time, males may benefit from always producing worthless gifts and becoming independent of the unstable prey availability. These selective pressures result in diminishing individuals' plasticity related to the gift production, and thus, in highly stressful populations males mostly produce worthless gifts. In this way, the different degrees of environmental variability experienced by the distinct populations can favour different levels of plasticity in the individuals' reproductive investment. These results indicate the importance of studying the effect of environmental conditions and more precisely of climatic variability and its interaction with sexual selection when studying the evolution of sexual traits.

General introduction:

Sexual selection is an evolutionary process that favours traits involved in improving reproductive success (Darwin, 1871). This selective pressure emerges because of the limited access to the opposite sex and can operate through diverse mechanisms and at different stages of the reproduction (Darwin, 1871; Eberhard, 1996; Evans & García-González, 2016; Parker, 1970). Agents of sexual selection can be classified into pre and post copulatory, both involving intersexual selection and intrasexual competition (Andersson & Iwasa, 1996; Eberhard, 1996; Parker, 1970; Trivers, 1972). Although there are exceptions to the rule, these mechanisms are related to gamete production and parental investment (Bateman, 1948; Trivers, 1972). Females tend to invest in gametes and sometimes in parental care, leading them to carefully select their partners before mating through the often-called female choice and/or after mating known as cryptic female choice. Males on the other hand, are generally assumed to invest little in their gametes, so their investment is directed to acquire and increase the number of mates by competing with their rival males to access females or after mating via sperm competition. Therefore, male fitness increases with mating rates, whereas female fitness is generally expected to reach its maximum with only one or a few matings (Bateman, 1948; Trivers, 1972). Given this, it would be more expected to find mating systems based in polygyny where males gain access to mate with several females, while females choose one male (Emlen & Oring, 1977). However, in many mating systems females are polyandrous, and thus they can acquire multiple ejaculates increasing selective pressures during and after mating (Evans & García-González, 2016; Kvarnemo & Simmons, 2013; Pélissié et al., 2014).

The resulting outcomes of sexual selection on individual fitness, however, can be strongly affected by environmental conditions at different time and space scenarios (Cornwallis & Uller, 2010; Cotton et al., 2006; Jennions & Petrie, 1997; Kasumovic et al., 2008; Miller & Svensson, 2014). Traits involved in reproduction are often adjusted to biotic environmental factors such as food availability, population demography, and predation risk, but also to abiotic factors such as climatic conditions (Clutton-Brock et al., 1997; Cockburn et al., 2008; Lima & Dill, 1990; Monteiro et al., 2017; Siepielski et al., 2017). Sexually selected traits are usually costly and displace individuals from their survival optimum (Lande, 1980), indicating that viability and sexual selection pressures can oppose each other (Jennions et al., 2001). Additionally, according to the resource allocation theory (Boggs, 2009), when resources are limited, individuals' reproductive investment must be counterbalanced with survival and maintenance requirements (Magrath & Komdeur, 2003; Morehouse et al., 2010). This implies that under limiting conditions, reproduction and survival not only may be opposite, but also may compromise each other. Environmental changes play a crucial role on the ultimate individual fitness in a population as it can alter the relative intensity of survival and reproduction. This drives different populations of the same species to differentially evolve reproductive traits increasing their success under their specific local conditions (Endler & Houde, 1995; Kwiatkowski & Sullivan, 2002; Simmons et al., 2001).

Overall, the interactive effects of the environment and sexual selective pressures modulate the evolution of sexual traits. Very good examples are the nuptial gifts, which particularly act as a link between environment and reproduction. Food gifts are prevalent in insects and in some spiders and it has been shown that in these taxa females can forage and enhance their fecundity through increasing the number of mates (Arnqvist & Nilsson, 2000). Hence, on the one hand post-copulatory processes becomes the main mechanisms of sexual selection due to individual fitness is highly determined by the effects of male sperm competition for fertilizations and cryptic female choice. On the other hand, when gift production is dependent on the environment, as in the case of gifts composed by prey, the ecological conditions can strongly influence the possibility of males to acquire such items. In fact, limited food availability leads to deceptive behaviours by the offering of inedible items instead of nutritive ones in several species (Albo, Melo-González, et al., 2014; Ghislandi et al., 2014; LeBas & Hockman, 2005; Preston-Mafham, 1999; Thornhill, 1976). Because nuptial gifts may take different forms, the costs and benefits of producing and receiving gifts differ across species and environments. Nuptial gifts have been classified as endogenous or exogenous, being endogenous those produced by the donor itself (e. g. glandular and salivary secretions, seminal fluids or even body parts), and exogenous those gathered from the environment (e. g. prey or inedible items) (Lewis et al., 2014; Lewis & South, 2012). Some gifts are composed by the two components, like the silk wrapped gifts in spiders, in which the silk wrapping is an endogenous production and the gift content is an exogenous item (Bristowe, 1958; Costa-Schmidt et al., 2008). This means that males can differentially allocate their energy between these two components. Silk wrapping of the gift is condition dependent as male spiders in better feeding condition invest more in gift production (silk wrapping) than those in poor condition (Albo, Toft, et al., 2011; Macedo-Rego et al., 2016; Trillo et al., 2014). The gift content can vary from fresh prey "nutritive gifts" to prey leftovers or even inedible items gathered from the surroundings "worthless gifts" (Albo, Winther, et al., 2011; Albo & Costa, 2010). Interestingly, males invest more silk when producing worthless than when producing nutritive gifts, indicating that they might be compensating a shorter investment in content with a higher investment in silk wrapping (Ghislandi et al., 2017; Pavón-Peláez et al., 2022). At last, producing nutritive gifts is directly dependent on prey availability, but also on male size and sperm competition (Albo et al., 2019, 2023; Ghislandi et al., 2014) creating complex eco-evolutionary scenarios.

The trade-off between investing in the endogenous or the exogenous part of the gift represents an opportunity for studying the maintenance of this sexual trait in relation to female choice and local environmental conditions. For this, we used the Neotropical gift-giving spider *Paratrechalea ornata* examining the nuptial gift across different populations with divergent environmental conditions and within a population along the mating season. In this species males mostly produce worthless instead of nutritive gifts (Albo, Melo-González, et al., 2014; Albo et al., 2023). In fact, even when prey are available, 20% of the males choose to wrap in silk inedible items (Pavón-Peláez et al., 2022). Based on the hypothesis that stressful environments relax sexual selection, particularly limiting female choosiness (Candolin et al., 2007; Jennions & Petrie, 1997), we predicted that deceptive worthless gifts in this riparian species would spread under large climatic variability and low prey availability (i.e. stressful conditions). A recent study in *P. ornata* reveals that in highly stressful environments worthless gifts are in high proportions and males mostly produced this mating tactic (Albo et al., 2023). On the other hand, when the environment is more benign deceptive gifts are in low proportions. In this thesis, the first chapter is dedicated to the study of six populations selected along the species distribution range (south, centre, north). We explored the worthless gifts proportions across this geographical scale and examined it in relation to climatic (i. e. precipitation variability), ecological (i. e. prey availability) and individual (i. e. male size) variables. Additionally, we analysed males' investment in gift production (i. e. silk wrapping) and female choosiness through the resulting mating duration acquired by males offering either nutritive or worthless gifts. In the second chapter, we focused on understanding the variation of worthless gifts proportions within a population with moderate stressful environmental conditions. For this, we analysed the interactive effects of pre- and post-copulatory mate competition, prey availability and males' size during the mating season.

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Chapter 1

Large climatic variations weaken sexual selection for nuptial gifts in spiders

Pavón-Peláez C., V. Diniz, W. Paredes, R. Teixeira, E. Costa-Schmidt, A. Santos, B. Buzatto and M.J. Albo. Large climatic variations weaken sexual selection for nuptial gifts in spiders (*in preparation*).

Resumen

Las condiciones ambientales pueden influir fuertemente en los costos y beneficios de los caracteres sexuales. Parte de la literatura afirma que los ambientes estresantes desafían la supervivencia de los individuos, limitando la elección de las hembras y la inversión reproductiva de los machos, lo que relaja las presiones de selección sexual. En este trabajo, probamos esta predicción utilizando la araña donadora de regalos nupciales *Paratrechalea ornata*, en la que los machos pueden envolver en seda regalos nutritivos (presa fresca) o simbólicos (restos de presas o partes vegetales). Examinamos los cambios en el rasgo sexual de los machos y la elección de las hembras en seis poblaciones expuestas a diferentes condiciones climáticas. Encontramos que la gran variabilidad en precipitaciones impone condiciones estresantes a los individuos que limitan la elección de la hembra y favorecen en la propagación de regalos simbólicos en la población. En poblaciones expuestas a condiciones altamente estresantes con las frecuencias más altas de regalos simbólicos (67%), los machos que ofrecen estos regalos adquieren cópulas con duraciones similares o incluso más largas que los que ofrecen regalos nutritivos. Por el contrario, las hembras penalizan a los machos que ofrecen regalos simbólicos reduciendo la duración de la cópula en las poblaciones expuestas a condiciones menos estresantes y con las frecuencias de regalos simbólicos más bajas (35%). Nuestros hallazgos son consistentes con la predicción de que las condiciones ambientales estresantes limitan la selectividad de las hembras relajando la selección sexual sobre los rasgos de los machos.

Abstract

Environmental conditions can strongly influence the cost and benefits of reproductive traits. Some literature argues that stressful environments challenge individuals' life cycle, limiting female choice and males' investment in reproduction, which relaxes sexual selection pressures. Here, we tested this prediction using the nuptial gift-giving spider *Paratrechalea ornata*, in which males can either wrap in silk nutritive (fresh prey) or worthless gifts (prey leftovers). We examined the changes in males' sexual trait and female choice along six populations living under different climatic conditions. We found that large variation in precipitation imposes stressful conditions to individuals limiting female choice and leading to the spread of deceptive worthless gifts in the population. In stressed populations with the highest proportions of worthless gifts (67%), males offering such gifts acquire similar or even longer matings than those offering nutritive gifts. In contrast, females penalize males offering worthless gifts by shortening mating duration in less stressed populations with the lowest worthless gift proportions (35%). Our findings are consistent with the prediction that stressful environmental conditions limit female choosiness, relaxing sexual selection over male traits.

Introduction

Individual reproductive traits are, over evolutionary time, adapted to the ecological factors (i.e., climatic variation, food resources, predation) that drive divergence among populations (Cornwallis & Uller, 2010; Miller & Svensson, 2014). However, there is a broad range of findings on whether environmental stresses strengthen or relax sexual selection in different taxa (Cally et al., 2019; Miller & Svensson, 2014; Passos et al., 2021). This is mostly due to the different life-history strategies that can be found across species. Part of the literature suggests that when local environmental conditions are stressful, individual survival becomes challenged and reproductive investment limited, which in turn relaxes the sexual selection pressures (Candolin et al., 2007; Cockburn et al., 2008; Janicke et al., 2015; Jennions & Petrie, 1997). Climatic variation has been suggested as a key factor affecting individuals' fitness and the evolution of sexual traits (Becker et al., 2018; Charmantier et al., 2008; Kozlovsky et al., 2018; Massot et al., 2017; Merilä & Hendry, 2013; Piersma & Drent, 2003; Siepielski et al., 2017). In a broad range of taxa, temporal and spatial variation in temperature affects the expression of sexual traits (Berger et al., 2014; Botero & Rubenstein, 2012; De Lisle et al., 2018; Rosenthal & Elias, 2019), whereas variation in precipitation alters fecundity and survival (Siepielski et al., 2017). For example, an increase in temperature results in more sneaky copulations in guppies (Endler, 1995) and diminish fighters' success in bulb mites (Plesnar-Bielak et al., 2018). Hence, stressful environments can change the costs and benefits arising from sexual selection and influence the population capacity of adaptation to new or changing conditions (Berger et al., 2014; Bussière et al., 2008; Candolin et al., 2007; Candolin & Heuschele, 2008; Jennions & Petrie, 1997; Kwan et al., 2008; Miller & Svensson, 2014).

Nuptial gifts in spiders are a male sexual trait that strongly depends on the environment, as they usually consist of a prey wrapped in silk. A recently postulated hypothesis is that stressful conditions, such as severe climatic variations and limited prey availability generates the opportunities for deceptive worthless nuptial gifts to evolve (Albo, Melo-González, et al., 2014; Albo et al., 2023). The spider *Paratrechalea ornata* is an outstanding model to test this prediction, as individuals live in riparian habitats that can be stressful environments when precipitation regimen and floods cause quick and unpredictable major changes (Hagen & Sabo, 2014; Iwata et al., 2003; Knight et al., 2005; Lytle, 2002; Sabater et al., 2022; Sanzone et al., 2003). Additionally, males can change their sexual trait, nuptial gift, by either wrapping fresh prey in silk (nutritive gifts) (Costa-Schmidt et al., 2008), or instead wrapping inedible items, such as prey leftovers or even small plant parts (worthless gifts) (Albo, Melo-González, et al., 2014; Albo & Costa, 2010). Furthermore, individuals are plastic in their gift-giving behaviour and can express these two mating tactics, offering a nutritive or a worthless gift (Albo, Melo-González, et al., 2014; Albo et al., 2023; Pavón-Peláez et al., 2022). A recent study comparing two populations with divergent environmental conditions (i.e. temperature and precipitation variation) found significant differences in the proportions of these mating tactics (Albo et al., 2023). In highly stressful conditions with permanent prey limitations, males produce worthless gifts in near 100% of the cases, whereas under moderate stressful conditions the proportions of the deceptive tactic vary between 0 and 80%. This outcome highlights a strong effect of local environmental conditions on this sexual trait.

Yet, very little is known on how the environment interacts with sexual selection determining the proportions of worthless gifts in *P. ornata* populations. The reproductive benefits of offering and receiving worthless and nutritive gifts seem to depend on a complex interaction of individuals' body sizes, gift-giving plasticity, prey availability and mate competition (Albo et al., 2014, 2023; Pavón-Peláez et al., in rev., 2022). In both studied populations, offering worthless gifts is better than offering no gift, as males without a gift face very low female acceptance rate and the shortest mating duration (Albo, Melo-González, et al., 2014; Albo et al., 2023; Albo & Costa, 2010). When producing worthless gifts, however, males reduce their investment in the gift content, and instead invest more in the silk wrapping, when compared to the production of nutritive gifts (Pavón-Peláez et al., 2022). Silk wrapping of the gift enhances female attraction (Macedo-Rego et al., 2016; Trillo et al., 2014) and females seem to not differentiate gift content prior accepting the mate, as they equally accept either tactic (Albo, Melo-González, et al., 2014; Albo et al., 2023). Under moderately stressful conditions and in absence of mate competition mating duration is similar, or even longer, for males offering worthless gifts compared to those offering nutritive gifts (Albo, Melo-González, et al., 2014; Albo et al., 2023; Pandulli-Alonso et al., 2022). Still, females are polyandrous and receiving multiple worthless instead of nutritive gifts reduce their fecundity (i.e. number of eggs) in such environment (Klein et al., 2014; Pandulli-Alonso et al., 2017). Not surprisingly, under sperm competition, males suffer from a reduction in mating duration, explaining the high proportions of worthless gifts, but also the maintenance of nutritive gifts in the population (Pavón-Peláez et al., in rev.). In contrast, in a highly stressful environment it seems that females suffer no costs associated with the deception (Albo et al., 2023). As such, female choosiness for gift content is limited or absent, creating the opportunity for the spread of the deceptive worthless gifts in the population. This is consistent with studies suggesting that under harsh environments female choice becomes limited (Candolin et al., 2007; Candolin & Heuschele, 2008; Jennions & Petrie, 1997).

