

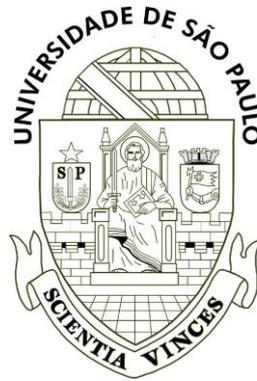
Sergio Nolazco Plasier

COMPENSAÇÃO FLEXÍVEL DO CUIDADO UNIPARENTAL:

As coisas nem sempre são o que parecem

FLEXIBLE COMPENSATION OF UNIPARENTAL CARE:

Things are not always what they seem



Instituto de Biociências
Universidade de São Paulo

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Sergio Nolazco Plasier

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EPIGRAPH

**The true beauty of science is that it's a
fantastic journey to the truth where you can
stumble across some amazing surprises.**

–The author

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RESUMO

Em algumas espécies com cuidado uniparental, quando o indivíduo parental deserta a prole ou morre, seu parceiro pode adotar as responsabilidades parentais, um comportamento conhecido como compensação flexível do cuidado uniparental. No entanto, para a maioria das espécies em que esta resposta comportamental tem sido relatada na literatura, não houve uma investigação completa de seus efeitos sobre a aptidão da prole. No opilião Neotropical *Serracutisoma proximum*, uma espécie com cuidado uniparental da fêmea, os machos donos de harem ficam sobre desovas desatendidas quando as fêmeas que normalmente cuidam dos ovos desertam ou morrem. Aqui, investigamos se esta espécie constitui um exemplo real de compensação flexível do cuidado uniparental, avaliando os efeitos de fatores ecológicos (como condições climáticas e disponibilidade de parceiras) e de história de vida (como sucesso reprodutivo passado do macho, tamanho da desova e canibalismo filial) sobre o comportamento dos machos e, em última instância, sobre a sobrevivência da prole. Esperamos que condições climáticas desfavoráveis, assim como baixa disponibilidade de parceiras e baixo sucesso passado dos machos, afetem negativamente a exibição de comportamentos compensatórios, mas que o tamanho da desova tenha um efeito positivo neste comportamento. Além disso, esperamos que um aumento na intensidade do canibalismo filial seja uma estratégia que alivie os custos da compensação. Contudo, exceto pelas condições climáticas que afetam tanto a intensidade do comportamento dos machos sobre as desovas quanto o canibalismo filial, os nossos resultados foram inconsistentes com as nossas previsões, e o comportamento dos machos em relação à prole desatendida não teve efeito sobre a sobrevivência da prole. Nossos resultados, portanto, não apoiam a existência de compensação flexível do cuidado uniparental em *S. proximum*. Ao invés de uma atividade parental, argumentamos que o comportamento dos machos corresponde a uma tática de acasalamento que aumenta o sucesso de fertilização e de acasalamento com as fêmeas que retornam às suas desovas ou com novas fêmeas que se alimentam dos ovos desprotegidos. Este estudo demonstra que, para os casos em que se pressupõe compensação flexível de cuidado uniparental, é necessário avaliar os efeitos sobre a aptidão da prole, uma vez que nem sempre um aparente comportamento parental é o que parece ser.

Palavras chave: *Cuidado amphisexual, Cuidado facultativo, Canibalismo filial, Esforço de acasalamento, Esforço parental.*

ABSTRACT

In some species with uniparental care, when the parental individual deserts the offspring or dies, its mate may adopt the parental responsibilities, a behaviour known as flexible compensation of uniparental care. However, for most of the species in which this behavioural response has been reported in the literature, there was no thorough investigation of its effects upon offspring fitness. In the Neotropical harvestman *Serracutisoma proximum*, a species with female uniparental care, harem-owning males stand on unattended clutches when the egg-tending females desert or die. Here, we investigated if this species constitutes an actual example of flexible compensation of uniparental care by evaluating the effects of ecological (namely, climatic conditions and mate availability) and life-history factors (namely, males' past mating success, clutch size and filial cannibalism) on males' behaviour and, ultimately, on offspring survival. We expected unfavourable climatic conditions, as well as low mate availability and males' past success, to negatively affect the exhibition of compensatory behaviours, but a positive effect of clutch size. Moreover, we expected an increase in the extent of filial cannibalism to be a strategy that alleviates the costs of compensation. With the exception of the effect of climatic conditions on the extent of both the behaviour of standing on unattended clutches and filial cannibalism, our results were inconsistent with our expectations, and males' behaviour towards unattended offspring had no effect on offspring survival. Our results, therefore, do not support the existence of flexible compensation of uniparental care in *S. proximum*. Rather than a parental activity, we argue that males' behaviour corresponds to a mating tactic that increases fertilization and mating success with the returning egg-tending females or newcomer mates foraging on the unattended offspring. This study demonstrates that for presumed cases of flexible compensation of uniparental care it is necessary to evaluate the effects on offspring fitness since not always an apparent parental behaviour is what it seems to be.

Key-words: *Amphisexual care, Facultative care, Filial cannibalism, Mating effort, Parental effort.*

INTRODUCTION

Parental care enhances offspring fitness in terms of improving survival, development, growth and/or overall quality (Clutton-Brock 1991; Alonso-Alvarez & Velando 2012; Santos et al. 2016), and ultimately the reproductive success of parents (Smiseth et al. 2012). However, it may also impose great costs on the caregivers (Clutton-Brock 1991; Gross & Sargent 1985; Alonso-Alvarez & Velando 2012), leading to a sexual conflict over care, in which each parent individually benefits from getting rid of the costs at the expense of its mate's effort (Lessells 1999; Houston et al. 2005). In this sense, when a caregiver alters its level of care, due to behavioural adjustments or offspring abandonment, its mate may adaptively respond by changing its own parental behaviour. For instance, a decrease in parental effort by one caregiver may be compensated by its mate increasing care according to its own interests, a pattern predicted by theoretical models (e.g., Winkler 1987; Houston & Davies 1985; McNamara et al. 2003; Johnstone 2011) and widely reported by empirical studies in species with biparental care (e.g., Itzkowitz et al. 2001; Hunt & Simmons 2002; Smiseth & Moore 2004; Harrison et al. 2009; Lehtonen et al. 2011) and cooperative breeders (e.g., Wright & Dingemanse 1999; MacGregor & Cockburn 2002; Zöttl et al. 2013).

Compensatory behaviours may also be present in species with uniparental care. In such cases, individuals of only one sex provide care, and when the caregiver dies or deserts the whole brood, the remaining parent may adopt the parental behaviour in order to compensate for its mate's absence ('flexible compensation of uniparental care', *sensu* Ringler et al. 2015). For example, in frogs with male-only care, the absence of a parental male results in females performing critical tadpole transportation to water (*Allobates femoralis*, Ringler et al. 2015; 2016) or brood protection (by repelling egg predators and preventing egg desiccation and fungal propagation) as efficient as their mates (*Eleutherodactylus johnstonei*, Bourne 1998). The assassin bug *Rhinocoris tristis* is another example in which males aggressively guard clutches, but in their absence, females behave likewise against predators, increasing offspring survival when compared to unattended clutches (Beal & Tallamy 2006). For each of these organisms, the compensatory response involves exhibiting a behaviour that is not regularly present in their repertoire, shifting from a non-parental to a parental state. Far from trivial, the expression of elaborate and complex compensatory parental behaviours must require the ability to perform them, but in most uniparental care species those behaviours have probably become evolutionarily constrained to one sex (Klug et al. 2012). This may explain, at least in

part, the rarity of reported cases of flexible compensation of uniparental care (also called 'facultative', or 'amphisexual' care [*sensu* Simon 1983]) in the literature.

The expression of adaptive compensatory behaviours is expected when the benefits surpass the costs, taking into account trade-offs between different components of fitness, for example, when time and/or energy expended in parental behaviours compromise mating activities (Gross & Sargent 1985; Stiver & Alonzo 2009). In such situation, parental effort (i.e., investment in current reproduction) should be favoured over mating effort (i.e., future reproduction), when mate availability or other factors that enhances mating success are relatively low (see review in Stiver & Alonzo 2009; Fig. 1). Likewise, when the brood is large, older and/or of high genetic quality (i.e., high offspring value), the benefits of providing care increase, favouring individuals that invest in parental behaviours rather than to mating effort (e.g., Carlisle 1985; Coleman et al. 1985; Montgomerie & Weatherhead 1988; Coleman & Fischer 1991; Curio & Onnebrink 1995; Koskela et al 2000; Fig. 1). The same positive association is expected regarding the effect of certainty of paternity (e.g., Alonzo & Klug 2012; Fromhage & Jennions 2016; Griffin et al. 2013), given that providing care to a larger proportion of genetically related offspring increases the male's reproductive success. Moreover, the benefits of care are boosted with increases in offspring predation pressure (Santos et al. 2016), favouring allocation to offspring protection over other competing activities (e.g., Rangeley & Godin 1992; Komdeur & Kats 1999, Steinhart et al. 2005). From an abiotic perspective, unfavourable conditions may directly affect parental effort, either through increases in offspring demands for higher levels of care (e.g., Jones & Reynolds 1999; Lindström et al. 2006; Klimczuk et al. 2015), or through decreases in parental abilities due to stressful physiological conditions (e.g., Chelini & Machado 2012; Consolmagno et al. 2016; see review in Wingfield & Sapolsky 2003; Fig. 1). The abiotic effect may also be indirect, through increases in the costs of care due to reductions in resource availability (e.g., Lavery & Kieffer 1994; Komdeur & Kats 1999; Barve & La Sorte 2016; Fig. 1) or due to changes in mates' reproductive activity and its above-mentioned consequences (Fig. 1). Therefore, multiple ecological and life-history variables can affect dynamically the cost-benefit differential of providing care, and thus the expression of related compensatory response patterns (Fig. 1).