Here we further test the hypothesis that stressful environments, represented by large climatic variation, relax sexual selection and favour the production of deceptive worthless nuptial gifts in spiders (Candolin et al., 2007; Cockburn et al., 2008; Janicke et al., 2015; Jennions & Petrie, 1997). We examined gift content across a broad geographic scale in the species *P. ornata*, whose distribution ranges from southern Brazil to southern Uruguay (Carico, 2005). For our experimental design, we selected locations in the extreme south, the centre and the extreme north of the species distribution, representing a gradient from highest to lowest annual climatic variability (Seager et al., 2003). First, we studied the proportions of worthless gifts in six populations during the reproductive season and related them to local variation in precipitation and temperature, as well as prey availability and individuals' body sizes. We predicted the proportions of worthless gifts to increase in stressful environments (those with larger climatic variation). Second, we examined the males' mating success associated with each mating tactic (worthless and nutritive gift) in relation to the proportions of worthless gifts at the population of origin. We performed laboratory experiments with individuals from four locations representing the geographic distribution. We predicted increased climatic variability to limit female's choosiness for nuptial gifts and allowing high mating success of males offering worthless gifts. Consequently, in populations with high proportions of worthless gifts, we expected females to not penalize males offering worthless gifts, and thus, those males would achieve comparable reproductive success than males offering nutritive gifts. In contrast, in populations with low proportions of worthless gifts, females should be more selective, and we expected males from those populations to be less successful in terms of mating duration when compared to males offering nutritive gifts. Third, we examined males' investment in gift wrapping, as we predicted males to invest more silk when producing worthless instead of nutritive gifts only in populations where females are more selective, which are those with low proportions of worthless gifts.

Methods

Biological model

Individuals from *P. ornata* are crepuscular/nocturnal and are usually found over stones and pebbles at the edge of freshwater courses (Costa-Schmidt et al., 2008; Costa-Schmidt & Machado, 2012). This species life-cycle occurs in a year, and in populations from Uruguay two different generations reproduce, one during March-June and another during September-December (Albo et al., 2014; Pavón-Peláez et al., in rev.), while in Brazil the reproductive season is documented from October to February (Costa-Schmidt et al., 2008). During these periods males can be found carrying nuptial gifts and courting females.

The courtship behaviour is triggered when the male detects the female silk (with pheromones) over the substrate (Albo et al., 2009). Once the male detects the presence of a female, he starts to walk vibrating his forelegs and pedipalps, while searching for an item to wrap in silk and offer as a nuptial gift. The male can either capture and wrap a fresh prey (usually a flying insect emerging from the watercourse), eat the prey and wrap the leftovers, or grab an inedible item. The silk wrapping of the item involves several bouts, afterwards the male offers it to the female by adopting a particular position called 'hyperflexion' in which he exposes the nuptial gift towards the female (Albo, Melo-González, et al., 2014; Albo & Costa, 2010; Costa-Schmidt et al., 2008). The female accepts the mating by grabbing the gift with her chelicerae, allowing the male to mount her and initiate the sperm transfer via pedipalp insertion. While inserting his pedipalp, the male holds the gift with the claws of his third pair of legs. This helps him to secure the gift and avoid that the female escapes with it. Between each pedipalp insertion, the male returns to grab the gift, remaining in a face-to-face position with the female, who simultaneously holds on to the gift. In this species the mating lasts about one or few minutes during which the female consumes the gift, and once the mating is complete, the female leaves with the gift (Albo & Costa, 2010; Costa-Schmidt et al., 2008).

Deceptive worthless gifts likelihood in a geographic scale

We explored natural populations to assess how the intensity of sexual selection and the occurrence of deceptive worthless gifts vary along the species distribution range. We studied the likelihood of worthless gifts in relation to variation in precipitation and temperature, prey availability and male size by conducting a field study during the mating season (September-December) of six populations (Figure 1). In 2015 and 2016 we sampled three populations from Uruguay: Minas, Lavalleja (34.278 S, 55.234 W) representing the extreme south; Queguay, Paysandú (32.178 S, 57.238 W) and Lunarejo, Rivera (31.191 S, 55.901 W) representing the centre-south. In 2021, we sampled three populations from Brazil, two in Rio Grande do Sul, representing the centre-north: Itaara (29.558 S, 53.833 W) and Candelária (29.503 S, 52.802 W); one in Santa Catarina representing the extreme north: Xanxeré (26.777 S, 52.500 W). In 2022, we sampled all populations (except Minas due to habitat fragmentation). In total we completed 26 sampling days for the Uruguayan populations (N = 8 in Minas, N = 9 in Queguay, N = 9 in Lunarejo) and 20 for the Brazilian ones (N = 8 in Candelaria, N = 7 in Itaara, N = 5 in Xanxeré), totalling 46 sampling days.

Following previous protocols (Albo et al., 2023; Pavón-Peláez et al., in rev.), during each sampling date, two people manually sampled all spiders from the same patch for two hours (in total 4,156 spiders collected: N = 577 in Minas, N = 796 in Queguay, N = 596 in Lunarejo, , N = 672 in Candelaria, N = 940 in Itaara, N = 422 in Xanxeré). We performed the sampling at night when the spiders were active (approximately from 9 to 11 pm), using headlamps. Spiders were kept individually for later data collection and released at the same site at the next morning. In the case of males carrying nuptial gifts, to prevent the male from eating the gift, we removed the gift from the males' chelicerae and kept it into a separate Eppendorf tube. In parallel, we collected small invertebrates (in total 49,609 potential spider prey) using a light trap consisting in a white fabric sheet (60 x 80 cm) and a camping lantern (10.5 cm diameter and 19.5 cm height), placed next to the watercourse during the two hours of the spiders sampling. We preserved the sampled invertebrates in 75% alcohol for later counting.

After sampling, we weighed gifts (mass, in nearest 0.0001g) and dissected them under a stereomicroscope using tweezers to register their content. Following previous protocols, the gifts were classified, according to their weight (and afterwards verified via dissections and visual inspection), as "nutritive" when containing fresh prey, or "worthless" when containing dry prey leftovers or other non-nutritive items (Albo, Winther, et al., 2011; Albo, Melo-González, et al., 2014). We recorded the number of males carrying gifts, and we weighed (live body mass, in nearest 0.001g) and measured the size (cephalothorax width, in nearest 0.1mm) of each. The proportions of males with worthless gifts were calculated as the number of males with a worthless gift divided by the total number of males with gifts (nutritive and worthless). Prey availability was estimated as the total number of prey (all taxonomic groups) found in the light traps.

We calculated the annual mean and variance (variability) in temperature and precipitation using the monthly earth skin temperature (°C) and precipitation corrected (mm/day) from 1981 to 2021. This data was obtained from the National Aeronautics and

Space Administration (NASA) Langley Research Centre (LaRC) Prediction of Worldwide Energy Resource (POWER) Project funded through the NASA Earth Science/Applied Science Program (NASA, 2022). The annual mean temperature and precipitation correlates with latitude (Pearson correlation: $r_{temperature} = -0.88$, $r_{precipitation} = -0.99$), decreasing from north to south across the species range of *P. ornata*. Temperature variability also correlated with latitude (Pearson correlation: $r = -0.79$) increasing towards the south, but precipitation variability did not (Pearson correlation: $r = -0.49$) (Figure 1S).

For data analyses, we used a matrix with means per collections and only from dates with more than three nuptial gifts (N = 6 in Minas, N = 7 in Queguay, N = 7 in Lunarejo, N = 7 in Candelaria, N = 7 in Itaara, N = 4 in Xanxeré). We explored the correlations of the climatic variables and the worthless gift proportions and found no relationship for the temperature (annual mean or variability), or the annual mean precipitation. Hence, we only used precipitation variability as a climatic variable in the models. We explored field data from the four locations by performing Generalized Linear Models (GLMs) with Binomial error distribution for worthless gift proportions, and Gaussian distribution for male size and prey availability (both log transformed) including only the locations as the independent variable.

To explain the likelihood of worthless gifts, we used GLMMs with Binomial error distributions to assess the effect of the independent variables (all variables scaled and not strongly correlated) (Pinheiro & Bates, 2006). Our set of candidate models included 11 models with the proportions of worthless gifts (number of males with a worthless gift divided by the total number of males with nutritive and worthless gifts) as the independent variable, and every possible combination between the fixed effects of precipitation variability, prey number, male size, as well as single two-way interactions between each pair of these variables. We included the combination of month (September, October, November, December) and year (2015, 2016, 2021,2022) as random effects in all models, as well as the population. We performed statistical analyses using R version 4.2.2 (R Core Team, 2022). Models were fit using functions of the packages lme4 and AICcmodavg (Bates et al., 2015; Mazerolle, 2019). We used the bias-corrected version of the Akaike Information Criterion (AICc) in a model selection approach (K. P. Burnham & Anderson, 2002).

Silk wrapping and mating success of the deceptive worthless gift across populations

We examined how the investment in silk wrapping of the gift and fitness success (mating duration) associated to each mating tactic (worthless gift, nutritive gift) varies in relation to the proportions of worthless gifts in the populations. We performed behavioural experiments for two of the studied populations in Brazil: Itaara (centre-north) and Xanxeré (extreme north) and analysed the data alongside a dataset from a previous study on the populations in Uruguay: Minas (extreme south) and Queguay (centre-south) (Albo et al., 2023).

We collected the individuals during the beginning of the reproductive season (September) in 2021, at the stage of juveniles or subadults, to perform the behavioural experiments using unmated individuals. We transported spiders to the laboratory, where we kept them individually into plastic jars (10cm diameter, 7cm height) with pebbles at the bottom and some small tree branches. Individuals were held in a room at an average temperature of 23.82°C (± 0.37 SE). We provided water daily in a cotton wool and we fed spiders twice a week with beetle larva (*Tenebrio molitor*) or an adult housefly (*Musca domestica*). To ensure spiders were sexually receptive to mate, we started the trials 20 days after males and females moulted to adulthood (Klein et al., 2012).

We followed the same protocol as for the Uruguayan populations (Albo et al., 2023), exposing each male to court a female into two different groups. In the Nutritive group, we allowed males to only produce nutritive gifts by providing them a live housefly (*M. domestica*). In the Worthless group, we allowed males to only produce worthless gifts by providing them inedible items consisting of exuviae of *T. molitor* larva. Sample sizes of both experimental groups in all populations (south, centre-south, centre-north, north) are shown in Table 2S. Individuals were assigned randomly to the groups, and we performed a lineal model to verify there was no difference in male size between groups within each population ($F_{1,\ 104} = 0.03$, $p = 0.82$; Table 3S). We performed the trials in transparent plastic jars (20cm diameter, 13cm height) with the bottom covered with pebbles to simulate natural conditions and a dish with water. We first placed the female 24h before the trial to allow her to deposit silk that stimulates male courtship and gift production (Albo et al., 2009; Albo, Melo-González, et al., 2014; Albo & Peretti, 2015). For the Worthless group, before introducing the male, we placed four exuviae distributed along the bottom of the cage. We introduced the male and after he contacted the female, we removed her from the experimental cage to prevent her for interfering with gift production. For the Nutritive group, we waited until the male started to court (vibrate forelegs) to offer him a live housefly by slowly approaching it with tweezers and letting the male perceive its wing vibrations. If the male did not grab the fly at the first attempt, we repeated the procedure every 15 minutes until he grabbed it. Once the male grabbed an item (either the exuviae in the Worthless group or the housefly in the Nutritive group), we waited 20 minutes for the male to wrap the item in silk, and then reintroduced the female into the cage. We finished the trial 30 min after the couple separated and the female left with the gift. If the male failed to grab any item or to wrap an item in silk, we re-used him in another trial.

We registered the occurrence of silk wrapping and duration of each bout, as well as mating occurrence and duration of each pedipalp insertion (proxy of the amount of sperm transfer). We calculated the silk wrapping duration in minutes as the sum of the duration of all wrapping bouts. We calculated mating duration as the sum of the duration of all insertions. We used Generalized Linear Models (GLM) to test for differences in silk wrapping duration, number of silk wrapping bouts, mating duration, and number of insertions, among the four populations. We included the worthless gift proportions of each population, the mating tactic (Nutritive group, Worthless group) and their interaction as independent variables. The models included a Gamma distribution of errors for silk wrapping duration and mating duration, and Poisson for number of silk wrapping bouts and number of insertions.

Results

Deceptive worthless gifts likelihood in a geographic scale

We collected a total of 607 males carrying a gift, 99 from south (Minas 40% worthless gifts), 247 from centre-south (Queguay 82% and Lunarejo 55% worthless gifts), 232 from centre-north (Candelaria 30% and Itaara 35% worthless gifts) and 22 from north (Xanxere 68% worthless gifts). The exploratory analysis showed worthless gift proportions were significantly higher for populations in the centre-south and north than for populations in the centre-north and south (Figure 2A, Table 1). We found significant differences in male size across populations (Figure 2B, Table 1). Post-hoc analyses show males in the north (N =131) and south (N = 227) were significantly larger than those in the centre-south (N = 613), whereas centre-north (N = 575) was not different from the rest (Supplementary material, Table 1S). We found no significant differences in prey number across locations (Figure 2C, Table 1), whereas the annual precipitation variability was higher for north (0.88 mm/day) and centre-south (0.81 mm/day) than for centre-north (0.44 mm/day) and south (0.11 mm/day) (Figure 2D).

Variation in precipitation affected positively the worthless gift proportions. Our model selection method explaining the worthless gifts likelihood given annual variability in precipitation, prey number and male size resulted in three best models (Table 2). In all models, the variation in precipitation appeared as the most important variable affecting the proportions of deceptive gifts (Table 3), and the AIC relative importance of this variable was 88% (calculated as the sum of the AIC weights of all models with this variable). Additionally, the second-best model showed a negative effect of prey availability on the proportions of worthless gifts, and the relative importance of this variable in the set of candidate models was 43% (Table 3).

Silk wrapping and mating success of the deceptive worthless gift across populations

Males' mating duration was significantly affected by the interaction between the mating tactic and the proportion of worthless gift at the population of origin (Figure 3A, Table 4). In the populations with the lowest worthless gift proportions, males offering worthless gifts acquired shorter mating duration than those offering nutritive gifts. In contrast, in the populations with the highest proportions of worthless gifts, mating duration was similar for both mating tactics or even slightly higher for the worthless gifts. The number of insertions was not affected by mating tactic or worthless gift proportions (Figure 3B, Table 4). Males' investment in silk wrapping, measured as the total silk wrapping duration and the number of the silk wrapping bouts, was unrelated to the mating tactic or the proportions of worthless gifts found in the field (Figure 3CD, Table 4).

Discussion

We confirmed our hypothesis that large climatic variation, and in particular local annual variation in precipitation was related to worthless gift proportions. Under this scenario, precipitation variability may be imposing stressful conditions for individual spiders due to its unpredictability, decreasing female choosiness for nuptial gifts and leading to the spread of deceptive worthless gifts in the populations. These results may exemplify how stressful environmental conditions can change the benefits and costs of nuptial gifts, ultimately reducing female choosiness and the strength of sexual selection, as previously found for other sexual traits (Berger et al., 2014; Bussière et al., 2008; Candolin et al., 2007; Candolin & Heuschele, 2008; Cockburn et al., 2008; Jennions & Petrie, 1997; Kwan et al., 2008; Miller & Svensson, 2014). Unpredictable and stressful environmental conditions are known to limit individual's investment in reproductive behaviours in several taxa (Clutton-Brock et al., 1997; Jensen et al., 2006; Kasumovic et al., 2008; Lima & Dill, 1990). This seems especially true for species in which males need to capture prey and court offering food resources (Gwynne & Simmons, 1990; Janicke et al., 2015). As such, we show that under highly stressful conditions male spiders more often reduce food investment in nuptial gifts, eating the prey, wrapping the leftovers and producing worthless, instead of nutritive gifts. The modification of the sexual trait is advantageous for males as they reduce the investment in gift content, but costly for females as they increase their fitness success (i.e. fecundity) through the food gifts (Pandulli-Alonso et al., 2017). Yet, the spread of deceptive gifts suggests that female choosiness for nuptial gifts is reduced under harsh environmental conditions.

Consistently with a recent metanalysis (Siepielski et al., 2017), large variation in precipitation is the primary factor explaining the increase of worthless gifts proportions. The effect of climatic variation may impact directly on the individuals or populations, or indirectly through their ecological interactions with prey or predators (Stenseth et al., 2002). The sexual trait studied here is certainly related to prey availability, as nutritive gifts consist of a captured prey wrapped in silk (Costa-Schmidt et al., 2008). Riparian gift-giving spiders feed from adult insects emerging from watercourses and therefore, changes in the rivers caused by precipitation (and in extreme cases floods) can dramatically change the insects life cycle, abundance and emergence (Akamatsu et al., 2004, 2007). We did not find a direct effect of precipitation variation over prey number, instead our model selection method retained current prey availability as an important factor affecting worthless gift proportions. This is probably because the abundance of prey is affecting individuals differently depending on the population of origin.

The dynamics of climatic conditions and variations in prey availability at each locality are expected to favour different levels of individual plasticity in gift-giving tactics. Spider males' plasticity in gift production is narrowed in highly stressed populations as even in the presence of prey, males mostly produce worthless gifts (Albo et al., 2023). In contrast, in less stressful environments males are largely plastic and can offer either mating tactic depending on prey availability, mate competition and their own size (Albo et al., 2023; Pavón-Peláez et al., in rev.). Thus, the abundance of prey would indicate the abundance of nutritive gifts only in less stressed populations. In addition, in such populations, the annual variability in precipitation may be translated into annual variability of prey. In fact, the effect of rainfall on communities of small invertebrates is relatively well understood (Shultz et al., 2006; Staley et al., 2007), and this effect is usually revealed after months or in different life stages of the individuals. Males of *P. ornata* experience this variability over their entire development, and as in this species food shortage has a long-term effect on male's gift-giving behaviour (Macedo-Rego et al., 2016), the increase in worthless gift production may be a response triggered by their overall feeding experience.

Hence, in environments with large precipitation variability males' gift-giving plasticity is limited but so is female choice for nuptial gifts. It is suggested that when the conditions are unpredictable and stressful, sexual selection pressures tend to be relaxed and female choice becomes limited (Candolin et al., 2007; Candolin & Heuschele, 2008; Jennions & Petrie, 1997). Mating duration represents an opportunity for female choice prevalent in many taxa (Evans & García-González, 2016), and especially in gift-giving species (Elgar et al., 2000; Gwynne, 2008; Lewis & South, 2012; Sauer et al., 1998; Thornhill, 1984; Vahed, 1998, 2007). Accordingly, female choice through mating duration seems to be responsible for maintaining the proportions of deceptive nuptial gifts in spiders. In the spider *Pisaura mirabilis* females feed from the gift during mating, resulting in mating durations determined by the mating tactic (Albo, Winther, et al., 2011). In such case, males offering worthless gifts suffer from a reduction in mating duration, which results in less sperm transferred and stored by females (Albo et al., 2013). Because females mate multiple times, offering a worthless gift would decrease males' paternity success under sperm competition. This is also happening in the least stressed populations of *P. ornata*, as in those populations we also found that females are selective and penalize males offering worthless gifts by shortening mating duration. Under more stressful conditions, however, female choice for nuptial gift content seems absent and males offering either mating tactic acquire similar mating durations. These differences in mating success are consistent with the proportions of worthless gifts found in the field. Altogether, our data adds evidence on how local environmental conditions interacting with sexual selection can differentially maintain mating tactics in different populations of the same species (Candolin et al., 2007; Janicke et al., 2015; Jennions & Petrie, 1997).

Mechanisms of female choice may also occur during courtship by selecting males prior to mating or after mating through cryptic female choice (Evans & García-González, 2016). Given that the nuptial gift is wrapped in silk, females of *P. ornata* cannot exert selection on its content prior to mating acceptance (Albo, Melo-González, et al., 2014). Yet, by adding more silk to the gift males may better lure females (Brum et al 2012 (Macedo-Rego et al., 2016; Trillo et al., 2014). Not surprisingly, in less stressful environments where females are selective, males increase their investment adding more silk to the item when producing worthless gifts than when producing nutritive ones (Pavón-Peláez et al., 2022). So far, we found no difference in silk wrapping between mating tactics across populations, which will require new experimental approaches. Additionally, we expected males body size to correlate with the environmental conditions. This is because under benign conditions males would be able to grow largest and highly invest in reproduction (Bonduriansky, 2007; Macedo-Rego et al., 2016; Trillo et al., 2014). Moreover, a recent study indicates that females can bias paternity towards large males when conditions are less stressful (Albo et al., 2023). Thus, competition for mates should then drive selection for male sizes, resulting in differences across populations. Nevertheless, we found that male size was not predicted by climatic variability.

In conclusion, by studying a particular sexual trait, the nuptial gift, here we present evidence on how stressful environmental conditions can weaken sexual selection. The effects of climatic variation on animal behaviour have been neglected for decades, and only recently some studies have revealed remarkable outcomes on individual survival and reproduction (Cockburn et al., 2008; Isotalo et al., 2022; Siepielski et al., 2017). Global climatic variability is increasing due to climate change, emphasizing the relevance of these processes for ecosystems (Nadeau et al., 2017; Stenseth et al., 2002) and reinforces the importance of understanding its effects over the ecology and evolutionary biology of species.

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Table 1. Parameter estimated and p-values using Generalized Linear Mixed Models to assess the differences in worthless gift proportions, male size and prey availability across locations (N=42). Significant differences are shown in bold.

	Worthless gift proportions			**Male size**			**Prey availability**		
	Estimate	SE	P	Estimate	SE	P	Estimate	SE	P
Intercept (Centre-North)	10.29	1.98	>**0.001**	1.33	0.02	>**0.001**	4.86	0.69	>**0.001**
South	-0.62	2.92	0.83	0.13	0.04	**0.001**	-0.64	1.02	0.53
Centre-South	-6.99	2.59	**0.01**	0.004	0.03	0.91	-0.08	0.89	0.93
North	-8.62	3.62	**0.03**	0.11	0.05	**0.02**	0.12	1.33	0.93

Table 2. Ranked (based on AIC$_c$) candidate models with combinations of the fixed effects of precipitation variability (‘var(Precip)’), prey availability (‘Prey’), and male size (‘M.size’) explaining the probability of males producing worthless gifts. Bold letters indicate the most parsimonious models.

N°	Fixed effects	*K*	AICc	ΔAICc	Weight	Log-Likelihoods	Cumulative weight
1	**var(Precip)**	**4**	**113.36**	**-**	**0.24**	**-51.73**	**0.236**
2	**var(Precip) + Prey**	**5**	**113.42**	**0.06**	**0.23**	**-50.21**	**0.465**
3	**var(Precip) + M.size**	**5**	**114.56**	**1.20**	**0.13**	**-50.78**	**0.595**
4	**Prey**	**4**	**114.65**	**1.29**	**0.12**	**-52.38**	**0.718**
5	var(Precip) + Prey + (var(Precip)*Prey)	6	115.81	2.45	0.07	-49.70	0.788
6	var(Precip) + Prey + M.size	6	115.97	2.61	0.06	-49.77	0.852
7	Null	3	116.21	2.84	0.06	-54.56	0.909
8	Prey + M.size	5	117.42	4.06	0.03	-52.21	0.940
9	M.size	4	117.81	4.45	0.03	-53.95	0.965
10	var(Precip) + M.size + (var(Precip)*M.size)	6	117.98	4.62	0.02	-50.78	0.989
11	Prey + M.size + (Prey*M.size)	6	119.45	6.09	0.01	-51.51	1.000

Table 3. Parameter estimated and confidence interval for the two firsts candidate models assessing the effect of precipitation variability and prey availability on worthless gift proportions. Significant differences are shown in bold.

Worthless gift proportions	**Model 1** (N=38)			**Model 2** (N=38)		
	Estimate (SE)	IC (95%)	z	Estimate (SE)	IC (95%)	z
Intercept	0.201 (0.237)	-0.26 – 0.67	0.854	0.164 (0.253)	-0.33 – 0.66	0.651
Precipitation variability	0.788 (0.166)	0.46 – 1.11	4.737	0.709 (0.247)	0.22 – 1.19	2.865
Prey availability				-0.182 (0.127)	-0.43 – 0.07	-1.43

Table 4. Parameter estimated and p-values for the Generalized Linear Mixed Models assessing mating duration (N= 70), number of insertions (N= 71), silk wrapping duration (N=107) and number of silk wrapping bouts (N= 106) in relation to the worthless gift proportions of their populations, the experimental group (Nutritive/Worthless) and their interaction. Significant differences are shown in bold.

	Intercept (Nutritive group)			**Worthless group**			**Worthless gift proportions**			**Worthless group* Worthless gift proportions**		
	Estimate	SE	P	Estimate	SE	P	Estimate	SE	P	Estimate	SE	P
Mating duration	0.33	0.22	0.14	0.86	0.38	**0.03**	0.42	0.40	0.29	-1.33	0.60	**0.03**
N insertions	0.98	0.37	0.01	-0.49	0.55	0.38	0.04	0.60	0.94	0.60	0.89	0.50
Silk wrapping duration	0.27	0.09	0.003	0.07	0.12	0.54	0.02	0.14	0.87	-0.19	0.18	0.29
N silk wrapping bouts	0.64	0.35	0.07	0.42	0.46	0.36	0.10	0.55	0.86	-0.29	0.73	0.69

Figure 1. Geographic distribution of *Paratrechalea ornata* studied populations. In Uruguay: the south population included Minas, Lavalleja (34.278 S, 55.234 W) represented in red, the centre-south populations included Queguay, Paysandú (32.178 S, 57.238 W) and Lunarejo, Rivera (31.191 S, 55.901 W) both represented in green. In Brazil: the centre-north populations included Itaara, Rio Grande do Sul (29.558 S, 53.833 W) and Candelária, Rio Grande do Sul (29.503 S, 52.802 W) both represented in light blue; the north population included Xanxeré, Santa Catarina (26.777 S, 52.500 W) represented in purple.

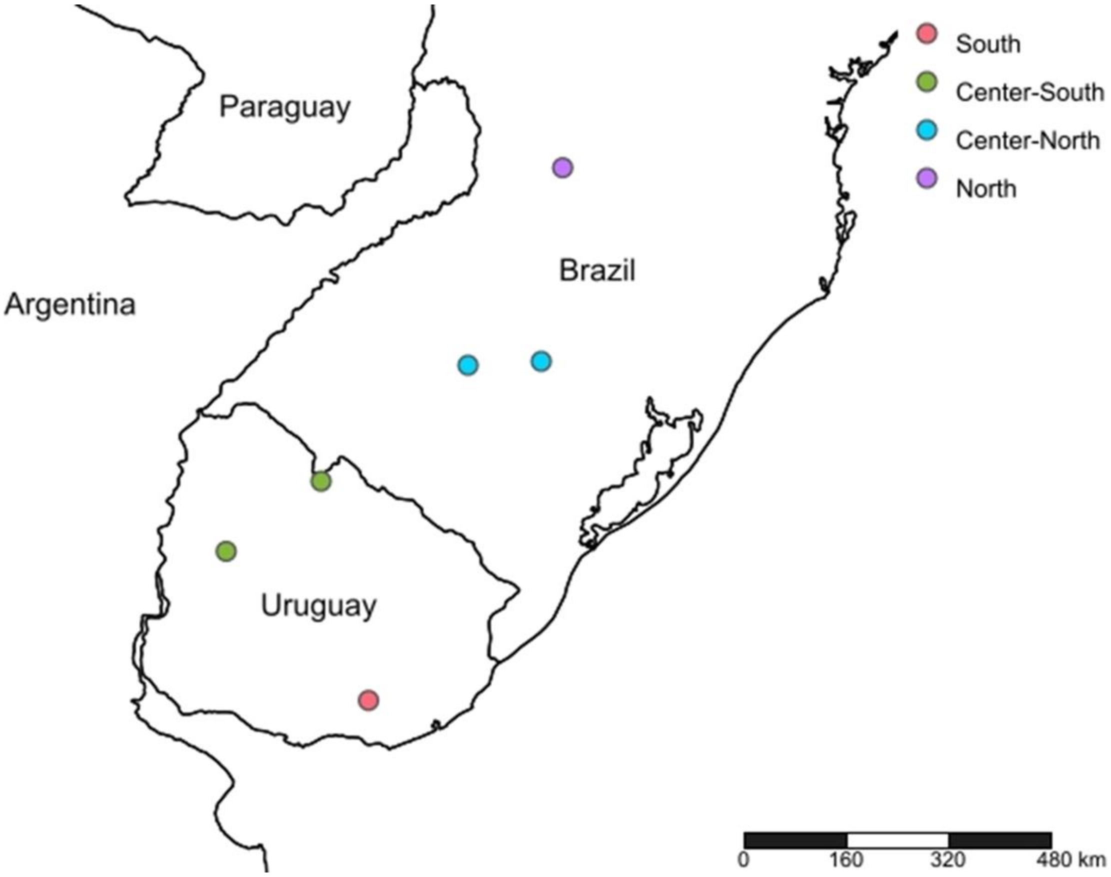


Figure 2. Nuptial gifts, individual and ecological variables in the field. A) Proportion of worthless gift (number of worthless gift/number of worthless and nutritive gifts), B) male body size (cephalothorax width in mm), C) prey availability (prey number) and D) the precipitation variability (mm/day) at the four locations of *P. ornata* populations.