Consuming part of its own brood (i.e., 'partial filial cannibalism') is argued to constitute an adaptive strategy that alleviates the energetic costs related to parental care (reviews in Manica 2002; Klug & Bonsall 2007), and may be of particular importance to species with compensatory responses. Although apparently counterproductive, by eating part of the brood, a parent gains energy and nutrients that are likely to be promptly allocated to its parental investment towards the remaining offspring, particularly when food availability is low (Manica

2002; Klug & Bonsall 2007; Fig. 1). Additionally, partial filial cannibalism is expected to increase with brood size because the relative costs of sacrificing a few eggs are likely to decrease with offspring number (Fitzgerald 1992; Manica 2002), while at the same time it may decrease sibling competition, increasing the per capita benefit of care to the remaining brood (e.g., Payne et al. 2002; Klug et al. 2006; Fig. 1). Moreover, the caregiver may avoid wasting time and energy caring for less valuable offspring by selectively consuming low quality offspring (Forbes & Mock 1998; Klug & Bonsall 2007), genetically unrelated offspring (e.g., Green et al. 2008; Neff 2003; Frommen et al. 2007; Gray et al. 2007), and even diseased or dead offspring, an action that can also prevent the spread of infections within the remaining brood (e.g., Kraak 1996; Bandoli 2016; Vallon et al. 2016). Given that filial cannibalism co-occurs with parental care, a more comprehensive understanding of flexible compensatory decisions should take into account their association.

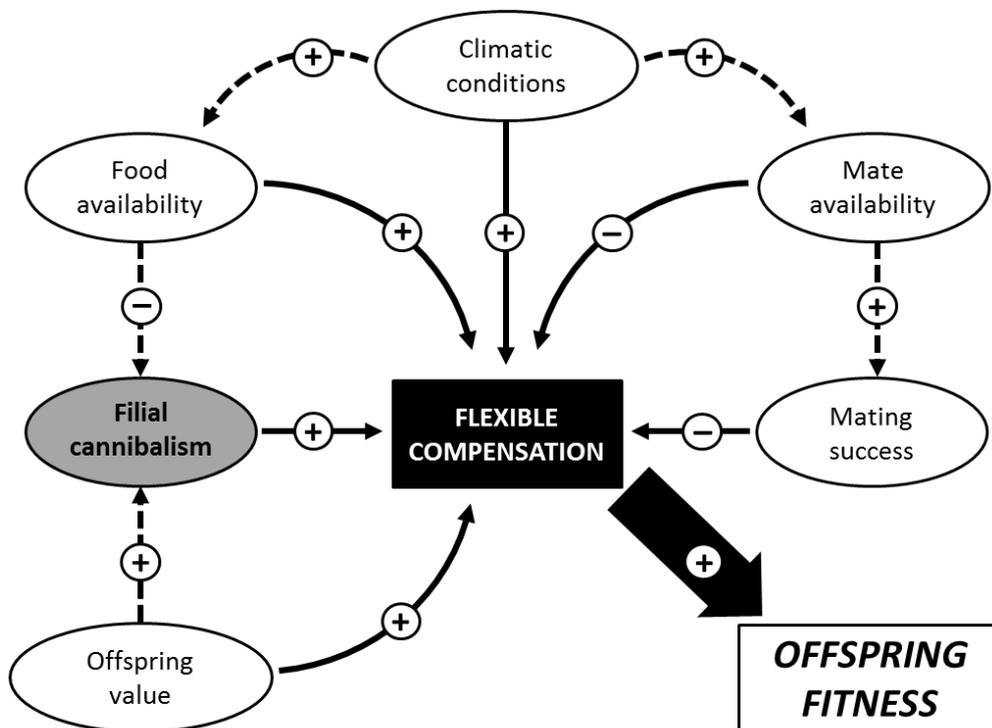


Figure 1. The expected effect of multiple ecological and life-history factors on flexible compensation of uniparental care and filial cannibalism. The arrows indicate the direction of positive (symbol '+') or negative (symbol '-') effects on parental decisions of males of the harvestman *Serracutisoma proximum*, which, in turn, should improve offspring fitness. Solid arrows represent direct effects while dashed arrows represent indirect effects. Although increases in egg predation pressure may promote compensatory behaviour, we do not include its effect in this schematic representation because we did not observe temporal variation on this ecological variable throughout the sampled period (see Supplementary Material S1). We also exclude the effect of certainty of paternity on this scheme because we assume that there is no considerable variation in this factor in our data because we restricted our sampling effort to clutches that only contained eggs from a first oviposition bout, which is preceded by intense mate-guarding and, consequently, reduced sperm competition risk.

In the Neotropical harvestman *Serracutisoma proximum* (Arachnida: Opiliones), territorial males defend host plants (used as oviposition sites by females) against other males during the breeding season, from September to April (peak in February; Buzatto & Machado 2008). At the beginning of the breeding season (i.e., September-October), territorial males engage in ritualistic fights using their second pair of legs in order to monopolize oviposition sites at the margin of forest streams (Buzatto & Machado 2008). When arriving at a territory, a female may copulate with the harem-owning male and lay a clutch of eggs, usually, on the underside surface of a leaf (Buzatto et al. 2007). Females provide care for the offspring until nymphal hatching and dispersal by standing on the eggs and aggressively repelling any egg predators in the close vicinity, which improve offspring survival (Buzatto et al. 2007). Although eggs can be attacked by fungal infections, parental females are not able to prevent this threat (as it occurs in other harvestmen; Mora 1990), and maternal care seems to be restricted to protection against offspring predators.

When *S. proximum* females die or desert their clutches temporarily, harem-owning males may approach and stand on the unattended offspring. However, while parental females generally tend to stay permanently on their clutches (Buzatto et al. 2007), harem-owning males usually spend little time with the unattended offspring within their territories, but considerable variation among males has been observed (Alissa et al. 2017). This is probably because harem-owning males also allocate time to other activities, such as patrolling the territory to repel other males and prevent territory takeovers, and female guarding, which consists on staying close to an ovipositing female, typically at up to 20cm (Buzatto & Machado 2008). Mate guarding may last for a few days in this species and is argued to be a tactic that prevents females to mate with other males, especially 'sneaker' males that invade territories and furtively seek mating opportunities (Buzatto et al. 2011). Moreover, females usually retain some unfertilized eggs in their reproductive tract after a first oviposition bout (Buzatto et al. 2011), which is likely to increase the importance of mate guarding behaviour in reducing the risk of sperm competition.

Apart from a few studies (e.g., Ringler et al. 2015, Bourne 1998, Beal & Tallamy 2006), flexible compensation of uniparental care is usually assumed based on observations of the behaviour towards abandoned offspring adopted by the sex that usually does not provide care, without testing its effects on offspring fitness (frogs: Simon 1983; Bickford 2004, harvestmen: Machado & Oliveira 1998; Willemart & Gnaspini 2004). This is also the case for the harvestman *S. proximum*, in which the behaviour of harem-owning males of standing on unattended clutches has been interpreted as flexible compensation of uniparental care (Buzatto & Machado 2009; Alissa et al. 2017). Here, we experimentally investigate under field conditions

whether the behaviours exhibited by *S. proximum* males indeed constitute a case of flexible compensation of uniparental care. If so, we hypothesise that these behaviours should improve offspring survival, exhibiting responses similar to parental females against egg predators. Moreover, we evaluated the effects of multiple ecological and life-history factors on the behaviour of harem-owning males, contrasting the observed patterns with theoretical predictions for parental behaviours (Fig. 1). First, we expect that unfavourable climatic conditions reduce the expression of potential compensatory behaviours due to males' physiological constraints (Santos 2007; Fig. 1), and/or due to indirect decreases in food availability (e.g., Barve & La Sorte 2016; Fig. 1). In the case of increased energetic costs of compensatory behaviour, we also expect an increase in the extent of partial filial cannibalism as a strategy that alleviates such costs (Fig. 1). Moreover, we expect a positive relationship between the expression of compensatory behaviours and offspring value due to its direct benefits on reproductive success (Fig. 1). Due to potential temporal trade-offs between mating and parental effort (Alissa et al. 2017), we also expect a negative effect of both mate availability and males' past mating success on compensatory parental behaviours (Fig. 1). Finally, we expect a positive relationship between partial filial cannibalism and offspring value in terms of clutch size because the relative costs of sacrificing a few eggs from large clutches should be lower than from small clutches (Fitzgerald 1992; Manica 2002; Fig. 1).

MATERIALS & METHODS

Study site

We carried out fieldwork in an Atlantic Forest fragment at Intervales State Park (24°14'S; 48°04'W; 800 m.a.s.l.), located in the state of São Paulo, south-eastern Brazil. The climate in the region is characterized by a well-marked seasonality, with a wet and warm period (October - March) and a dry and cold period (April - September). We collected the data between February and April 2016, which consists in the second half of the breeding season of the harvestman *S. proximum* (Buzatto & Machado 2008). Monthly precipitation ranged from 25 to 200 mm during the sampled period, while the average temperature ranged from 20 to 22 °C (data collected from the station F-5-046 at Intervales State Park).