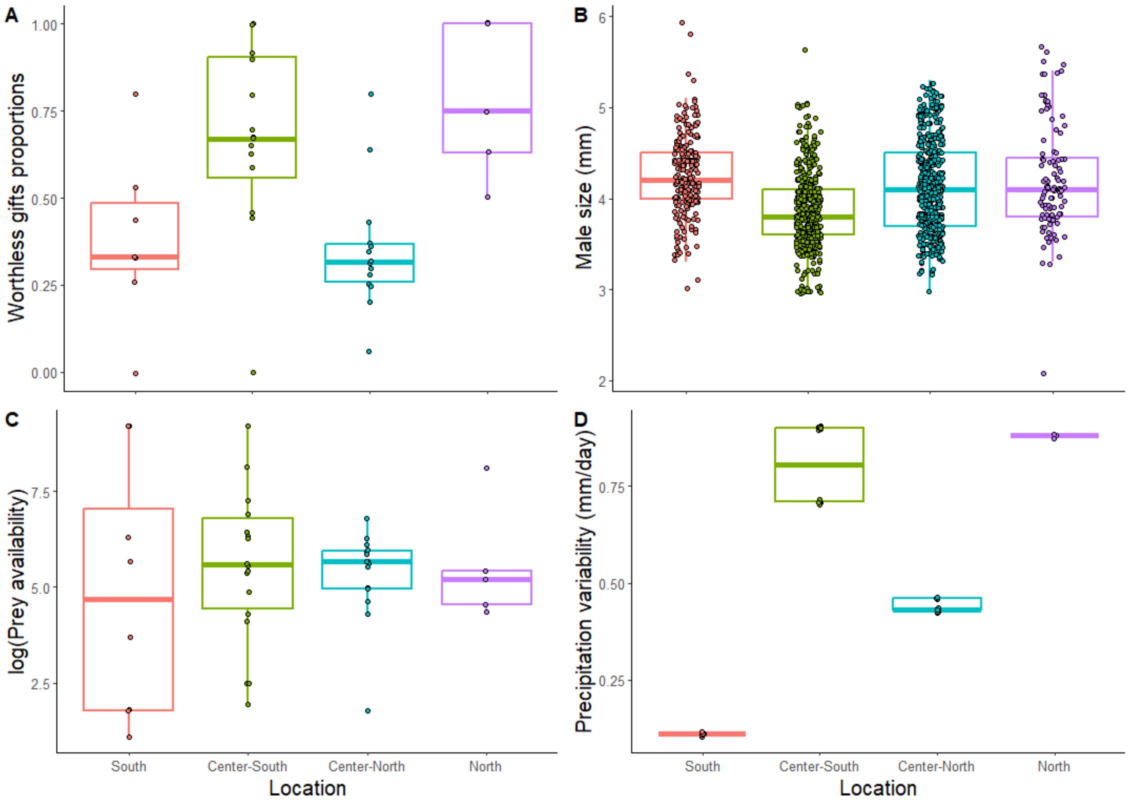
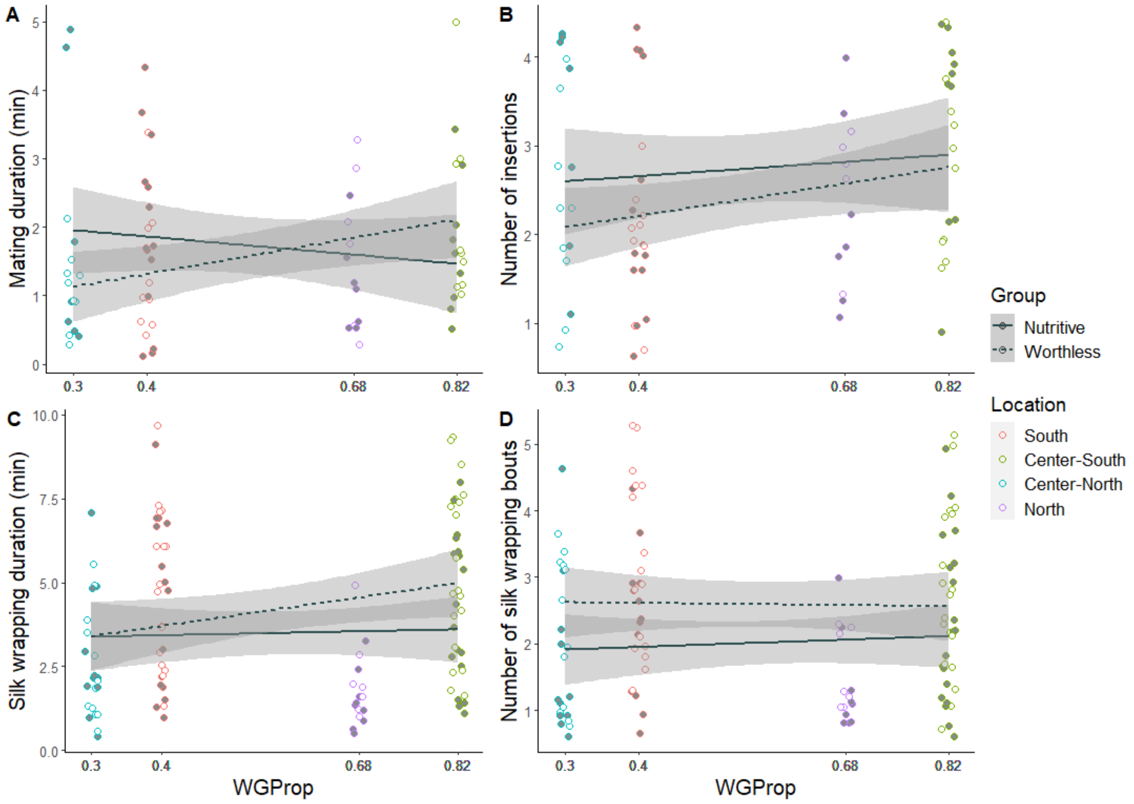


Figure 3. Males' silk investment and mating success under laboratory conditions. A) Mating duration (min), B) number of insertions, C) silk wrapping duration (min), and D) number of silk wrapping bouts in relation worthless gift frequencies at the population of origin (south, centre-south, centre-north, north) and mating tactic (nutritive/worthless gift). The data for the south and centre-south populations was extracted from Albo et al (2023), and the data for the centre-north and north populations was collected in this study. Final sample sizes are shown in Table 2S.



SUPPLEMENTARY MATERIAL

Table 1S. Parameters estimated and p-values for post-hoc analyses comparing male size between locations. Significant differences are shown in bold.

	Estimate (SE)	t	P
South – Centre South	0.121 (0.037)	3.257	**0.012**
South – Centre-North	0.057 (0.038)	1.527	0.423
South – North	-0.004 (0.051)	-0.070	0.999
Centre South – Centre-North	-0.064 (0.029)	-2.162	0.147
Centre South – North	0.125 (0.046)	2.719	**0.044**
Centre-North – North	0.061 (0.046)	1.320	0.5476

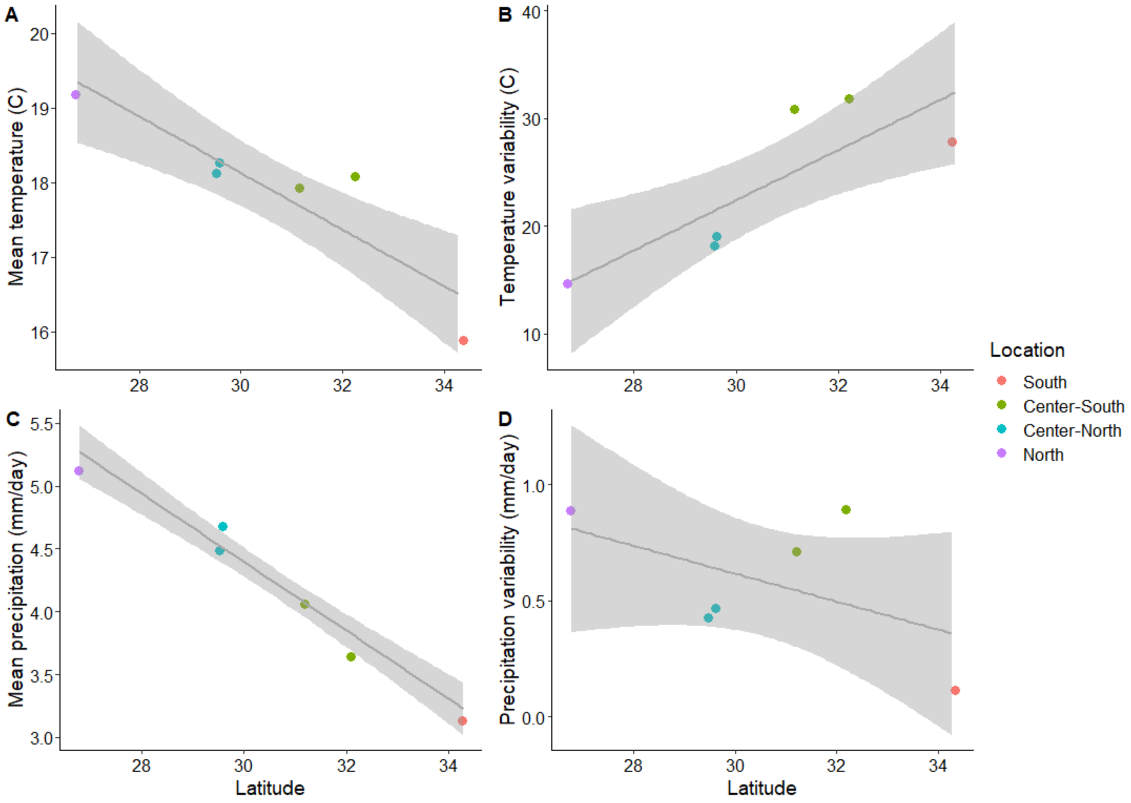
Table 2S. Sample sizes of the experimental groups for the analyses of nuptial gift production (silk wrapping duration and number of silk wrapping bouts) and mating success (mating duration and number of insertions).

	Nuptial gift production		Mating	
	Nutritive gift	Worthless gift	Nutritive gift	Worthless gift
South	16	16	14	9
Centre-South	19	19	10	10
Centre-North	12	12	7	9
North	9	7	7	6

Table 3S. Mean value (X) and standard error (SE) for males' body size and its range for individuals used in the behavioural experiments from each population.

Latitude	Group	N	X ± SE (mm)	Range
South	Nutritive	15	3.84 ± 0.05	3.3 – 4.1
	Worthless	16	3.90 ± 0.06	3.5 – 4.6
Centre- South	Nutritive	19	3.19 ± 0.05	2.8 – 3.6
	Worthless	19	3.16 ± 0.04	2.8 – 3.6
Centre- North	Nutritive	11	3.61 ± 0.14	3.2 – 4.8
	Worthless	11	3.54 ± 0.06	2.6 – 3.6
North	Nutritive	9	3.85 ± 0.08	3.5 – 4.2
	Worthless	6	3.85 ± 0.10	3.6 – 4.2

Figure 1S. Climatic variables across latitudes. Annual data extracted from NASA (2022) registering temperature (^{0}C) and precipitation (mm/day) from 1980 to 2020 at each studied locality (south, centre-south, centre-north, north). A) Mean temperature, B) temperature variability C) mean precipitation and D) precipitation variability in relation to the latitude.



Chapter 2

When all males cheat, post-copulatory competition limits worthless gifts success in spiders

Pavón-Peláez, C., M. Martínez Villar, V. Franco-Trecu and M.J. Albo. When all males cheat, post-copulatory competition limits worthless gift-giving success in spiders. *Behavioral Ecology* (*in revision*).

Resumen

Las condiciones ambientales junto con los agentes de selección sexual (por ejemplo, competencia por cópula) regulan la expresión de las tácticas de apareamiento. Asimismo, cuando los recursos necesarios para la reproducción son limitados surgen tácticas alternativas de apareamiento. Estas tácticas son comúnmente realizadas por machos menos competitivos (por ejemplo, de pequeño tamaño) y restringidas a bajas proporciones en las poblaciones. Excepcionalmente, en la araña donadora de regalos nupciales *Paratrechalea ornata*, los machos ofrecen regalos nutritivos (presas frescas), pero más a menudo regalos simbólicos (restos de presas o partes vegetales) como táctica alternativa. Las frecuencias de regalos simbólicos varían entre 0-80% durante el período reproductivo en algunas poblaciones. Predecimos que esto es el resultado de la interacción entre la disponibilidad de presas y la competencia por cópulas, alterando los costos y beneficios asociados a cada tipo de regalo. En el campo, encontramos que los machos pequeños y medianos en su mayoría produjeron regalos simbólicos cuando la disponibilidad de presas fue baja y la competencia post-copulatoria alta. En cambio, los machos grandes no se vieron afectados por la disponibilidad de presas, produciendo regalos simbólicos solo bajo competencia post-copulatoria baja. Por lo tanto, esta táctica engañosa es realizada por todos los machos independientemente de su competitividad, pero está en desventaja ante la competencia. Bajo condiciones de laboratorio aislamos el efecto de la competencia controlando la disponibilidad de presas y el tamaño de los machos y encontramos que, incluso teniendo disponibilidad de presa, los machos de tamaño mediano aumentaron la producción de regalos simbólicos bajo competencia post-copulatoria. Esto da como resultado un acceso cópulas ligeramente mayor, pero con una duración reducida en comparación con los machos que ofrecieron regalos nutritivos. Por lo tanto, bajo competencia post-copulatoria ofrecer regalos simbólicos puede ayudar a los machos a maximizar su éxito de cópulas al aumentar su número, pero no la transferencia de esperma, lo que explica el mantenimiento de los regalos nutritivos en la población.

Abstract

Environmental conditions together with agents of sexual selection (i.e., mate competition) regulate the expression of mating tactics. Likewise, alternative tactics arise when resources needed for reproduction are limited. These tactics are commonly performed by less competitive males (e.g., small size) and restricted to low proportions in the populations. Exceptionally, in the gift-giving spider *Paratrechalea ornata* males offer nutritive gifts (prey), but more often worthless gifts (inedible items) as an alternative tactic. The deceptive tactic frequencies range between 0-80% along the mating season in some populations. We predict this is the result of the interaction between prey availability and mate competition altering the benefits and costs associated to each mating tactic. In the field, we found that small-medium males mostly produced worthless gifts under low prey availability and high post-copulatory competition. Instead, large males were not affected by prey, producing worthless gifts only under low post-copulatory competition. Thus, this deceptive tactic is performed by all males regardless of competitiveness, but it is disadvantageous under competition. We disentangle the competition effect by controlling prey availability and male size under laboratory conditions, and we found that even when having a prey, medium size males increased the production of worthless gifts under post-copulatory competition. This result in a slightly increased mating access but with reduced duration compared to males offering nutritive gifts. Hence, when facing post-copulatory competition, the deceptive tactic may help males to maximize their fitness by increasing the mating rate but not sperm transfer, explaining the prevalence of nutritive gifts in the population.

Introduction

Environmental factors and agents of sexual selection (mate choice and competition) fluctuate across time and space and can act either to the same or opposite direction on the expression of reproductive traits (Alpedrinha et al., 2019; Cornwallis & Uller, 2010; Cotton et al., 2006; Emlen & Oring, 1977; Miller & Svensson, 2014). The changes in selective forces can alter the benefits and costs associated to the traits throughout the mating season, creating the scope for diverse male mating tactics to succeed in a population (Hendrickx et al., 2015; Kasumovic et al., 2008). A well-known phenomenon is the occurrence of alternative mating tactics, performed by males to maximize their fitness in situations where they are not able to display the dominant tactic (Brockmann et al., 2008; Gross, 1996b; Kvarnemo & Ahnesjö, 1996; Taborsky, 1998; Taborsky et al., 2008). Frequently alternative mating tactics are part of a conditional strategy (status-dependent selection) in which individuals can switch from one tactic to another along lifespan (Byrne & Roberts, 2004; Engqvist & Taborsky, 2016; Taborsky, 1994). These mating tactics are mostly dependent on environmental (i.e., food) or intrinsic cues (i.e., male condition) allowing individuals to adjust reproduction to their own status (Engqvist & Taborsky, 2016; Fraser et al., 2014; Gross, 1996a). For instance, it is widespread acknowledged that less competitive males would perform alternative mating tactics commonly when food resources are scarce and/or mate competition is high. This behavioural plasticity is incredible advantageous in nature as alternative tactics are usually less costly to perform than the dominant tactics, except that they are associated with lower fitness and thus, males are making “the best of a bad job” (Brockmann et al., 2008; but see Fraser et al., 2014; Gross, 1996a; Taborsky et al., 2008). Alternative mating tactics are likely to occur in several taxa, including nuptial gift-giving species, which are prevalent in insects and spiders. Males have the strategy of producing and offering a nuptial gift, but each individual has the ability of producing different gift types (tactics) by varying its content (Albo, Toft, et al., 2014; Engels & Sauer, 2006; Jia et al., 2000; LeBas & Hockman, 2005; Lehmann, 2012; Lewis et al., 2014; Preston-Mafham, 1999; Vahed, 1998).

Food gifts have been suggested as initially evolving through males’ sensory exploitation of female foraging motivation in spiders (Albo et al., 2017; Albo, Toft, et al., 2014; Bilde et al., 2007). But, limited resources have led males to switch the gift investment by reducing the nutritious content and investing in more silk for producing worthless gifts as an alternative tactic (Albo, Melo-González, et al., 2014; Albo, Winther, et al., 2011; Ghislandi et al., 2017; Pavón-Peláez et al., 2022). The production of worthless gifts is advantageous for males because females usually reject mates without gifts, especially if they have already mated (Albo, Melo-González, et al., 2014; Albo & Costa, 2010; Stålhandske, 2001). Individual males can, thus, switch between the two gift-giving mating tactics and tightly adjust the gift production according to prey availability (Pavón-Peláez et al., 2022). When prey are present, males wrap it in silk and produce nutritive gifts, but when prey are absent, they can perform an alternative tactic by wrapping prey leftovers or plant material and producing worthless gifts (Albo, Melo-González, et al., 2014; Albo, Winther, et al., 2011; Bristowe, 1958; Costa-Schmidt et al., 2008). The prevalence of these tactics is, therefore, unequivocally influenced by prey availability, but it is also predicted to change within the mating season and across populations depending on the particular interaction arising from local prey availability, mate choosiness and level of competition (Brockmann, 2001; Brockmann et al., 2008; Gross, 1996b; Taborsky et al., 2008). For instance, pre- and post-copulatory mate competition may act in different directions (Chung et al., 2021; Devigili et al., 2015; McDonald et al., 2017; Morimoto et al., 2019; Pélissié et al., 2014; Simmons & Buzatto, 2014; Tuni et al., 2017) favouring either the nutritive or the worthless gift-giving tactic. Independently of the mosaic resulting from these selective pressures, in all cases males producing deceptive worthless gifts are expected to gain lower reproductive success (i.e. fertilizations) than the prevailing dominant tactic of producing and offering nutritive gifts (Brockmann, 2001; Croll et al., 2019; Gross, 1996b; Taborsky et al., 2008). This is because deception is costly for females and they commonly penalise these tactics reducing males' fitness (Alonzo & Calsbeek, 2010; Buoro et al., 2011; Croll et al., 2019; Maynard-Smith, 1974; Mokkonen & Lindstedt, 2016; Stuart-Fox, 2005; Tomkins & Hazel, 2007). This has been shown in a gift-giving spider, as females reduce mating duration and sperm transfer when receiving worthless gifts (Albo et al., 2013, 2019; Albo, Winther, et al., 2011). Thus, selection against deceptive gifts was shown to maintain the alternative tactic at low proportion in this spider population (Albo et al., 2019).

An exceptional case is the spider *Paratrechalea ornata* which reveals unexpected patterns, since males produce deceptive worthless gifts in very high proportions (Albo et al., 2023; Albo, Melo-González, et al., 2014), suggesting that this mating tactic can be performed by all males regardless their competitiveness (i.e. small size or poor condition). In fact, a recent study has shown that even when prey is available, 20% of the males still choose to produce a worthless gift (Pavón-Peláez et al., 2022). This is a semiaquatic species living in riparian habitats from the Neotropical region (Carico, 2005). These ecosystems are known to be stressful environments for organisms limiting their survival and reproduction (Hagen & Sabo, 2014; Iwata et al., 2003; Knight et al., 2005; Lytle, 2002; Sanzone et al., 2003). As such, worthless gifts have been found to occur in almost 100% in populations under highly stressful conditions (i.e. permanent prey limitations) (Albo et al., 2023; Albo, Melo-González, et al., 2014). In contrast under moderate stressful conditions, worthless gifts frequencies vary along the season from 0 to 80% (Albo et al., 2023). Thus, the worthless gift-giving tactic changes from alternative to dominant tactic in different dates. This suggests a strong and changing interaction between local environmental conditions and the different agents of sexual selection (mate choice and competition), and that offering worthless gifts may even reward males with higher reproductive success under certain dates. There is a knowledge gap in relation to the effects of competition on the male mating tactics. Laboratory studies using the population under moderate stressful conditions indicate that for males, eating the prey or grabbing inedible items from the surroundings for producing deceptive worthless gifts seems to be a very successful choice in a non-competitive environment. There is no evidence for pre-copulatory female choice in relation to the gift content because males offering worthless gifts acquire similar female acceptance to those with nutritive gifts (Albo, Melo-González, et al., 2014; Albo, Winther, et al., 2011), whereas both tactics confer males similar mating duration (Albo et al., 2023; Albo, Melo-González, et al., 2014; Pandulli-Alonso et al., 2017). Further, males offering worthless gifts can even acquire longer matings than when offering nutritive gifts (Albo & Peretti, 2015; Pandulli-Alonso et al., 2022). Since sperm stored by females is positively correlated to mating duration (Albo & Peretti, 2015), both mating tactics may have equal opportunities for males in post-copulatory choice and competition. In contrast to males, females can gain nutritional benefits (improving their fecundity) when receiving multiple nutritive food gifts (Pandulli-Alonso et al., 2017). Thus, they may cryptically bias paternity towards those males thereby increasing the selective pressures on post-copulatory traits (i.e. sperm competition) (Eberhard, 1996; Firman et al., 2017; Parker, 1970; Simmons et al., 2001) and explaining the prevalence of nutritive gifts in the population.

Here, we aimed to explore how both mating tactics are maintained in a population with large variation in the frequencies of nutritive and worthless gifts. We first performed a field study to understand the shifts in the gift-giving tactics during the mating season in relation to the fluctuations in prey availability and pre- and post-copulatory mate competition. Given the stressful characteristics of the aquatic environment, we expected to find high variation in prey availability (Hagen & Sabo, 2014; Iwata et al., 2003; Kato et al., 2003; Lytle, 2002); and because of the seasonality of this species (see below) we expected mate competition to progressively increase with the season. Considering the gift-giving behaviour as a conditional strategy (Brockmann et al., 2008; Engqvist & Taborsky, 2016; Gross, 1996a) with two mating tactics (nutritive and worthless gifts), our first hypothesis implied that less competitive males (i.e., small males) would produce worthless gifts when prey is limited, and when pre- and post-copulatory mate competition is high. Therefore, we predicted the mating tactic performed by small males would depend on the strength of these selective forces when interacting. Additionally, the present data on this species also suggests the worthless gifts production may occur regardless male competitiveness (Pavón-Peláez et al., 2022). Large males have gathered enough food resources to reach large body sizes, which should favour them by prolonging mating duration (Pandulli-Alonso et al., 2022) and thus, our second hypothesis included the mating tactic decision of large males to be less affected by prey availability. In contrast, as it has been shown in several species, males can highly invest in reproduction under the risk of sperm competition (Dore et al., 2020; Kelly & Jennions, 2011; Wedell et al., 2002), then, our third hypothesis was large males investing in nutritive gifts when competition is high. We predicted this males would produce worthless gifts when either pre- or post-copulatory mate competition is low or absent (Albo et al., 2023). Secondly, we disentangled the potential effects of mate competition by performing laboratory experiments with constant prey availability and controlling for male size. For that we studied changes in males' gift production, mating access and duration under one of two competitive environments: pre- and post-copulatory mate competition. As in the field, we expected these less competitive males (medium size) to increase worthless gift production under the effect of mate competition. However, since females gain benefits when receiving multiple nutritive gifts (Pandulli-Alonso et al., 2017), our fourth prediction was that females would favour mating duration with males offering food gifts under mate competition. A schematic figure of the hypotheses is shown in supplementary material (Figure 1S).

Material and methods

Biological model

Individuals of *Paratrechalea ornata* are usually found during the night, while walking or settling over stones and pebbles at the edge of the freshwater courses (Costa-Schmidt et al., 2008). The mating season in Uruguay occurs twice a year during March-June and September-December, (Albo, Melo-González, et al., 2014). This species has a clear seasonality starting early September with mostly immature individuals (MJAlbo unpublished data) and ending in December where near half of the individuals are females with an eggsac and only few males are found (this study). Males can be observed carrying nuptial gifts and courting females during the season. Male courtship behaviour is triggered by female silk (presumably pheromones) deposited on the substrate (Albo et al., 2009). At that time, the male vibrates his forelegs and pedipalps while searching for an item (prey or inedible item) to eventually wrap it in silk and offers it to a female (Albo, Melo-González, et al., 2014; Albo & Costa, 2010). Once the female accepts the mating, she grabs the gift, and the male mounts and initiates sperm transfer via pedipalp insertions into her genitalia. The male holds the gift with the claws of his third pair of legs and returns to a face-to-face position between each pedipalp insertion. During mating the female consume part of the gift and once the mating is complete, she leaves with the remaining of the gift (Albo & Costa, 2010; Costa-Schmidt et al., 2008).

Effects of food availability and mate competition in the field

Here, we aimed to examine the prevalence of the two mating tactics and the potential effects of prey availability and mate competition along the mating season in a natural population. We predicted less competitive (small) males producing worthless gifts when prey is limited and competition is high, whereas more competitive (large) males would produce worthless gifts when competition is low. We conducted a field study during the second mating season, from September to December in 2015 and 2016 at a population located in Santa Lucia river in Minas, Lavalleja (34.278 S, 55.233 W), Uruguay. We visited the site during each month, totalling 8 collections, but we excluded one date due to only one gift was found, reducing the dates to 7.

We examined the likelihood of worthless gifts in relation to pre- and post-copulatory mate competition, male size/body condition and prey availability. On every sampling date, four people manually collected all spiders from the same patch for one hour. The sampling method involved colleting the spiders by hand and placed them into small plastic jars (8 cm diameter and 7 cm height). This was done along the river coast (pebbles and water) being the patch size approximately of 96 meters long, providing a good representation of the population (i.e., near 100 individuals per hour). We performed the sampling using headlamps during the night, when the spiders are active (approximately from 10 to 11 pm). We kept all spiders individually in vials for data registration and when males carrying nuptial gifts were found, we removed the gift from the males' chelicerae using tweezers and transferred it into an Eppendorf tube. To assess the gift content, we first weighed gifts (mass, in nearest 0.0001g) and later dissected them to register their content using tweezers under a stereomicroscope. We classified gifts as "nutritive" (containing fresh prey) or "worthless" (containing prey leftovers or other non-nutritive items) following previous protocols (Albo, Winther, et al., 2011). This classification was verified by examining the gift weight in relation to its type of content (mean ± SE: Nutritive gifts 0.0046 ± 0.0003, N = 59, Worthless gifts 0.0014 ± 0.0001, N = 40; GLM (Gaussian): Estimate = -0.0032, $P < 0.001$).

We collected a total of 577 spiders and classified individuals into juveniles, subadults, adult males or females, and recorded whether males were carrying gifts and females were carrying an eggsac. We used the operational sex ratio (OSR) as a measure of the intensity of pre-copulatory competition and calculated it as the number of adult males divided by the number of adult males plus the number of receptive adult females (without an eggsac) (Kvarnemo & Ahnesjö, 1996). As in other gift-giving spiders, females of *P. ornata* are polyandrous, and they only have their eggs fertilized and produce an eggsac after multiple matings late in the season (Albo et al., 2019; Pandulli-Alonso et al., 2017; Tuni et al., 2013). Thus, finding more females with an eggsac indicate that more females have mated with multiple males, suggesting high sperm competition. Thus, following a previous study (Albo et al., 2019), we account for post-copulatory competition using the proportion of females carrying an eggsac, calculated as the number of females carrying an eggsac in relation to the total number of adult females. We weighed (live body mass, in nearest 0.001g) (mean ± SE: 0.11 ± 0.002) and measured the size (cephalothorax width, in nearest 0.1mm) of each adult male (mean ± SE: 4.27 ± 0.029; range: 3.0-5.9), after which all animals were released at the same site of collection. This data allowed us to calculate the male body condition (residual index) from the residuals of the weight~size regression (Jakob et al., 1996). Finally, during each date we obtained samples of small invertebrates in the riparian habitat (a total of 20.892 potential spider prey) by using a light trap consisting in a white fabric sheet (60 x 80 cm) and a camping lantern (10.5 cm diameter and 19.5 cm height), placed next to the watercourse at approximately 50cm above ground level for two hours (including the hour of the spiders sampling). We preserved the sampled invertebrates in 75% alcohol for later counting under a stereomicroscope. We estimated prey availability as the total number of prey (all taxonomic groups) found in the light traps.

First, we performed exploratory analyses using Generalized Linear Models (GLM) to examine the variables measured along the mating season (days). This allowed us to understand which variables were relevant (and not correlated) for the main model to explain the probability of worthless gifts along the season. We calculated the proportion of males with worthless gifts as the number of males with a worthless gift divided by the total number of males with gifts and explored this variable using

Quasibinomial distribution. The ecological variables examined were prey availability (Gamma distribution), OSR (Quasibinomial distribution) and females carrying an eggsac (Quasibinomial distribution). In all explorations we included the days as the independent variable. Similarly, we examined the individual variables as males' size (Gaussian distribution), weight (Gaussian distribution), and body condition (Gaussian distribution) along the season and between the two years of fieldwork by including days, year and their interaction as independent variables. Because significant differences in relation to the male individual variables (male size and body condition) were found between years, (supplementary material Table S1) we performed all the analysis including the year in interaction with the individual variable. During the exploratory analyses we found no effect of mating season over female size ($p = 0.262$) or female weight ($p = 0.920$). Females gained weight near their oviposition at the end of the season, and we found a significant effect of the proportion of females with eggsac on the female weight ($p = 0.038$). Further, season (days) and proportion of females carrying an eggsac were strongly correlated, and therefore we only included females carrying an eggsac excluding days from the models, preventing multicollinearity. We performed statistical analyses using R version 4.2.2 (R Core Team, 2022).