We conducted naturalistic observations and manipulations on adults and clutches found on the vegetation flanking a 5-m wide stream that follows the 'Trilha da Caçadinha' trail. The sampling area comprised two 1-m wide transects along both sides of the stream (Fig. 2). Because *S. proximum* reproductive activity decreases from February to April (see Buzatto & Machado 2008 and *Results*), the density of reproductively active adults (territorial males, as well as parental and ovigerous females) also decreases throughout these months. Therefore, in order to sustain reasonable sample sizes, we progressively increased the sampling effort over time by extending our sampled area down the stream, with the total area varying between sampled months (Fig. 2).

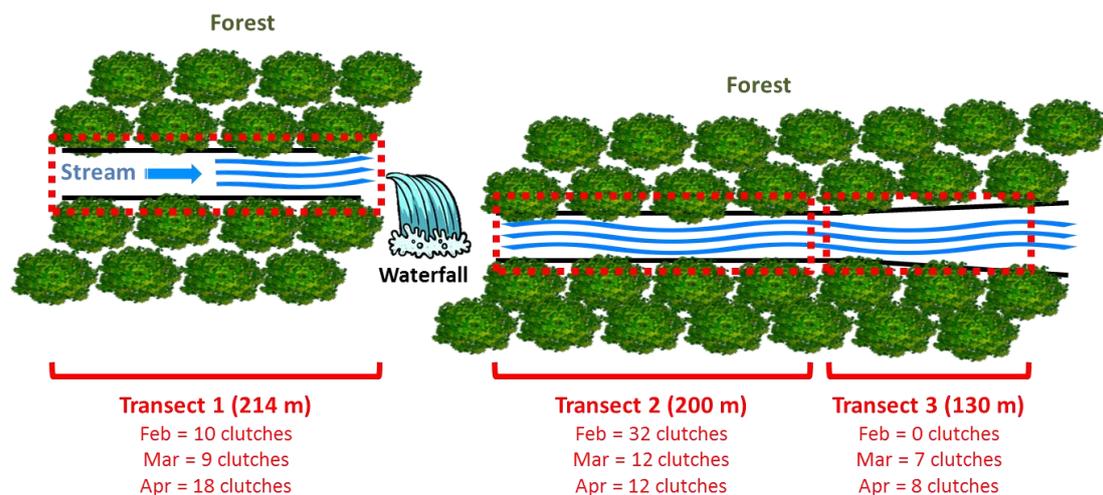


Figure 2. Schematic representation of the study site and sampling effort. The sampled areas (within the red dashed rectangles) comprised two 1-m wide transects along both sides of the stream. In February, we sampled transects 1 and 2, while in March and April, we increased the sampling area down the stream, including also transect 3.

Naturalistic observation and manipulation

Every sampled month, we repeated the same manipulation and data collection procedure (Fig. 3). On the first two days (stage 1 in Fig. 3), two observers performed an intensive search for *S. proximum* clutches in the sampled area. In order to avoid nymphal hatching during the sampled period, we only considered clutches that had been recently laid, which we estimated based on egg coloration (i.e. uniform cream to light brown coloration, corresponding to initial embryonic development stages according to Gnaspini 2007). We classified females in the sampled areas observed on a clutch in resting position and not consuming eggs as the parental females associated with the clutches. We individually marked every parental female with enamel ink since this procedure seems to not affect *S. proximum* behaviours (e.g., Buzatto et al. 2007, 2011; Alissa et al. 2017).

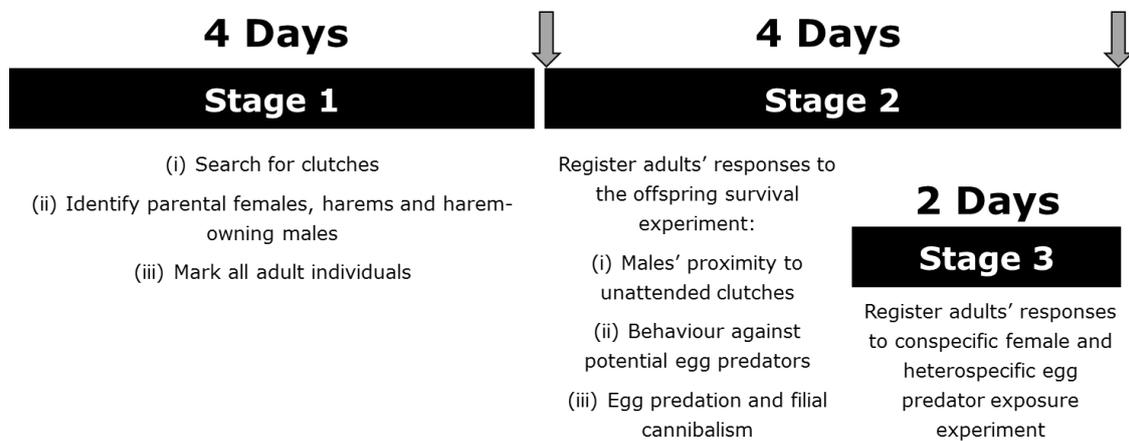


Figure 3. Schematic representation of the manipulation and data collection process. Arrows indicate when photographs of clutches were taken to calculate egg predation rates.

We also performed systematic observations of all clutches during two additional days (stage 1), visiting them between four and six times per afternoon (from 14h00 to 18h00) and between three and five times per night (from 21h00 to 01h00). During the entire period of stage 1, we individually marked with enamel ink all males found within a radius of 2 m around each clutch. We classified harem-owning males as associated with any particular parental female and her clutch if we observed at least one of the following behaviours: (a) copulation, where males grasp females' pedipalps frontally using their own pedipalps, before and during penis intromission (Machado et al. 2015); (b) mate-guarding, where a male extends his prolonged second pair of legs towards the female after copulation, usually staying in close proximity (at a distance up to 20 cm from the female), while she lays eggs (Buzatto & Machado 2008; Machado et al. 2015); (c) territory defence within a radius of up to 1 m around a parental female, where territorial males ritualistically fight conspecific males, characterized by

face-to-face confrontations using their second pair of legs or more aggressive attacks that include strikes using also their pedipalps (Buzatto & Machado 2008, 2014). Since *S. proximum* mating system is based on males' monopolization of harems within their territories (Buzatto & Machado 2008), we classified parental females as belonging to the same harem when they were spatially aggregated (in the same plant or rock, at a distance up to 1.5 m from each other) and shared the same harem-owning male.

At the beginning of a subsequent second stage (Fig. 3), we performed a field manipulation to evaluate the expression of harem-owning males' behaviours towards unattended clutches and its effects on one component of the offspring fitness: egg survival. We randomly assigned clutches to one of the following groups: (i) 'no adult', in which we removed the parental females and harem-owning males, keeping them in captivity during the experimental period; (ii) 'only male', in which we removed both adults, keeping parental females in captivity but immediately returning harem-owning males to their territory; and (iii) 'with female', in which we removed the parental female but immediately returned her to the clutch. By manipulating all individuals, we attempted to standardize any potential effect on their behaviour.

In February, we did not sample clutches to which we were not able to assign a harem-owning male during stage 1 through the observational diagnosis described above. In March and April, however, due to the significant decrease in the number of clutches found in the sampled areas (see *Results*), whenever we were unable to observe and determine the identity of the harem-owning male to a particular clutch, we only removed the female and designated the clutch to the 'no adult' group. In order to avoid uncertainty regarding harem-owning males' behaviours, however, we discarded clutches in this group where a male exhibited territorial behaviours during observations in stage 2.

After assigning clutches to the experimental groups, we performed systematic observations of all of them for four consecutive days (stage 2 in Fig. 3). We visited the clutches between two and five times per afternoon and between three and five times per night, registering events of egg predation. For clutches in the 'only male' group, we additionally estimated the distance of the harem-owning males to the unattended clutches within their territory and registered males' behaviours towards potential egg predators and events of filial cannibalism. We photographed and counted the number of eggs (using ImageJ software - Schneider et al. 2012) of every experimental clutch at the beginning and at the end of stage 2 (indicated by the grey arrows in Fig. 3).

Finally, in a last stage during the last two days of stage 2 (corresponding to stage 3 in Fig. 3), we performed an additional field manipulation to evaluate aggressive behavioural

responses of individuals standing on the clutch against two potential egg predators: conspecific females and males of the sympatric heterospecific harvestman *Longiperna concolor*, which are known to feed upon *S. proximum* eggs (Buzatto et al. 2007, *Results*). We presented these two potential egg predators to either the harem-owning males (from the 'only male' experimental group) or the parental females (from the 'with female' group) when they were standing on their clutches. We kept the potential egg predators in separate plastic containers until calmly releasing them close to the experimental clutches, allowing them to walk towards the *S. proximum* adult. We registered the harem-owning males' and parental females' responses to the manipulation (Fig. 3), particularly attack behaviours, characterized by rapid strikes using mainly their second pair of legs and pedipalps, attempts to grasp the intruder's body using their pedipalps, and, ultimately, to bite appendages joints. In the trials using conspecific females as egg predators, we presented individuals from a different harem to males in order to avoid the potential influence of mate recognition on behavioural responses. At the end of stage 3, we returned all males and females kept in captivity to their respective clutches and territories.

STATISTICAL ANALYSES

Given that we did not manipulate any of our predictor variables, but just explored their natural variation, the first step in our statistical analyses must be to check for potential multicollinearity problems, a relatively common situation in ecological data (Graham 2003). Correlations between predictor variables not only break the independence assumption of most statistical tests, but also decrease statistical power and generate inaccurate estimates of the regression coefficients, with potentially great impacts on the conclusion derived from the observed data. Therefore, checking and solving multicollinearity problems is strongly recommended (Allison 1999; Graham 2003). We used 'tolerance' as an indicator of multicollinearity problems, estimated as $1 - R^2$, where R^2 is calculated by regressing each predictor variable onto the remaining predictors in a multiple regression analysis. Conservative values greater than 0.4 are interpreted as weak linear dependencies between predictor variables that would not lead to multicollinearity problems (Allison 1999). Because the proxies for climatic conditions and mate availability are strongly correlated to each other (see Supplementary Material S2), we analysed their effects in separate models, never combined. Although there are other significant pairwise correlations between our predictor variables, their linear dependencies are not strong if the isolated effect of mean precipitation or mate availability is analysed with the remaining predictor variables (see Supplementary Material S2), and, therefore, we were able to evaluate their respective additive effects.