To explain the probability of worthless gifts, we performed two GLMs with binomial error distribution using the mating tactic (0: nutritive gift, 1: worthless gift) as the dependent variable. In both models we included as independent variables prey availability, OSR, females carrying an eggsac and year, each variable in interaction with one of the individual variables: a) one model including the male size and b) one model including male body condition. Males size accounts for long-term feeding regime due to prey availability affects spiders' growth during immature stages until adulthood, when they reach a fixed body size. In contrast, body condition (weight ~ size) accounts for short-term feeding regime as the weight will strongly depend on the amount of prey available and individual foraging ability. We transformed prey number (log) to meet the assumption of homoscedasticity. We used the step-wise model selection with Akaike Information Criterion (AIC), in order to select the best model explaining worthless gift probability (K. Burnham & Anderson, 2003). Models were fit using functions of the R packages lme4 and AICcmodavg (supplementary material Table S2, S3) (Bates et al., 2015; Mazerolle, 2019).

Effects of mate competition when food is available under laboratory conditions

Here, we aimed to assess whether the competitive environment, regarding pre- or post-copulatory mate competition, affects male gift investment, courtship duration, mating access and duration. We predicted females favouring mating duration with males offering nutritive food gifts when competition is high. We collected juveniles and subadults (n = 146) between 9 pm and 11 pm during the beginning of mating season (August-September) in 2017 from the same locality of the field study and transported them to the laboratory where they were maintained individually in plastic jars (8 cm diameter and 7 cm height) with pebbles at the bottom and a small tree branch. To accelerate their development, we held individuals in a temperature-controlled room at 26.1 °C (± 0.23 SE). We provided water in a cotton wool daily and twice a week we fed them with fruit flies (*Drosophila* sp.). Once individuals reached adulthood, we transferred them to the experimental room at an average temperature of 21.66 °C (± 0.15 SE). We continued the same feeding regimen for adult spiders during the whole experimental period. Virgin adult males and females commenced trials 20 days after their moult to adulthood. This adult maturation period ensured all spiders were sexually mature and receptive to mate (Klein et al., 2012). Due to the interactive effect of male size with ecological variables over the probability of worthless gifts found in the field study, we measured male body size and, in all trials, we used medium size males (range: 3.9-4.4 mm) that were randomly assigned to the experimental groups (see below). All individuals were preserved in 75% alcohol after concluding the behavioural study.

Worthless gifts likelihood

We examined male changes on gift production (nutritive/worthless gifts) in three groups. In the 'No competition group' (*NoC,* males n =17), we exposed males to unmated females in the absence of a competitor male. In the 'Pre-copulatory competition group' (*PreCopC,* males n = 19), we exposed males to unmated females in the presence of a competitor male. In the 'Post-copulatory competition group' (*PostCopC,* males n = 10), we exposed males to already mated females in the absence of a competitor male. We verified no differences in males' sizes across groups (mean ± SE: *NoC* group 4.18 ± 0.04 mm; *PreCopC* group 4.17 ± 0.04 mm; *PostCopC* group 4.12 ± 0.04 mm; $F_{2, 43} = 0.40$, $p = 0.67$). Note that the final sample size in *PostCopC* was reduced to 10 due to 7 males did not fit into the medium size selection, as they were largest. We assigned each male to one of the three groups and repeatedly exposed (every four days) them to court (but not mate) a different female over five consecutive trials. For trials replicates, we assigned the 74 unmated females in the *NoC* and *PreCopC* trials, but assuring each male was exposed to five different ones; 19 mated females were assigned with a similar procedure in the *PostCopC* trials. For the *PostCopC* group, mated females were previously exposed to a male offering a wrapped housefly one week before trials. In the three groups, males had the opportunity to wrap in silk and offer either a nutritive gift, consisting of a recently captured housefly (*Musca domestica),* or a worthless gift by grabbing an exuviae of *Tenebrio molitor* larva. Males sometimes can offer the prey item unwrapped, but for the purpose of this paper and in concordance with our field data, we considered only the items wrapped in silk as nuptial gifts.

In the first trials, females' adulthood age averaged 31.8 days (± 22.2 SD) and males' adulthood age averaged 27.6 days (± 18.2 SD). We performed the trials in transparent glass cages (30 x14 cm base, 20 cm height), in which we simulated natural conditions by covering the bottom with pebbles and water. Following previous protocols (Albo, Melo-González, et al., 2014; Albo & Peretti, 2015), we first placed females in the experimental cages 24h before trials, allowing them to habituate and deposit silk that stimulates male courtship and gift production (Albo et al., 2009). The day of the trial, in the groups *NoC* and *PostCopC* (without a competitor male), we placed each male in the experimental cage with the corresponding female and six exuviae distributed along the bottom of the cage. For the *PreCopC* group (with competitor male), we removed the female from the cage immediately before the trial and placed both males (focal and competitor) into it. Once they made physical contact and the contest began (pushing legs towards each other), we enclosed the competitor male in a small mesh, keeping them separate but allowing leg contact during the trial. At that time, we placed the female again in the cage and distributed six exuviae along the cage. For the three groups, we waited until the male started courting the female (fast vibrations of forelegs) and then offered him a live housefly with tweezers. This procedure allows males to detect the prey wing vibrations, promoting its capture (Albo et al., 2009; Albo, Melo-González, et al., 2014; Albo & Costa, 2010; Albo & Peretti, 2015; Pavón-Peláez et al., 2022), while it also allows us to homogenise the access to prey among males, and avoids female capturing the prey. We repeated this action every 15 min, until the male grabbed and captured the housefly, or grabbed any exuviae from the pebbles. We finished the trials when the male offered the wrapped gift to the female, preventing males from mating using a paintbrush and ensuring that all individuals were unmated. From a total of 220 trials, in 7% of the cases males did not grab any item and in 13% of the cases the males grabbed an item but did not wrap it in silk, and thus we finished these trials an hour after the experiment started. We used and analysed only the data from 80% of the cases (177 trials) in which males offered a wrapped gift to the female (*NoC* group = 64 trials; *PreCopC* group = 67 trials; *PostCopC* group = 46 trials).

During courtship males could grab the prey or an inedible item to wrap in silk. We registered the gift production as the occurrence of silk wrapping of an item (housefly or exuviae) by males during courtship. Using an individual data matrix, we tested differences in the probability of producing worthless gifts (dependent variable; 1: worthless, 0: nutritive) by using Generalised Linear Mixed Model (GLMM) with Binomial error distribution including groups (*NoC, PreCopC* and *PostCopC*) as fixed effects. In order to consider repeated measurements within males and females, we included both sexes ID as a random intercept and male adulthood age as a covariate. During exploratory analysis we found no effect of experiment number and therefore this variable was not included in the model. The model was fit using functions of the R packages lme4 (Bates et al., 2015).

Mating access and duration

We analysed the mating access and duration in the three groups (*NoC, PreCopC* and *PostCopC*) by exposing the same males to a subsequent final trial (number six) under the same competitive environment and this time we allowed them to mate. We followed the previous experimental protocol. We allowed males to mate only after they offered a wrapped gift to the female, and the interaction was considered finished when the male stopped mounting and the female walked away or when the female rejected to mate.

We registered courtship and mating occurrence. Courtship duration (min) was calculated as the time since the male started courting until he started the pedipalp insertion, whereas mating duration (min) was calculated as the sum of all pedipalp insertion durations. We used GLMs to examine the differences in courtship duration, mating access and mating duration by using them as dependent variables and including the mating tactic (nutritive gift/worthless gift), group (*NoC*, *PreCopC* and *PostCopC*) and the interaction as independent variables. The models included a Binomial error distribution for occurrence of mating, Gamma error distribution for courtship duration and Gaussian error distribution for mating duration. We transformed mating duration (log) to meet the assumptions of normality and homoscedasticity. The models were fit using functions of the R packages lme4 (Bates et al., 2015).

Results

Effects of food availability and mate competition in the field

In the field, we collected a total of 222 males of which 44% were carrying nuptial gifts. From all gifts collected (n = 97), 60% were nutritive and 40% were worthless. We found that worthless gift proportion (p = 0.980), prey number (p = 0.439) and pre-copulatory competition measured by the OSR (p = 0.745) did not correlate with the mating season as these fluctuated along it (Figure 1A). In contrast, the intensity of post-copulatory competition quantified by the percentage of females carrying an eggsac increased significantly over time (β = 0.006, p = 0.017) (Figure 1A). Males' size varied, and individuals at the beginning of the season were smaller than the ones found later in the season; males' weight and body condition did not change (Supplementary material Table S1) (Figure 1BCD). Both male size and weight differed between years (Supplementary material Table S1), but male body condition did not.

When considering the full model including prey availability, OSR, proportion of females carrying an eggsac, year and male size, the probability of worthless gifts decreased in the dates where large prey number occurred, while it increased when larger number of females carrying an eggsac were found (Table 1). Both variables interact with male size, and as it is shown in Figure 2AB, this interaction was restricted to small males. For large males, the probability of worthless gifts was not affected by prey availability, but it was moderately high at the beginning of the season when the number of females carrying an eggsac was low. We did not find any effect of the OSR on the worthless gift probability. Except for the interaction with individual male trait, similar effects were found when including male condition, instead of size, in the model (Table 1).

Effects of mate competition when food is available under laboratory conditions

Worthless gifts likelihood

The probability of offering a worthless gift significantly differed according to the competition context (Table 2; Figure 3A). Even when prey is available, males under post-copulatory competition (*PostCopC*) increased the usage of inedible items offering significantly more worthless gifts (41%) than males from the other groups (20% *NoC* and 13% *PreCopC*).

Mating access and duration

We did not find differences in courtship duration neither depending on the group (*NoC*, *PreCopC*, *PostCopC*) nor on the mating tactic (nutritive gift/ worthless gift) (Table 2; Figure 3B). We found that in the post-copulatory competition group males offering worthless gifts increased their mating access with no significant effect, whereas they acquired shorter mating durations compared to those offering nutritive gifts (Table 2; Figure 3CD).

Discussion

We show that the maintenance of gift-giving tactics in the studied population of *P. ornata* strongly depends on the interaction between prey availability and post-copulatory competition. As expected for riparian habitats we found high variation on prey availability (Hagen & Sabo, 2014; Iwata et al., 2003; Kato et al., 2003; Lytle, 2002), whereas post-copulatory mate competition increases along the mating season. In this population the frequencies of nutritive and worthless gifts highly vary in time (this study). This suggests that the changes in the selective forces probably alter the benefits and costs of the mating tactics, driving individual males to maximize their fitness success according to their own size, as reported for other mating systems (Hendrickx et al., 2015; Kasumovic et al., 2008). We also found males' decision on the alternative mating tactic (worthless gift) can occur regardless of low competitiveness (i.e., small size). Both small-medium and large males produce worthless gifts, but prey availability and post-copulatory mate competition act differently on each male size. Small-medium males mostly produce worthless gifts when prey availability is low and post-copulatory competition is high, which is consistent with a conditional strategy (Brockmann et al., 2008; Engqvist & Taborsky, 2016; Gross, 1996a). In contrast, very large males do not rely on prey availability for gift production as even under low prey numbers these males produce nutritive gifts, whereas they only produce worthless gifts when post-copulatory competition is low. Dominant males have been seen benefiting and parasitizing the courtship effort from subordinate males in some fish species. This usually happens when the competition context is high and therefore males favour their fertilization success by changing from the dominant tactic to a new alternative tactic (Pires et al., 2021; Taborsky, 1994, 2001; Taborsky et al., 1987; van den Berghe, 1988). Unlike those cases, in *P.*

ornata more competitive large males perform the same alternative tactic as less competitive small-medium males, though in a different context.

Living under highly changing environmental conditions is challenging for organisms survival and reproduction (Candolin & Heuschele, 2008; Endler, 1995; Janicke et al., 2015). In an evolutionary time-scale, ephemeral resources, such as riparian insects, most probable have favoured the large flexibility of the gift-giving tactic in the studied population. Consequently, in an ecological daily time-scale these plastic males can maximize their fitness by shifting the mating tactic depending on food and competition. Individual sizes seem a fundamental matter for the mating tactic decision in gift-giving spiders since males need to cope with changes in prey availability. When food resources are scarce, small-medium males would benefit from eating the prey to gain energy and producing worthless gifts. But, present prey limitations do not affect large males and they probably have enough energy to invest in offering a nutritive gift instead of consuming it (Zhang et al., 2021). In fact, when analysing body condition instead of body size, the probability of offering nutritive gifts also increases with better conditions. This verified previous field data (Albo, Melo-González, et al., 2014) and was recently tested under semi-natural conditions for another gift-giving spider (Heimerl et al., 2022). For achieving large sizes or good body condition males need to be well fed in the recent past or during juvenile stages (Bonduriansky, 2007). In spiders, silk investment and gift content are dependent on the short- and long-term feeding regimes of males, and poorly fed males tend to avoid starvation instead of investing in the gift (Albo, Toft, et al., 2011; Macedo-Rego et al., 2016; Trillo et al., 2014).

Large males are highly competitive as they are able to invest in nutritive gifts and in addition they benefit from longer mating durations because of their size (Pandulli-Alonso et al., 2022). This is an advantage late in the season when post-copulatory competition is increasing, because sperm transfer is positively correlated with mating duration (Albo & Peretti, 2015). This can explain why large males only offer worthless gifts in absence of mate competition, which is also benefiting them as they would acquire similar mating duration from performing either mating tactic (Albo, Melo-González, et al., 2014). Our laboratory experiments showed that post-copulatory competition increases the probability of medium males of producing worthless gifts. Further, they may eventually access more matings but with shorter duration compared to those offering nutritive gifts. Thus, small-medium size males advantage offering nutritive gifts early in the season when mate competition is low and can even acquire matings with unmated females that accept males without gifts (Albo, Melo-González, et al., 2014; Albo & Costa, 2010). Later, when post-copulatory mate competition is present, these less competitive males benefit from doing the “best of a bad job” and invest least by offering worthless gifts. Similarly, a recent study on this species showed that when facing sperm competition risk, males decrease their investment in silk wrapping of the gift, enabling them to increase the number of gifts produced and therefore the courted females (Macedo-Rego et al., 2021). Thus, under post-copulatory competition males benefit through increasing the number of mates instead of the success of each. We did not measure silk investment, but males can add more silk when producing worthless than nutritive gifts (Pavón-Peláez et al., 2022). The fact that *P. ornata* females seem attracted to the silk wrapping of the gift (Trillo et al., 2014) may explain the increased mating access acquired by males offering worthless gifts here. Given their shortest mating durations, these small-medium males would have low number of sperm stored (Albo et al., 2013; Albo & Peretti, 2015; Tuni et al., 2017) and a disadvantage in sperm competition (Parker, 1970; Parker & Pizzari, 2010; Simmons, 2001). Additionally, as found in other taxa it is possible that smaller males could produce less sperm than larger males (Chung et al., 2021) or have low sperm performance and endurance (Taborsky, Schütz, Goffinet, & Sander van Doorn, 2018; but see Kustra & Alonzo, 2020). Therefore, our conclusion from these findings is that under post-copulatory competition large competitive males would invest in nutritive gifts, whereas less competitive males would advantage in producing worthless gifts investing in number of mates rather than in sperm transfer time. Because large males are less in number (67% small-medium and 33% large) this explains the prevalence of high proportions of worthless gifts in the population.