We built alternative generalized linear models (GLMs) to represent different biological hypotheses for each particular effect evaluated in this study. We analysed the data by comparing the adjustment of these alternative models to the observed data through a model selection approach based on the Akaike Information Criterion corrected for small samples AIC_c (Burnham & Anderson 2002), always including the null effect model in our set of alternative models. We ranked all alternative models and calculated the difference between them and the model with the smallest AIC_c (i.e., ΔAIC_c). We considered that all models whose ΔAIC_c lies within the range between 0 and 2 represent equally plausible explanations for the observed data within the list of alternative models (Burnham & Anderson 2002). If only one model met this criterion, we considered it as the best explanation overall (Burnham & Anderson 2002). However, if two or more nested models met this criterion, we considered the simplest one to be the best explanation for the observed data and dismissed the models with additional parameters (namely 'uninformative parameters' *sensu* Arnold 2010). This occurs when the addition of extra parameter(s) with poor explanatory power into a simpler model does not improve the adjustment of the more complex model enough to surpass the ΔAIC_c distance by 2 units between models, and thus their inclusion becomes irrelevant (Burnham & Anderson 2002; Arnold 2010). In addition, we calculated the 95% profile likelihood confidence intervals for all estimated parameters (Venables & Ripley 2002). We built, fit, and selected models using the in-built packages in the statistical environment R v.3.0.2 (R Core Team 2014), in addition to the packages '*bbmle*' (Bolker & R Core Team 2016) and '*aods3*' (Lesnoff & Lancelot 2015).

Effects on males' behaviour

To evaluate if harem-owning males' decisions towards unattended clutches within their territory represent flexible compensatory parental behaviours, we built a set of GLMs to analyse the effect of ecological and life-history variables on two proxies for paternal care. The first proxy is the proportion of the observations during stage 2 that a harem-owning male was in the close vicinity of the unattended clutch in the 'only male' group (hereafter called 'male proximity'). Harvestmen have limited visual abilities and rely mostly on close-range olfaction, contact chemoreception and mechanoreception to detect food, predators and conspecifics (Willemart et al. 2009). Therefore, we only included observations where harem-owning males were at a distance up to 20 cm from the clutches, since this is usually the distance that males stay from females during mate-guarding after copulation (Buzatto & Machado 2008), and thus, where they are potentially capable to physically detect egg predators.

We used a set of alternative models that considered a beta binomial distribution of the errors to account for overdispersed data and where male proximity depended on (i) the mean

precipitation during the whole sampled period at each sampled month (eight days, encompassing stages 1 and 2), used as a proxy for climatic conditions, (ii) the number of eggs at the beginning of stage 2 (hereafter called 'clutch size'), used as a proxy for offspring value, (iii) the number of parental females found in transect 2 at stage 1 during each sampled month that were either ovipositing their first bout of eggs or associated with eggs at the very beginning of their embryonic development, characterized by creamy small solid appearance (Gnaspini 2007), used as a proxy for the recent influx of ovigerous female at the population level (hereafter called 'mate availability'), and (iv) the number of clutches inside each harem-owning male's territory (hereafter called 'harem size'), used as a proxy for individual males' past mating success. We also included models considering their additive effects. We excluded data from clutches where all the eggs disappeared during stage 2 because male proximity is likely to be affected by the absence of eggs.

The second proxy for parental care is the frequency of attacks against potential egg predators (conspecific females and heterospecific *L. concolor* males) in the manipulation at stage 3. We used a set of models that considered a binomial distribution of the errors to model the frequency of attacking responses of *S. proximum* adults in separate analyses for the two types of potential egg predators. In both cases, we explicitly built models for alternative hypotheses where the probability of attacking egg predators depended on the mean precipitation, clutch size, the sex of the adult tested, and their additive effects. Although clutch size during the manipulation at stage 3 was not measured at the exact prior moment to the predator exposure trials (Fig. 3), we consider it as a valid predictor since most clutches lost less than 20 eggs (mean = 18 eggs) throughout the whole sampled period, when the median clutch size was 103 eggs (see *Results*). While mate availability and males' past mating success are expected to affect male proximity due to temporal trade-offs between mating and parental effort, they are not expected to affect aggressiveness against egg predators once harem-owning males are standing on the unattended clutches.

In all analyses, we expect males to respond to variation in ecological and life-history variables, so that male behaviours (both male proximity and males' probability of attacking) would (i) be positively related to precipitation (Fig. 1), as favourable climatic conditions favour the acquisition of food resources and, consequently, decrease the associated costs of caring and/or improve adult's ability to protect the brood; and (ii) be positively related to clutch size (Fig. 1), as the benefits of spending time and energy caring for large clutches should be greater than caring for small clutches. Additionally, considering the temporal trade-offs between parental and mating effort, we expect male proximity to be negatively related to mate availability and harem size, given that the benefits of providing care should be smaller than

searching for mates when there are more females available and for males that are generally more successful in obtaining mates, respectively (Fig. 1). Moreover, we expect males to be as aggressive towards egg predators as parental females or at least as effective in repelling them if they are actually providing care.

Effects on filial cannibalism

We built a set of GLMs that consider a beta binomial distribution of the errors to analyse the effect of males' proximity, as well as ecological and life-history variables, on the overdispersed occurrence of egg consumption performed by the harem-owning males in the 'only male' group. Our response variable was the proportion of observations where the harem-owning males were consuming eggs while being standing on unattended clutches. We explicitly built models for alternative hypotheses where the occurrence of egg consumption from the unattended clutches within their territories depended on the mean precipitation, clutch size, male proximity, and their additive effects. If harem-owning males' egg consumption represents instances of filial cannibalism, we expect it to be (i) negatively related to precipitation (Fig. 1), as unfavourable abiotic conditions difficult the acquisition of food resources and, consequently, increase the benefits of sacrificing eggs from their own clutches; (ii) positively related to clutch size (Fig. 1), as the relative cost of sacrificing a few eggs from large clutches should be lower than from small clutches; and (iii) positively related to male proximity (Fig. 1), as the probability of filial cannibalism should increase naturally with the amount of time males spend close to the offspring. We excluded data from clutches where all the eggs disappeared during stage 2 and where males were never seen standing on the clutch.

Effects on offspring survival

To evaluate if males' behavioural decisions towards unattended clutches within their territory constitute parental behaviours that improve offspring fitness, we built a set of GLMs to analyse offspring survival. We used the difference in the number of eggs in the unattended clutches between the beginning and the end of stage 2 (discarding any new eggs laid by parental females in the 'with female' group) as a proxy for egg predation rate (hereafter called 'number of eggs lost per clutch') and the response variable in our analyses. First, we explicitly built a set of GLMs for alternative hypotheses that considered a negative binomial distribution of the errors and the effect of manipulation groups on the overdispersed count data of eggs lost per clutch. In particular, we explored alternative arrangements of the manipulation groups, where the number of eggs lost per clutch would be: (i) different among all groups; (ii) similar between 'with female' and 'only male' group, but different from 'no adult' group; or (iii) similar between 'only male' and 'no adult' group, but different from 'with female' group. We did not include

amongst the candidate models the implausible scenario where the number of eggs lost is similar between ‘with female’ and ‘no adult’ groups because this species is already known to exhibit maternal care that improves egg survival (Buzatto et al. 2007). Moreover, we also excluded data from one clutch lost due to tree fall. If harem-owning males do provide compensatory care, we expect egg losses in the ‘only male’ group to be (i) lower than in the ‘no adult’ group, since parental care improves offspring survival; and (ii) similar or lower in comparison to the ‘with female’ group, since paternal care may be, respectively, equally or less efficient than maternal care. Due to great variance among harem-owning males regarding their proximity to the unattended clutches in the ‘only male’ group (see *Results*), we performed a second analysis to evaluate the effect of male proximity on the number of eggs lost in the ‘only male’ group. If harem-owning males do provide care while being close to the unattended clutches within their territories, we expect the number of eggs lost to be negatively related to male proximity, as the chances of successful egg predation events should be reduced by increments in males' intensity of care.

Because some clutches lost all of their eggs during stage 2, we cannot estimate the exact egg loss rate for them. We only know that egg loss rate for these clutches are at least above a certain value (i.e., equal or larger to the number of eggs present at the beginning of stage 2), but it is unknown to what exact extent. Data with this type of uncertainty are known as right-censored observations, and assuming that they represent actual egg loss rates can lead to inaccurate estimates of the models' parameters, in particular, underestimation of egg loss rates, which can be potentially greater than a given value. To deal with this type of data, we included an additional term to the likelihood functions of the alternative models described before for the two analyses:

$$L = \prod_{i=1}^U f(x_i; \theta_1, \theta_2, \dots, \theta_k) \cdot \prod_{j=1}^C 1 - F(y_j - 1; \theta_1, \theta_2, \dots, \theta_k) \quad ,$$

where $\theta_1, \theta_2, \dots, \theta_k$ are the unknown model parameters to be estimated, and x_i and y_j are the number of eggs lost from clutches during stage 2. For the observations with partial clutch predation (uncensored observations), we used the traditional probability density function, represented by the first term $f(x; \theta)$ of the equation. The second term represents the right-censored observations and incorporates the cumulative density function $[1 - F(y - 1; \theta)]$, denoting the probability of y_j eggs or more being lost during stage 2. Therefore, the adjusted likelihood function above takes into account data from clutches that suffered both partial and total egg predation.

RESULTS

Fluctuations on ecological and life-history predictor variables

The median precipitation, which was the abiotic variable used as proxy for climatic conditions in our analyses, declined gradually from February to April (Fig. 4A). The number of females that were either ovipositing their first bout of eggs or associated with eggs at the very beginning of their embryonic development in transect 2, which was our proxy for mate availability at the population level, also declined throughout the sampled months, with six females found in February, three in March and only one in April. The harem size, which was our proxy for individual males' past mating success, ranged from one to four clutches and shows a slight declining trend from February to April (Fig. 4B). Finally, clutch size, which was our proxy for offspring value, varied largely amongst females, ranging from 32 to 208 eggs and also shows a decline over the course of the sampled months (Fig. 4C).

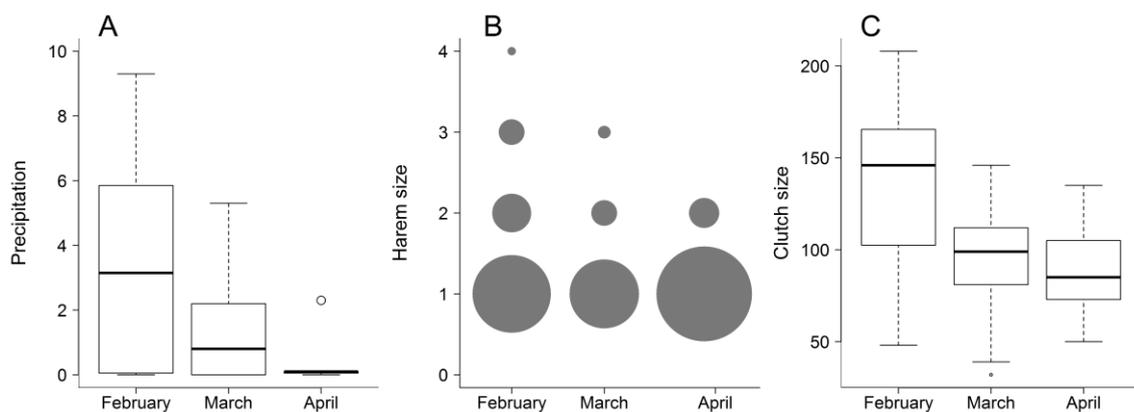


Figure 4. Fluctuations on ecological and life-history predictor variables throughout the sampled months. (A) Precipitation (mm); (B) Number of clutches per territory of sampled males of the harvestman *Serracutisoma proximum* (i.e., harem size), where the size of the circles is proportional to the number of observations; and (C) Number of eggs per sampled clutch of *S. proximum* (i.e. clutch size).

Effects on males' behaviour

Male proximity

We observed large variation in the relative frequency of observations that the harem-owning males were in close proximity to the unattended clutch (≤ 20 cm) within the 'only male' group (median = 30% of observations, range = 0 – 100% of observations). This pattern differs notoriously from females' behaviour towards their offspring, usually spending most of the time standing on their clutches (median = 100% of observations, range= 81 – 100% of observations for the 'with female' group; see also Buzatto et al. 2007). The large variation observed in males' proximity is better explained by a positive association with precipitation, but also with

mate availability (Table 1; Fig. 5). Although other competitive models are equally plausible to explain the observed data on harem-owning males' proximity ($\Delta AIC_c \leq 2$), the additional inclusion of clutch size has a negligible effect since it did not improve the fit enough to surpass the ΔAIC_c distance by 2 units in relation to the former models (i.e., 'uninformative parameter' *sensu* Arnold 2010, Table 1).

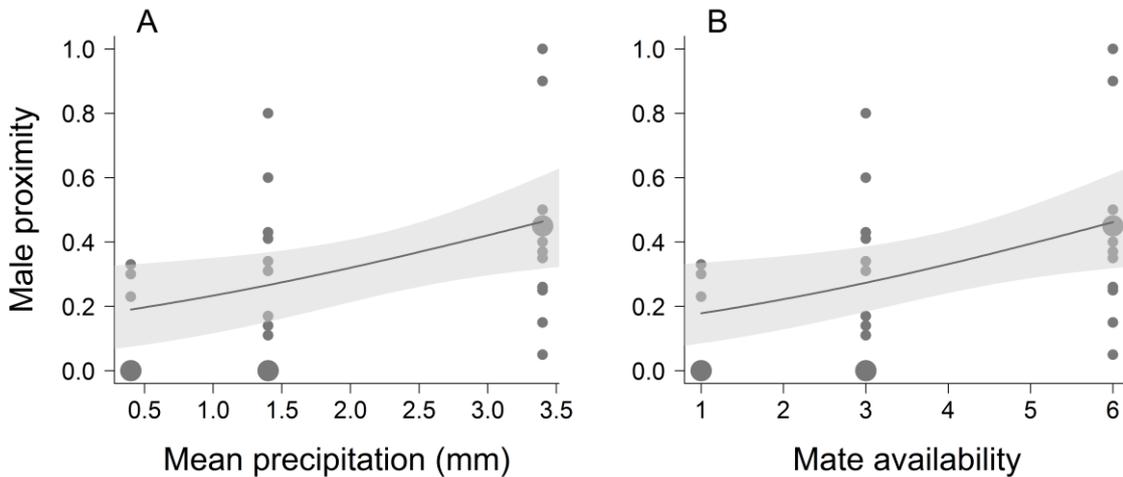


Figure 5. Variation in males' proximity to unattended clutches within their territories for the harvestman *Serracutisoma proximum*. Male proximity represents the proportion of observations that harem-owning males were in close proximity to the unattended clutch (≤ 20 cm). Association with (A) mean precipitation (mm) during the sampled period and (B) the number of females with recently laid clutches in transect 2 (i.e., mate availability at the population level). The size of the circles is proportional to the number of observations and the black lines represent the values predicted by the respective model, along with 95% confidence intervals (grey shadows). We excluded data from clutches where all the eggs disappeared during the sampled period.

Responses to potential egg predators

Parental females standing on their clutches attacked the heterospecific predator (*L. concolor*) on 38 out of 61 trials, while harem-owning males attacked only once out of 23 trials (Fig. 6). Moreover, in 57% of the trials when males did not attack, they run away for more than 1 m from the clutch, while females did it only in 23% of those trials. Variation among individuals on the probability of attacking the heterospecific predator is better explained by the sex of the adult standing on the clutches than by any other variable (Table 2). In fact, the estimated probability of harem-owning males attacking a heterospecific predator is extremely lower (= 0.04; 95% CI = 0.002 – 0.29) than the probability estimated for parental females (= 0.62; 95% CI = 0.50 – 0.74).

Table 1. Summary of candidate models ranked by Akaike Information Criterion corrected for small samples (AIC_c) relating the proportion of observations where the harem-owning males of the harvestman *Serracutisoma proximum* were found in close proximity (≤ 20 cm) to unattended clutches to ecological and life-history variables, including the null effect model.

| Candidate models | Coefficients' estimates | | | | | | K | AIC_c | ΔAIC_c | w_i |
|--|--------------------------|-------------------------|-------|------|-------------------------|-------------------------|----------|--------------|----------------|-------------|
| | I | Prec | CS | HS | MA | ϕ | | | | |
| <i>Mate availability</i> | -1.80[†] | – | – | – | 0.28[†] | 0.28[†] | 3 | 181.0 | 0.0 | 0.27 |
| <i>Precipitation</i> | -1.62[†] | 0.43[†] | – | – | – | 0.28[†] | 3 | 181.1 | 0.1 | 0.26 |
| <i>Clutch size + mate availability</i> | -1.33 [†] | – | -0.01 | – | 0.36 [†] | 0.27 [†] | 4 | 182.5 | 1.5 | 0.13 |
| <i>Clutch size + precipitation</i> | -1.09 | 0.57 [†] | -0.01 | – | – | 0.27 [†] | 4 | 182.6 | 1.6 | 0.13 |
| Harem size + precipitation | -1.80 [†] | 0.41 [†] | – | 0.14 | – | 0.28 [†] | 4 | 183.6 | 2.6 | 0.07 |
| Null effect model | -0.69 [†] | – | – | – | – | 0.31 [†] | 2 | 184.1 | 3.1 | 0.06 |
| Harem size | -1.23 [†] | – | – | 0.33 | – | 0.31 [†] | 3 | 185.3 | 4.3 | 0.03 |
| Clutch size + harem size + precipitation | -1.17 | 0.56 [†] | -0.01 | 0.05 | – | 0.27 [†] | 5 | 185.5 | 4.5 | 0.03 |
| Clutch size | -0.90 | – | 0.002 | – | – | 0.31 [†] | 3 | 186.5 | 5.5 | 0.02 |
| Clutch size + harem size | -1.52 | – | 0.003 | 0.34 | – | 0.31 [†] | 4 | 187.9 | 6.9 | 0.01 |

Best models based on AIC_c in bold and competitive models ($\Delta AIC_c \leq 2$) with uninformative additional parameters in italics. The symbol “+” between variables represents additive effects models, and the “–” symbol indicates coefficient estimates whose 95% confidence intervals do not include zero. Coefficients: I represents the intercept; Prec represents mean precipitation (mm); CS represents clutch size (i.e., number of eggs at the beginning of stage 2); HS represents harem size (i.e., number of clutches within each males' territory); MA represents mate availability (i.e., number of females in the population with recently laid clutches in transect 2); ϕ represents the over-dispersion parameter of the beta-binomial distribution of the errors. K: number of estimated parameters; ΔAIC_c : difference between the AIC_c of each model and the one with the lowest AIC_c ; w_i : AIC_c weight for each model. Sample size for all models is 28 males.