Overall, our findings add evidence to the body of literature evaluating the synergetic effects of competitive environments in reproductive investment on pre- and post-copulatory traits (Chung et al., 2021; Devigili et al., 2015; Macedo-Rego et al., 2021; McDonald et al., 2017; Pélissié et al., 2014; Simmons & Buzatto, 2014; Tuni et al., 2017). From the two components of mate competition, we found that the expression of the alternative mating tactic in gift-giving spiders is mostly modulated by the effects of post-copulatory but not by pre-copulatory competition. Pre-copulatory sexual selection usually favours traits that maximize mating access (Markow, 2002), and in *P. ornata* mating access is not differentially favoured by any gift-giving tactic. Instead, as gifts are wrapped in silk, females appear to not differentiate between gift contents and accept mating with similar frequencies with males offering either nutritive or worthless gifts (Albo, Melo-González, et al., 2014; Pandulli-Alonso et al., 2017). The importance of post-copulatory sexual selection increase in gift-giving species due to females gain food resources through multiple matings and food gifts (Arnqvist & Nilsson, 2000; Collet et al., 2012; Morimoto et al., 2019). For example, in a population of the spider *Pisaura mirabilis,* females counteract male deception by shortening mating duration hence, reducing sperm transfer (Albo, Winther, et al., 2011). However, while in this species mating duration can last more than one hour giving females enough time to assess gift content (Stålhandske, 2001), *P. ornata* mating duration hardly exceeds one minute (Albo & Costa, 2010), leaving no time for them to distinguish between mating tactics. Additionally, for males the investment in food gifts would be inevitably shared with the fertilizations of other males and thus, they should invest in nutritive gifts when the paternity to acquire is highly probable. Double mated females can bias the full paternity towards large males regardless of the mating tactic and mating order (Albo et al., 2023). However, in another gift-giving spider, priority patterns for paternity success vary from the longest mating duration, to the first male, to no pattern at all, according to the number of matings acquired by the females (Drengsgaard & Toft, 1999; Matzke et al., 2022). Thus, even though paternity can be monopolised by large males, there might be a chance for small-medium males (that mate first) to obtain paternity when females mate with multiple males.

Understanding the interactive effects of changing environmental conditions and the agents of sexual selection on individual phenotypes is a challenging research area to explore. Using a spider population with high variation in the frequencies of the gift-giving tactics we disentangle the effects of prey availability and mate competition showing that these selective pressures act differently on males according to their size. As expected, small-medium males invest in deceptive tactics in a highly competitive environment, but also more competitive large males acquire benefits from performing the deceptive tactic when post-copulatory mate competition is low. As far as we know these are novel findings showing that the same alternative tactic is chosen by more and less competitive males and brings the opportunity to further develop research on the eco-evolutionary dynamics of deceptive tactics along populations of this species.

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Table 1. Worthless gifts probability in relation ecological and individual variables. Parameter estimated and p-values of the final models selected to explain worthless gift probability along the mating season. Models were performed using GLM with binomial error distribution. Initial models included prey number (log), females carrying an eggsac (proportion), OSR and year, all four in interaction with A) male size (mm), or B) male body condition as independent variables. Final models selected included A) prey number (log), females carrying an eggsac (proportion) both in interaction with male size (mm), B) prey number (log), females carrying an eggsac (proportion) and male body condition. Significant differences are shown in bold.

	Worthless gift probability (N = 97)		
A: Ecological variables + male size	Estimate (SE)	IC (95%)	z value
Intercept	-0.140 (0.258)	-0.64 – 0.38	-0.541
Prey number (log)	-2.017 (0.624)	-3.37 – -0.92	-3.231
Male size	-0.639 (0.273)	-1.20 – -0.12	-2.337
Females carrying an eggsac	1.980 (0.710)	0.73 – 3.53	2.789
Prey number*Male size	1.479 (0.602)	0.40 – 2.79	2.457
Females carrying an eggsac*Male size	-1.836 (0.732)	-3.45 – -0.55	-2.509
B: Ecological variables + male condition	Estimate (SE)	IC (95%)	z value
Intercept	-0.481 (0.229)	-0.94 – -0.04	-2.105
Prey number (log)	-0.834 (0.338)	-1.54 – -0.20	-2.471
Male body condition	-0.520 (0.253)	-1.05 – -0.04	-2.052
Females carrying an eggsac proportion	0.662 (0.377)	-0.05 – 1.4 4	1.757

Table 2. Males gift-giving behaviours under mate competition. Parameter estimates, standard error (SE), test and p-values to explain the probability of worthless gifts, courtship duration, mating access and mating duration. A) Model (GLMM) for assessing worthless gift probability across groups: No competition (*NoC*), Pre-copulatory competition (*PreCopC*) and Post-copulatory competition (*PostCopC*); including male and female identity as random effect and age as a covariate. B) Model (GLM) for assessing courtship duration (min), mating access and mating duration (min); including group, mating tactic (nutritive gift/worthless gift) and their interaction. Significant differences are shown in bold.

	Worthless gift probability (N = 176)		
A: Group	Estimate (SE)	z	P
Intercept (*NoC*)	-1.406 (0.396)	**-3.550**	**<0.0001**
PreCopC	-0.655 (0.550)	-1.192	0.233
PostCopC	1.158 (0.561)	**2.063**	**0.039**

	Courtship duration (N = 31)			**Mating access** (N = 39)			**Mating duration** (N = 31)		
A: Mating tactic + Group	Estimate (SE)	t	P	Estimate (SE)	z	P	Estimate (SE)	t	P
Intercept (*NoC*, NG)	0.012 (0.002)	5.157	**<0.0001**	2.197 (1.054)	2.084	**0.037**	-0.321 (0.221)	-1.450	0.159
PreCopC	0.002 (0.003)	0.508	0.616	-0.993 (1.243)	-0.799	0.424	0.436 (0.305)	1.429	0.165
PostCopC	0.004 (0.006)	0.777	0.444	-1.792 (1.394)	-1.285	0.199	0.866 (0.443)	1.956	0.062
WG	0.008 (0.008)	0.981	0.336	-1.504 (0.616)	-0.931	0.352	0.733 (0.519)	1.412	0.170
PreCopC *WG	0.001 (0.013)	1.063	0.951	0.993 (2.132)	0.466	0.641	-1.142 (0.731)	-1.940	0.064
PostCopC *WG	-0.005 (0.011)	-0.480	0.635	19.665 (2917.013)	0.007	0.995	-1.674 (0.711)	**-2.356**	**0.027**

Figure 1. Ecological and individual variables along the mating season in a *Paratrechalea ornata* population. Field data showing A) the occurrence of worthless nuptial gifts and potential explanatory variables. Data points show in the left axis the proportion of worthless gifts (number of worthless gifts collected on date/number of total gifts collected on date), sexes proportion (number of males/ number of males + number of receptive females), the proportion of females carrying an eggsac (number of females carrying an eggsac/ total number of adult females) and in the right axis the prey availability on date (log); male traits along the season: B) size (mm), C) weight (g), and D) body condition (residuals of weight ~ size regression), presented as boxplots (thick horizontal line the median, black dots represent the mean, lower and upper hinges correspond to the first and third quartiles, and whiskers represent the 95% confidence interval; black dots out of the boxplot represent outliers). White and grey colours represent years 2015, 2016, respectively.

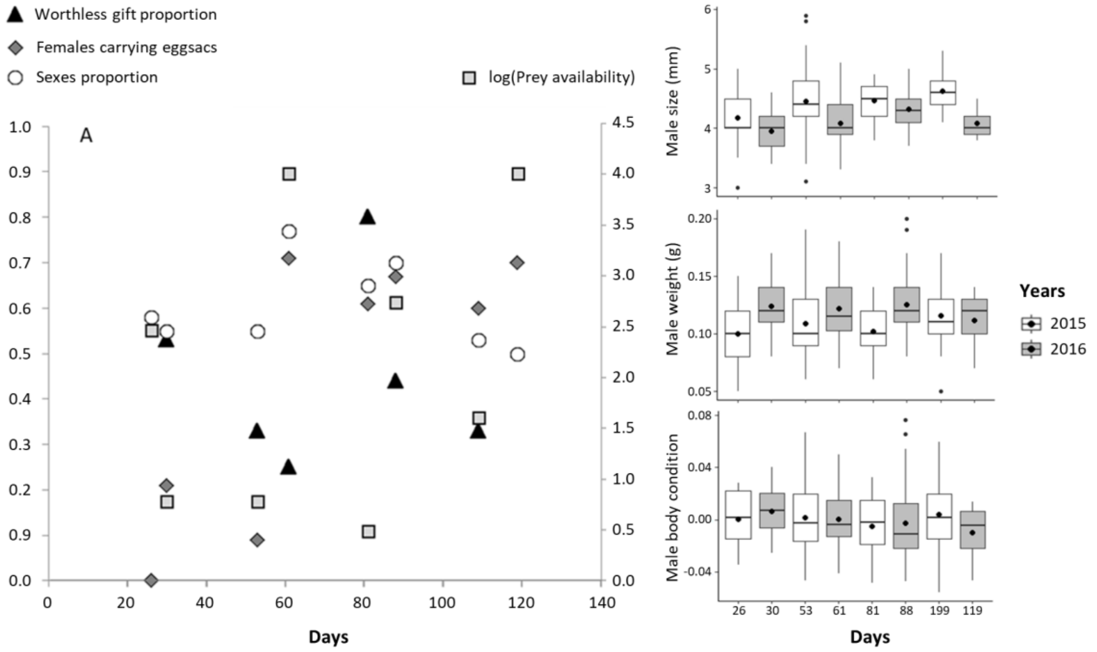


Figure 2. Worthless gifts probability in relation to prey and post-copulatory competition. Generalized Linear Mixed Models showing the probability of worthless gifts in relation to: A) number of prey, B) proportion of females carrying an eggsac, in an interaction with male size (mm). Both models have year as random effect. Model prediction represented in black line, confidence interval in grey and observed data as tick marks. Cross-sections are taken at the 10th, 50th, and 90th quantiles.

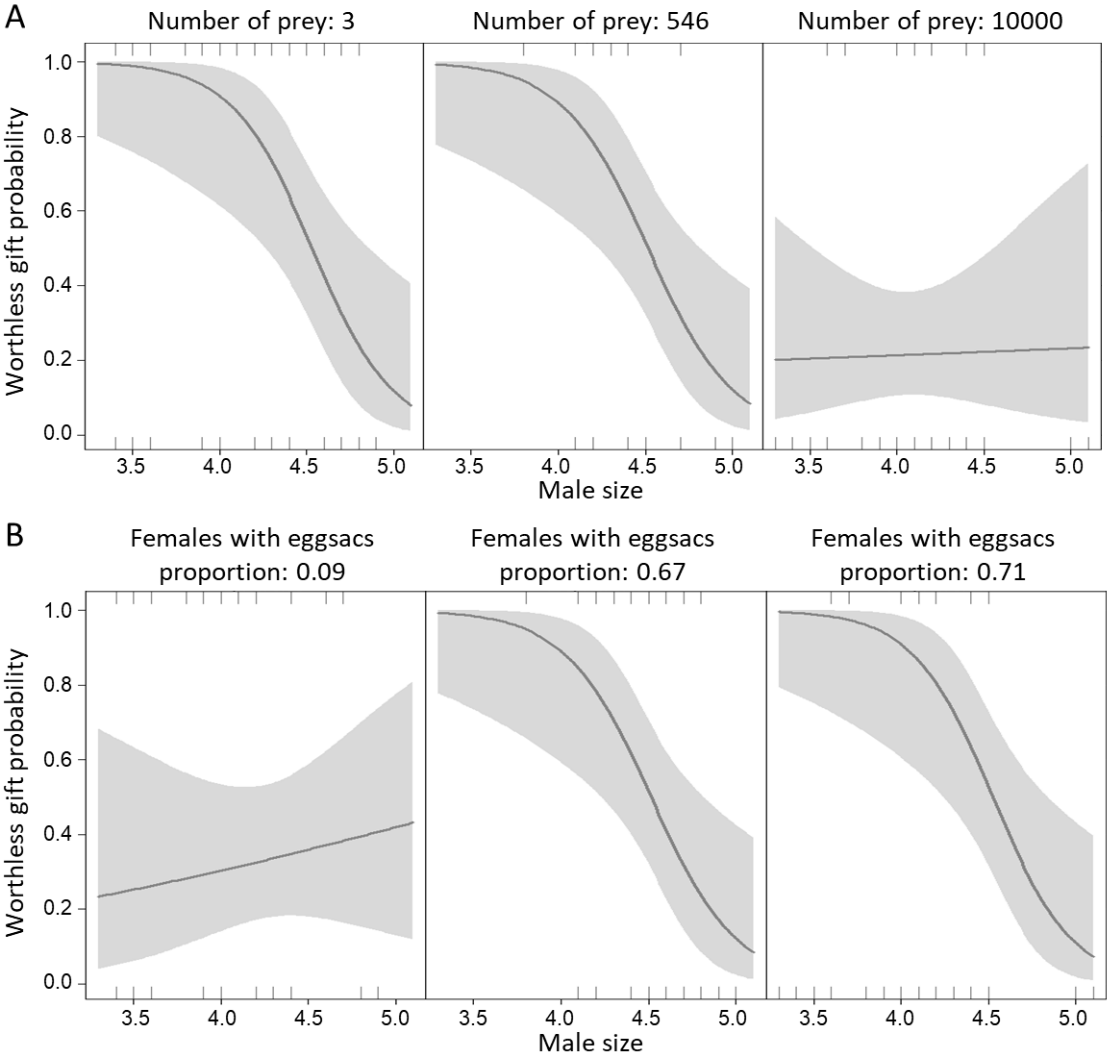
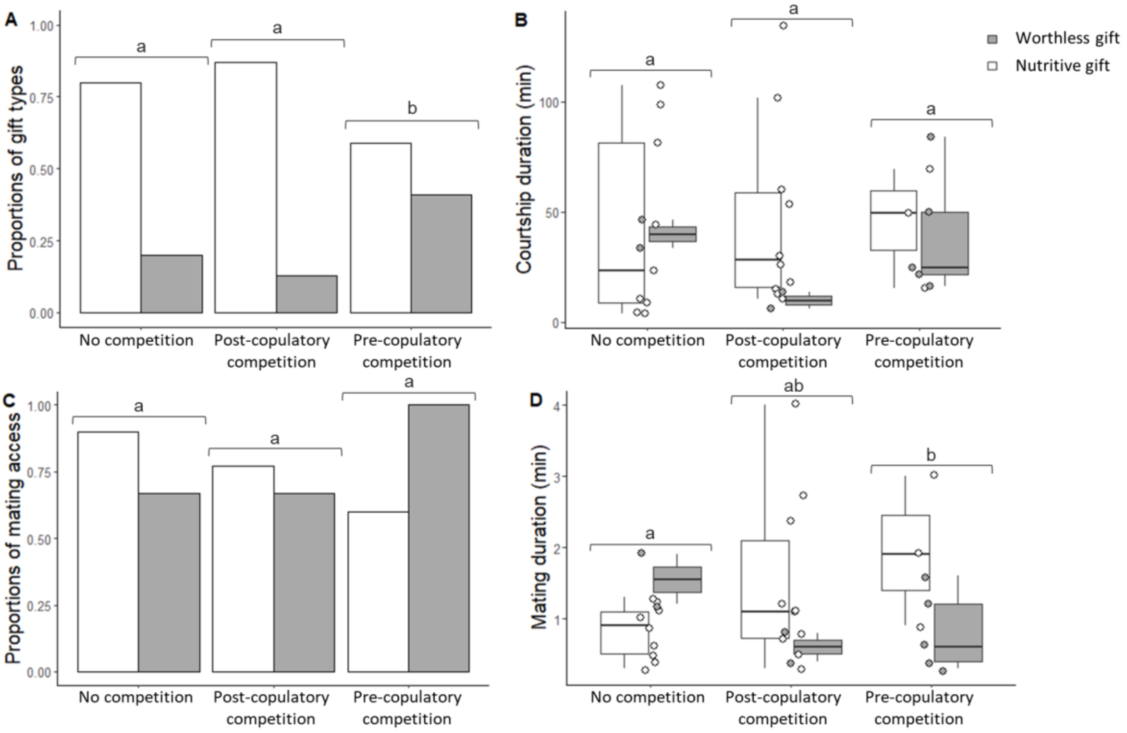