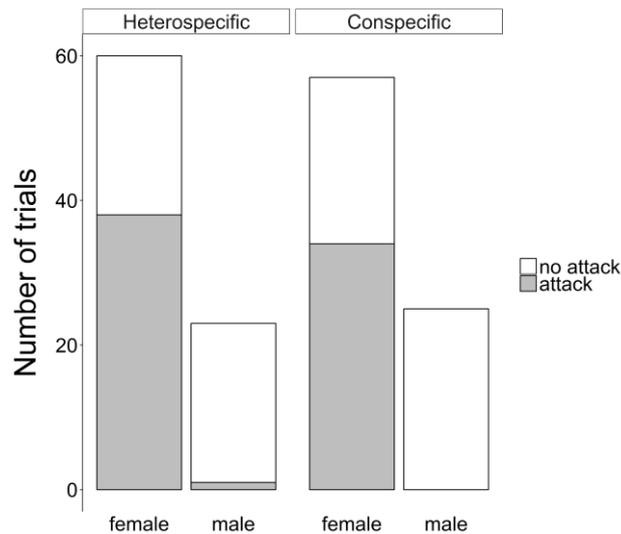


Figure 6. Frequency of attacking responses of parental females and harem-owning males of the harvestman *Serracutisoma proximum* to potential egg predators while standing on clutches. The responses are classified as attack (represented by the grey bars) or no attack (white bars). The potential predators included males of the harvestman *Longiperna concolor* and conspecific females. Plot created using package ‘*ggplot2*’ (Wickham 2009).

We observed a similar pattern when using conspecific females as potential egg predators: parental females standing on their clutches performed the attacking behaviour in 34 out of 56 trials, while harem-owning males never attacked on 25 trials (Fig. 6). Once again, variation among individuals on the probability of attacking the conspecific predator is better explained by the sex of the adult standing on the clutches than by any other variable (Table 2). The estimated probability of parental females attacking a conspecific female is 0.61 (95% CI = 0.48 – 0.73), while the probability estimated for a harem-owning male is less than 0.0001 (0 – 0.12; 95% CI approximated using the ‘rule of three’ [0 – 3/n], since no attack events were performed by males against conspecific females — Jovanovic & Levy 1997). Although other competitive models are equally plausible to explain the observed variation in the frequency of attacks towards heterospecific or conspecific egg predators ($\Delta AIC_c \leq 2$), the inclusion of clutch size or precipitation has a negligible effect on the probability of attacking and they both are interpreted as uninformative parameters (*sensu* Arnold 2010; Table 2).

Table 2. Summary of candidate models ranked by Akaike Information Criterion corrected for small samples (AIC_c) relating the probability of manipulated adults of the harvestman *Serracutisoma proximum* attacking potential egg predators to ecological and life-history variables, including the null effect model.

| Candidate models | Coefficients' estimates | | | | K | AIC_c | ΔAIC_c | w_i |
|--|-------------------------|--------------------------|-------|-------------------|----------|-------------|----------------|-------------|
| | I | Male | Prec | CS | | | | |
| Attack response towards males of the heterospecific harvestman <i>Longiperna concolor</i> | | | | | | | | |
| <i>Sex + precipitation</i> | 1.04 [†] | -3.58 [†] | -0.32 | – | 3 | 92.9 | 0.0 | 0.38 |
| Sex | 0.50 | -3.59[†] | – | – | 2 | 93.2 | 0.3 | 0.32 |
| <i>Sex + clutch size</i> | 1.50 | -3.70 [†] | – | -0.01 | 3 | 94.0 | 1.1 | 0.21 |
| Sex + clutch size + precipitation | 1.27 | -3.61 [†] | -0.27 | -0.003 | 4 | 95.0 | 2.1 | 0.12 |
| Precipitation | 0.42 | – | -0.33 | – | 2 | 116.6 | 23.7 | <0.001 |
| Null effect model | -0.14 | – | – | – | 1 | 118.1 | 25.2 | <0.001 |
| Clutch size + precipitation | 0.02 | – | -0.42 | 0.01 | 3 | 118.3 | 25.4 | <0.001 |
| Clutch size | 0.29 | – | – | -0.004 | 2 | 119.8 | 26.9 | <0.001 |
| Attack response towards conspecific females | | | | | | | | |
| Sex | 0.44 | -19.00 | – | – | 2 | 79.2 | 0.0 | 0.40 |
| <i>Sex + clutch size + precipitation</i> | -0.80 | -19.95 | -0.43 | 0.02 | 4 | 80.4 | 1.2 | 0.22 |
| <i>Sex + precipitation</i> | 0.76 | -20.01 | -0.18 | – | 3 | 80.6 | 1.4 | 0.19 |
| <i>Sex + clutch size</i> | -0.36 | -19.97 | – | 0.01 | 3 | 80.8 | 1.6 | 0.18 |
| Clutch size + precipitation | -1.64 | – | -0.41 | 0.02 [†] | 3 | 111.8 | 32.6 | <0.001 |
| Null effect model | -0.32 | – | – | – | 1 | 112.2 | 33.1 | <0.001 |
| Clutch size | -1.28 | – | – | 0.01 | 2 | 112.9 | 33.7 | <0.001 |
| Precipitation | -0.08 | – | -0.13 | – | 2 | 113.8 | 34.6 | <0.001 |

Best models based on AIC_c in bold and competitive models ($\Delta AIC_c \leq 2$) with uninformative additional parameters in italics. The symbol “+” between covariates represents additive effects models, and the “†” symbol indicates coefficient estimates whose 95% confidence intervals do not include zero. Coefficients: I represents the intercept; Male represents the harem-owning male category (reference sex: female); Prec represents mean precipitation (mm); CS represents clutch size (i.e., number of eggs at the beginning of stage 2). K: number of estimated parameters; ΔAIC_c : difference between the AIC_c of each model and the one with the lowest AIC_c ; w_i : AIC_c weight for each model. Sample size for all models is 84 clutches.

Rather than attacking conspecific females, harem-owning males attempted to copulate with them on approximately 30% of trials (eight out of 25 trials; Fig. 8a). In such cases, males grasped the females' pedipalps with their own pedipalps, usually with the penis everted. This contrasts with the notoriously aggressive attack behaviour that includes strikes, appendage grasping and bites, commonly exhibited by parental females against potential egg predators (reported here and in Buzatto et al. 2007) and observed only in one occasion by the harem-owning male against the heterospecific predator (but also reported in Buzatto & Machado 2009). Copulation attempts were generally unsuccessful, as females walked away after being released, with only one exception (Fig. 8a). After this successful occasion, the male guarded

the female while she cannibalized eggs from the unattended clutch within his territory for a few minutes (Fig. 8b) until she left the territory.