Figure 3. Males gift-giving behaviours under mate competition. Data from groups, No competition (*NoC*, n males = 17, N trials = 64), Pre-copulatory competition (*PreCopC*, n males = 17, N trials = 67) and Post-copulatory competition (*PostCopC*, n males = 10, N trials = 46), according to mating tactic (nutritive gift/worthless gift): A) proportion of mating tactics performed (all gifts per group), and B) courtship duration (min), C) proportion of mating access (only matings per group), D) mating duration (min). Black dots represent the raw data, thick horizontal line the median, lower and upper hinges correspond to the first and third quartiles, and whiskers represent the inter-quartile range. For each group, the proportions of nutritive gifts are shown in white and worthless gifts in grey. Different letters indicate significant differences among groups; post-hoc Tukey test showed no statistical differences between all categories.



SUPPLEMENTARY MATERIAL

Table S1. Parameters from models for male size (mm), male weight (g) and male body condition along mating season for the years 2015 and 2016. Statistical analyses were performed by using Linear Models, and the complete models included days and year as fixed effects. Significant differences are shown in bold.

	Male size (mm)		**Male weight (g)**		**Male body condition**	
	Estimate (SE)	P value	Estimate (SE)	P value	Estimate (SE)	P value
Intercept	4.147 (0.108)	**<0.0001**	<0.0001 (<0.0001)	**<0.0001**	<0.0001 (<0.0001)	0.973
Days	0.004 (0.002)	**0.004**	<0.0001 (<0.0001)	0.243	<0.0001 (<0.0001)	0.971
Year 2016	-0.256 (0.144)	**0.077**	<0.0001 (<0.0001)	**0.003**	<0.0001 (<0.0001)	0.193
Days:Year 2016	-0.000 (0.002)	0.640	<0.0001 (<0.0001)	0.149	<0.0001 (<0.0001)	0.164

Table S2. Comparison models for selection based on their AIC. GLM for worthless gift probability were performed using binomial error distribution and including prey availability (Prey), operational sex ratio (OSR), females carrying an eggsac (Feggsac), year (2015/2016) and male size (Msize) in interaction with each variable. Best model with the lowest AIC is shown in bold.

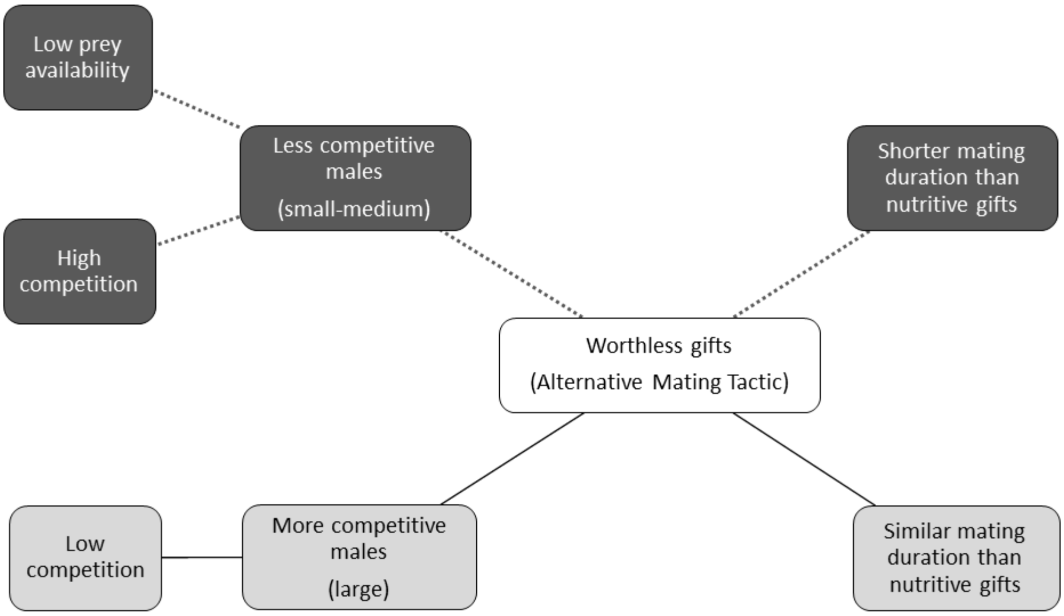
Model	Independent variables	AIC
1	**Msize:Feggsac + Msize:Prey**	**123.66**
2	Msize:Feggsac + Msize:Prey + Year	124.84
3	Msize:Feggsac + Msize:Prey + Msize:Year	126.48
4	Msize:Feggsac + Msize:Prey + Year + OSR	126.62
5	Msize:Feggsac + Msize:Prey + Msize:Year + OSR	128.39
6	Msize:Feggsac + Msize:OSR + Msize:Prey + Year	128.62
7	Msize:Feggsac + Prey	129.45
8	Feggsac + Msize:Prey	130.22
9	Msize:Feggsac + Msize:OSR + Msize:Prey + Msize:Year	130.38
10	Msize:Feggsac + Msize:OSR + Msize:Year + Prey	130.73
11	Msize:Feggsac + Prey + Year	131.02
12	Msize:Feggsac + Prey + Msize:Year	131.16
13	Feggsac + Msize:Prey + Year	132.22
14	Msize:Feggsac + Prey + Msize:Year + OSR	133.08
15	Msize:OSR + Msize:Prey + Msize:Year + Feggsac	133.28
16	Feggsac + Msize:Prey + Msize:Year	134.17
17	Feggsac + Msize:Prey + Msize:Year + OSR	135.94

Table S3. Comparison models for selection based on their AIC. GLM for worthless gift probability were performed using binomial error distribution and including prey availability (Prey), operational sex ratio OSR, females carrying an eggsac (Feggsac), year (2015/2016) and male body condition (Mbc) in interaction with each variable. Best model with the lowest AIC is shown in bold.

Model	Independent variables	AIC
1	**Mbc+ Feggsac + Prey**	**126.82**
2	Mbc + Feggsac + Prey + Year	126.82
3	Mbc:Feggsac + Prey + Year	127.17
4	Mbc + Prey	128.08
5	Mbc:Feggsac + Prey	128.39
6	Mbc:Feggsac + OSR + Prey + Year	128.73
7	Mbc + Prey + Year	128.81
8	Mbc:Feggsac + OSR + Prey + Year	129.11
9	Feggsac + Prey	129.44
10	Feggsac + Mbc:OSR + Prey + Year	130.06
11	Mbc:Feggsac + OSR + Prey + Year	130.22
12	Feggsac + Prey + Year	130.6
13	Mbc:Feggsac + Mbc:OSR + Prey + Year	130.79
14	Mbc:Feggsac + OSR + Mbc:Prey + Year	131.1
15	Feggsac + Mbc:OSR + Mbc:Prey + Year	131.39
16	Mbc + Feggsac	131.58
17	Mbc:Feggsac + Mbc:OSR + Prey	132.11
18	Mbc:Feggsac + Mbc:OSR + Mbc:Prey + Year	132.25
19	Mbc:Feggsac + Mbc:OSR + Prey + Mbc:Year	132.7
20	Mbc:Feggsac + OSR + Mbc:Prey + Mbc:Year	133.1
21	Feggsac + Mbc:OSR + Mbc:Prey + Mbc:Year	133.38
22	Mbc + Feggsac + Year	133.47

23	Mbc:Feggsac + Mbc:OSR + Male:Prey	133.66
24	Mbc:Feggsac + Mbc:OSR + Male:Prey + Mbc:Year	134.25
25	Mbc:Feggsac + OSR + Prey + Year	135.36
26	Mbc:Feggsac + Year	135.39
27	Mbc:Feggsac + Mbc:OSR + Year	137.3

Figure 1S. Schematic representation of the expected effects of prey and mate competition over the males size and the alternative mating tactic. Less competitive males (small) are expected to produce worthless gifts when food resources are limited and mate competition is high (conditional strategy), gaining lower fitness than when producing nutritive gifts. More competitive males (large) are also expected to produce worthless gifts but only when competition is low, acquiring similar mating duration than when offering nutritive gifts.



Final considerations and perspectives

The evolution of sexual traits has been subject of research for decades, yet there is a restricted understanding on the general patterns resulting from the interaction between the environment and sexual selection. In fact, there are contrasting findings on whether stressful environmental conditions strengthen or weaken sexual selection pressures (Candolin et al., 2007; Candolin & Heuschele, 2008; Jennions & Petrie, 1997; Passos et al., 2021). This is an outstanding discussion revealing large variations on individual responses that mostly rely on the different life-history strategies across the animal kingdom. A very important life-history trade-off is the one between investing in reproduction or in survival and maintenance (Boggs, 2009; Williams, 1966). Individuals need to cope with this type of decisions, especially when resources are limited (Magrath & Komdeur, 2003; Morehouse et al., 2010), or when environmental conditions change fast during their life-time (Bårdsen et al., 2011; Botero & Rubenstein, 2012). Unpredictably changing environments usually favour phenotypic plasticity as individuals benefit from the ability to switch between different traits or behavioural tactics to face different conditions (Bårdsen et al., 2011; Charmantier et al., 2008; Pigliucci, 2001). Additionally, as mating encounters vary with demographic and environmental conditions mating behaviours are usually plastic (Cornwallis & Uller, 2010; Dore et al., 2020). Therefore, when environmental cues are reliable, individuals can use this information to adjust their reproductive investment increasing their success according to the conditions. This, for instance, occurs in some birds as they increase their clutch-size when perceiving wetter climatic conditions which would improve offspring success (Rotenberry & Wiens, 1991), and in some guppies whose females decrease their sexual receptiveness when exposed to the presence of a predator (Gong & Gibson, 1996).

The genetic basis of plasticity and its potential to improve the fitness of individuals, implies that it can be target of natural selection and evolve according to the local conditions (Via & Lande, 1985). In fact, different conditions experienced by different population can result in a conditional evolutionary stable strategy with different levels of individual plasticity in mating tactics, a phenomenon known as genotype-environment interaction (Tomkins & Hazel, 2007). In this line, nuptial gift-giving mating systems with more than one mating tactic are determined both by the environmental conditions (e. g. prey availability) and the genetic basis of the sexual trait (Albo et al., 2023). This is, at the individual level, the production of either mating tactic (nutritive gift versus worthless gift) would be triggered by specific environmental cues, while the switch point between producing one or other would be genetically determined. Therefore, different populations exposed to different environmental conditions would be subject to different selective pressures acting on this switch point. This can result in different plastic expressions, which translates to divergent mating tactic proportions across populations.

Here, we take advantage of the semiaquatic spider *Paratrechalea ornata* as a biological model to examine the behavioural responses of individuals at both between and within population levels. This species is ideal for understanding the effects of the interaction between environment and sexual selection, first because individuals are plastic in the production of the sexual trait, wrapping in silk either fresh prey (nutritive gifts) or inedible items (worthless gifts) (Pavón-Peláez et al., 2022). Second, they are commonly exposed to stressful environments as conditions can change fast and unpredictably with precipitation regimen and floods in the riparian habitats (Hagen & Sabo, 2014; Iwata et al., 2003; Knight et al., 2005; Lytle, 2002; Sabater et al., 2022; Sanzone et al., 2003).

We found that, additionally, local environmental conditions can change due to local precipitation variability, and this directly affects the frequencies of deceptive worthless gifts at each population. This means that in the different populations there is a scope for different levels of plasticity in the reproductive investment. Males from populations exposed to extremely variable precipitation regimes would find it more successful to maintain almost fixed the production of deceptive worthless gifts. This allows them to be independent of the environment because the production of worthless gifts helps them to avoid relying on prey availability. This is also possible due to a relaxed selection on female preferences for the nuptial gift content under highly stressful environments (Albo et al., 2023; chapter 1, this thesis). In contrast, female choice is possible under moderate stressful conditions as we showed that when the population is exposed to a low precipitation variability *P. ornata* females can favour mating duration with males offering nutritive gifts. Thus, sexual selection can operate when environmental conditions are relatively favourable for individuals. As such, when studying the behavioural responses within a population under moderate stressful conditions, we show that mate competition has a significant effect on the mating tactics production and the resulting mating success. In the absence of competition males performing either mating tactic acquires similar mating durations, but when increasing post-copulatory competition females discriminate between mating tactic, favouring those males that offer nutritive gifts.

Overall, these findings unravel a very interesting evolutionary discussion exemplifying the conditions in which deceptive tactics can be maintained in high frequencies across populations. Deceptive mating tactics usually reduces female fitness and therefore are related to a decrease in males' reproductive success (Albo, Winther, et al., 2011; LeBas & Hockman, 2005). Selection against these tactics acts to maintain them at low frequencies in the populations (Brockmann, 2001; Croll et al., 2019; Gross, 1996b; Taborsky et al., 2008). However, under permanent changing environmental conditions where females cannot rely on the gift content, their fitness must become independent of the mating tactic, which relaxes their preferences. This explains the increase in the reproductive success of males using deceptive tactics, and its spread in such populations (Albo et al., 2023). As a perspective from these findings and discussion, an interesting approach for studying the maintenance of plasticity in spider nuptial gifts would be to develop a theoretical model to evaluate the possible evolutionary paths in the face of climate change and the increasing climatic instability. Examining males and females' responses according to their plasticity level, the risk of extreme events of precipitation, permanent prey availability along multiple generations, would give remarkable insights on the potential changes in female choice and the evolution of plastic and fixed sexual traits.

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