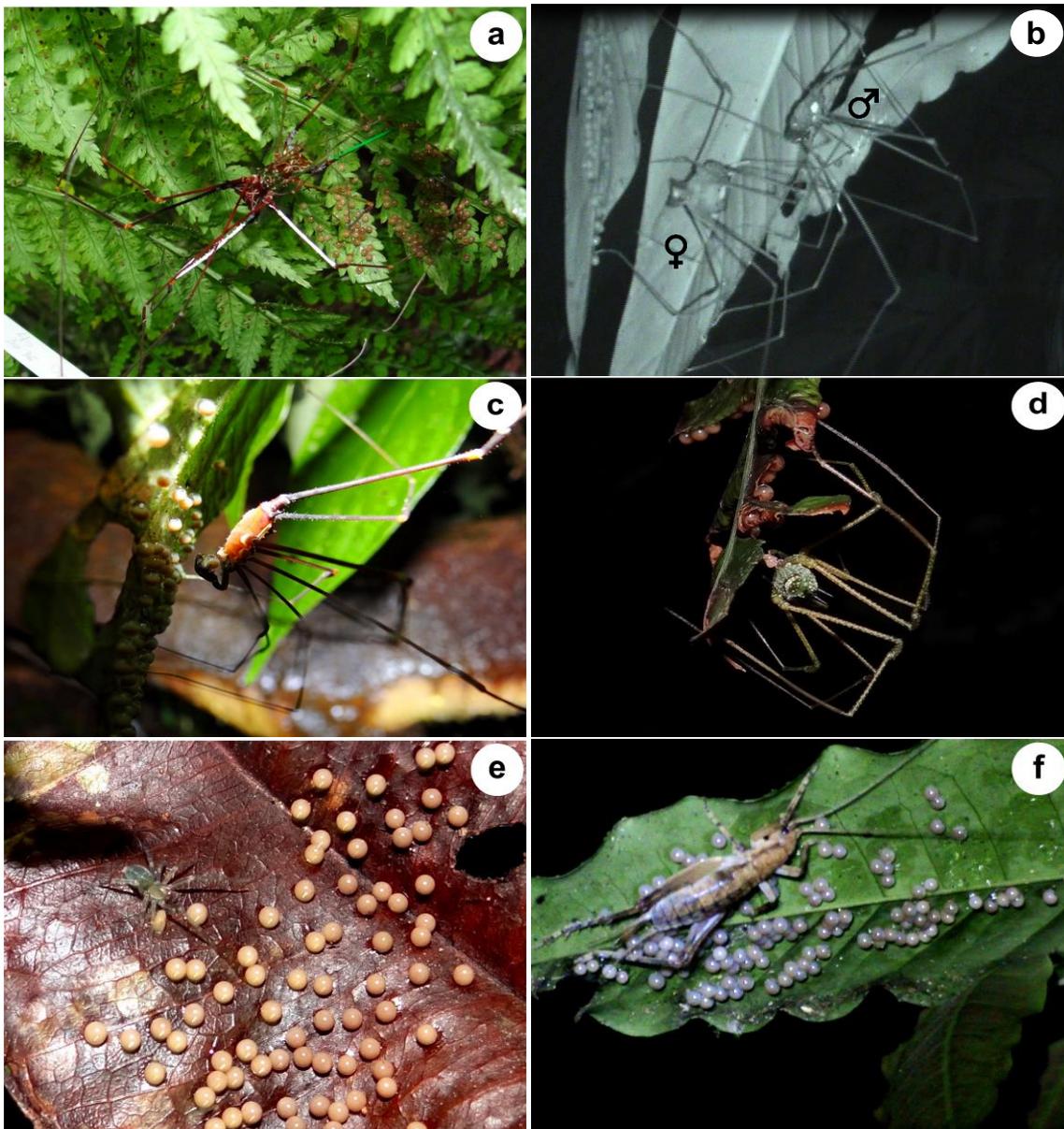


Figure 8. Photographs of clutches of the harvestman *Serracutisoma proximum*. (a) Harem-owning male on an unattended clutch copulating with a female released during the egg predator exposure experiment (see main text for details); (b) harem-owning male guarding a female that was not from his harem while she was consuming eggs from his unattended clutch (egg visible between retracted pedipalps). (c-f) Conspecific and heterospecific egg predators consuming eggs from unattended clutches: (c) a sneaker conspecific male; (d) an adult of the harvestman *Iporangaia pustulosa*; (e) an individual of an unidentified species of spider; and (f) an individual of an unidentified species of cricket.

Effects on filial cannibalism

We rarely observed harem-owning males consuming eggs from the unattended clutches within their territories. Only nine out of 33 manipulated males performed such behaviour during stage 2 and never more than 3 events were recorded per male. The variation among males on the occurrence of egg consumption is better explained by a negative effect of precipitation (Table 3; Fig. 7). Although another competitive model is equally plausible to explain the occurrence of egg consumption from the unattended clutches within their territories ($\Delta AIC_c \leq 2$), clutch size has a negligible effect on the probability of egg cannibalism and is interpreted as uninformative parameters (*sensu* Arnold 2010; Table 3). Most of the time that we observed a harem-owning male standing on the unattended clutch within its territory, it was just standing still, with their second pair of legs extended, in a similar position adopted by parental females. Interestingly, we also observed sneaker males (in eight occasions) and other territorial males from a different harem (in 13 occasions) in this position on the unattended clutches when harem-owning males were absent.

Table 3. Summary of candidate models ranked by Akaike Information Criterion corrected for small samples (AIC_c) relating the proportion of egg predation events by the harem-owning male while standing on the clutch to environmental and ecological and life-history variables, including the null effect model.

| Candidate models | Coefficients' estimates | | | | | K | AIC_c | ΔAIC_c | w_i |
|------------------------------------|-------------------------|--------------------------|--------------------|-------|-------------------------|----------|-------------|----------------|-------------|
| | I | Prec | CS | MP | ϕ | | | | |
| <i>Precipitation</i> | 0.23 | -1.31⁺ | – | – | 0.30⁺ | 3 | 55.6 | 0.0 | 0.63 |
| <i>Clutch size + precipitation</i> | 2.00 | -1.26 ⁺ | -0.02 | – | 0.27 ⁺ | 4 | 56.9 | 1.3 | 0.32 |
| Clutch size | 0.51 | – | -0.03 ⁺ | – | 0.36 ⁺ | 3 | 61.7 | 6.1 | 0.03 |
| Male proximity | -0.46 | – | – | -0.15 | 0.28 ⁺ | 3 | 63.5 | 7.9 | 0.01 |
| Null effect model | -1.69 ⁺ | – | – | – | 0.40 ⁺ | 2 | 63.8 | 8.2 | 0.01 |

Best model based on AIC_c in bold and competitive models ($\Delta AIC_c \leq 2$) with uninformative additional parameters in italics. The symbol “+” between covariates represents additive effects models, and the “+” symbol indicates coefficient estimates whose 95% confidence intervals do not included zero. Coefficients: I represents the intercept; Prec: represents mean precipitation (mm); CS represents clutch size (i.e., number of eggs at the beginning of stage 2); MP represents male proximity (i.e., the proportion of the observations during stage 2 that a harem-owning male was at up to 20 cm from the unattended clutch); ϕ represents the over-dispersion parameter of the beta-binomial distribution of the errors. K : number of estimated parameters; ΔAIC_c : difference between the AIC_c of each model and the one with the lowest AIC_c ; w_i : AIC_c weight for each model. Sample size for all models is 22 clutches.

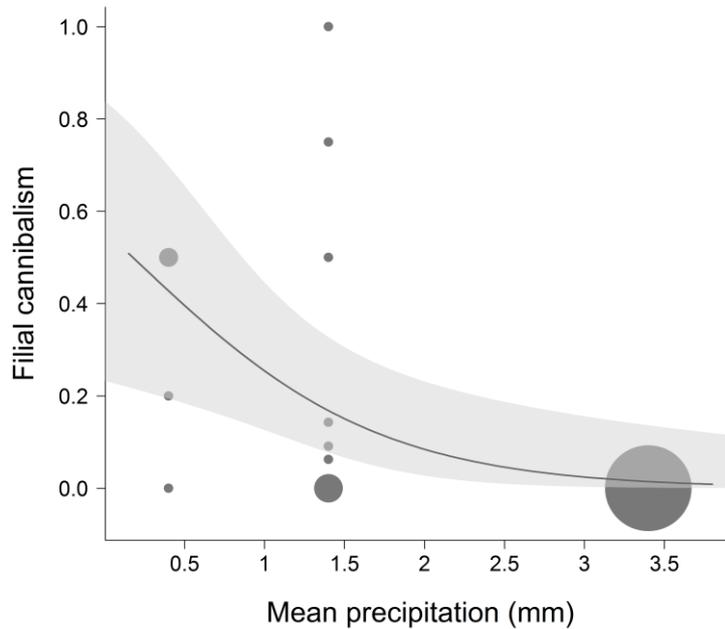


Figure 7. Proportion of the observations of harem-owning males of the harvestman *Serracutisoma proximum* standing on unattended clutches where they consumed eggs in relation to mean precipitation. The size of the circles is proportional to the number of observations and the black line represents the prediction of the most plausible model along with 95% confidence intervals (grey shadow).

Effects on offspring survival

We observed 48 egg predation events by seven species, including insects and conspecific and heterospecific harvestmen (Table 4). Except for *S. proximum* males, egg predators always feed voraciously upon eggs, consuming several eggs in the same predation attempt. Filial cannibalism by parental females also occurred, but rarely: we only observed it twice. Despite conspecific adult males being the most common egg predators (ca. 44% of the observed events), they usually stayed in guarding position on the clutch after feeding on a few eggs (Fig. 8c).

Table 4. Number of observations where egg predators were found consuming *Serracutisoma proximum* eggs in each manipulation group.

| Type | Manipulation groups | | |
|---|---------------------|-----------|----------|
| | With female | Only male | No adult |
| ORDER OPILIONES | | | |
| <i>Serracutisoma proximum</i> | | | |
| Parental females ^a | 2 | – | – |
| Other females ^b | – | 8 | 5 |
| Harem-owning males ^a | – | 9 | – |
| Other males ^b | – | 4 | 8 |
| <i>Promitobates ornatus</i> | – | 3 | 1 |
| <i>Longiperna concolor</i> | – | – | 2 |
| <i>Iporangaia pustulosa</i> | – | 2 | – |
| ORDER ARANEAE | | | |
| <i>Unidentified spider^c</i> | – | – | 2 |
| ORDER HYMENOPTERA | | | |
| <i>Unidentified wasp</i> | – | 1 | – |
| ORDER ORTHOPTERA | | | |
| <i>Unidentified cricket^d</i> | – | – | 1 |

‘With female’ = clutches where the parental female was present; ‘only male’ = clutches where the parental female was removed but the harem-owning male was present; ‘no adult’ = clutches where both parental female and harem-owning male were absent. ^a indicates filial cannibalism events; ^b indicates cannibalism events on unrelated clutches (depicted in Fig. 8b-c); ^c indicates the spider depicted in Fig. 8e; and ^d indicates the cricket depicted in Fig. 8f.

Regarding the differences in the number of eggs lost per clutch between manipulation groups, clutches from the ‘with female’ group showed the lowest observed values (median = 1 egg, range = 0 – 37 eggs), followed by “only male” clutches (median = 10 eggs, range = 0 – 101 eggs) and ‘no adult’ clutches (median = 16 eggs, range = 0 – 132 eggs; Fig. 9). The observed variation in egg loss rates was better explained by an arrangement that considers the median values differing between clutches from the ‘with female’ group and clutches from the other two groups, but not between ‘no adult’ and ‘only male’ clutches (Table 5). Although a model considering egg loss rates to differ between all groups was equally plausible ($\Delta AIC_c \leq 2$), the inclusion of the additional parameter discriminating between ‘no adult’ and ‘only male’ clutches has a negligible effect on the response variable and is interpreted as an uninformative parameter (*sensu* Arnold 2010, Table 5). Therefore, the presence of harem-owning males does not enhance the offspring survival when compared to clutches without any parent. Moreover, despite the large variation in the frequency of observations that the harem-owning males were in close proximity to the unattended clutch within the ‘only male’ group, it also does not explain the observed pattern of egg loss rate within the group (Table 6, Fig. 10).

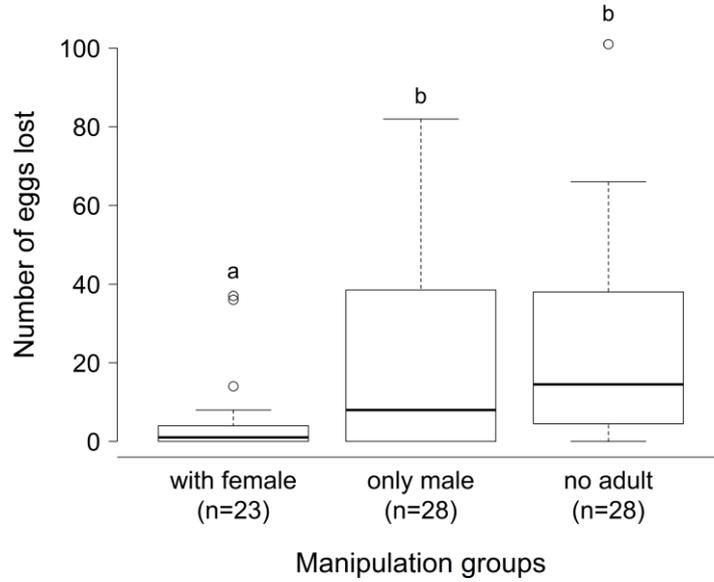


Figure 9. Number of *Serracutisoma proximum* eggs lost per clutch over four days in three manipulation groups. ‘With female’ represents clutches where parental females were present; ‘only male’ represents clutches where parental females were removed but harem-owning males were present; and ‘no adult’ represents clutches where both parental females and harem-owning males were absent. Distinctive letters above the box-plots denote significant differences based on the model selection results. Censored observations are excluded.

Table 5. Summary of candidate models ranked by Akaike Information Criterion corrected for small samples (AIC_c) relating the number of lost eggs over four days in clutches of the harvestman *Serracutisoma proximum* to plausible combinations of comparison groups, including the null effect model.

| Candidate models | Coefficients' estimates | | | | | K | AIC_c | ΔAIC_c | w_i |
|--|-------------------------|-------------------------|-------------------------|-------------------------|-------------------------|----------|--------------|----------------|-------------|
| | I | OM | NA | {OM·NA} | Θ | | | | |
| Only “with female” group differ | 1.66[†] | – | – | 1.86[†] | 0.37[†] | 3 | 586.7 | 0 | 0.69 |
| <i>All groups differ</i> | <i>1.66[†]</i> | <i>2.04[†]</i> | <i>1.68[†]</i> | – | <i>0.37[†]</i> | 4 | 588.3 | 1.6 | 0.31 |
| Null effect model | 3.24 [†] | – | – | – | 0.32 [†] | 2 | 598.4 | 11.7 | 0.002 |
| Only “no adult” group differ | 3.17 [†] | – | 0.17 | – | 0.32 [†] | 3 | 600.3 | 13.7 | <0.001 |

Best model based on AIC_c in bold and competitive models ($\Delta AIC_c \leq 2$) with uninformative additional parameters in italics. The “[†]” symbol indicates coefficient estimates whose 95% confidence intervals do not include zero. Coefficients: I represents the intercept; OM represents ‘only male’ clutches category (where parental females were removed but harem-owning males were present); NA represents ‘no adult’ clutches category (where parental female and harem-owning males were absent); {OM·NA} represents ‘only male’ and ‘no adult’ clutches categories pooled (reference category: ‘with female’ clutches [where parental female is present]); Θ represents the shape parameter of the negative binomial distribution of the errors. K : number of estimated parameters; ΔAIC_c : difference between the AIC_c of each model and the one with the lowest AIC_c ; w_i : AIC_c weight for each model. Sample size for all models is 85 manipulated clutches (‘with female’ = 23 clutches, ‘only male’ = 33 clutches, ‘no adult’ = 29 clutches).

Table 6. Summary of candidate models ranked by Akaike Information Criterion corrected for small samples (AIC_c) relating the number of eggs lost over four days in clutches of the harvestman *Serracutisoma proximum* to the proportion of observations that the harem-owning males were in close proximity to unattended clutches ($\leq 20\text{cm}$), including the null effect model.

| Candidate models | Coefficients' estimates | | | K | AIC_c | ΔAIC_c | w_i |
|--------------------------|--------------------------------|--------------|--------------------------------|----------|--------------|----------------|-------------|
| | I | MP | Θ | | | | |
| Null effect model | <i>3.78[†]</i> | – | <i>0.28[†]</i> | 2 | 228.8 | 0.0 | 0.73 |
| <i>Proximity</i> | <i>4.08[†]</i> | <i>-0.85</i> | <i>0.28[†]</i> | 3 | 230.8 | 2.0 | 0.27 |

Best model based on AIC_c in bold and competitive models ($\Delta AIC_c \leq 2$) with uninformative additional parameters in italics. The “+” symbol indicates coefficient estimates whose 95% confidence intervals do not include zero. Coefficients: I represents the intercept; MP represents male proximity (i.e., the proportion of the observations during stage 2 that a harem-owning male was at up to 20 cm from the unattended clutch); Θ represents the shape parameter of the negative binomial distribution of the errors. K : number of estimated parameters; ΔAIC_c : difference between the AIC_c of each model and the one with the lowest AIC_c ; w_i : AIC_c weight for each model. Sample size for all models is 33 clutches.

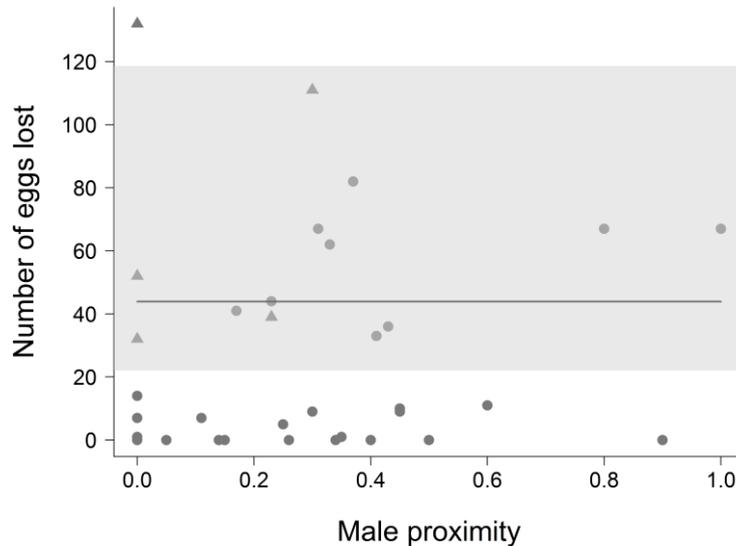


Figure 10. Number of *Serracutisoma proximum* eggs lost per clutch over four days and male proximity in the ‘only male’ group. Male proximity represents the proportion of observations that harem-owning males were in close proximity to the unattended clutch ($\leq 20\text{ cm}$). Triangles represent right-censored observations, and circles represent uncensored observations. The line corresponds to the prediction of the most plausible model (null effect) along with 95% confidence intervals (grey shadow).

DISCUSSION

Our results show no evidence to support the suggestion that the behaviour of *Serracutisoma proximum* males towards unattended clutches consists in an instance of flexible compensation of uniparental care. Males spend significantly less time standing on the clutches than parental females and rarely attack potential egg predators or consume eggs from the clutches within their territory. In fact, the exhibition of all these behaviours is mainly affected by climatic conditions, probably due to physiological constraints (Santos 2007), and/or indirect decreases in food availability (e.g., Barve & La Sorte 2016), and, ultimately shows no effect on offspring survival (Fig. 11). It is important to notice that egg predation pressure was far from being negligible during the sampled period, given that parental females reduced egg loss rates around 10-fold when compared to clutches without any adult assistance (see similar results in Buzatto et al. 2007), presenting a situation in which offspring survival greatly depends on parental care. Although an alternative interpretation would be that harem-owning males are inefficient compensators, we argue that such strategy would not be adaptive since males would only waste time in activities that do not provide any relevant improvement on offspring fitness and that could otherwise be invested in mating activities (such as territory patrolling and mate guarding; Buzatto & Machado 2008), thus compromising their lifetime reproductive success. Therefore, despite previous claims (e.g., Buzatto & Machado 2009, Alissa et al. 2017), our results reveal that an important question remains unanswered: why do *S. proximum* males exhibit this seemingly counterproductive behaviour towards unattended clutches?

A first reasonable explanation is that males simply perceive the unattended clutch within their territories as a food resource. Indeed, our findings show that the occurrence of filial cannibalistic events increases when climatic conditions are unfavourable, probably because males' behaviour of consuming eggs from their own clutches simply responds to the difficulty of finding food resources. In general, however, harem-owning males rarely cannibalize eggs while being next to unattended clutches (see Alissa et al. 2017 and *Results*) and when they do so, they only consume a few eggs. This is a pattern completely different from the voracious behaviour exhibited by other conspecific egg cannibals (females unrelated to the unattended clutch and juveniles) and other egg predators (see Buzatto et al. 2007 and *Results*). In fact, there is no relationship between the amount of time that harem-owning males spend next to an unattended clutch and the occurrence of filial cannibalism. For example, in February, when mate availability was at its highest and males spent most of their time in close proximity to unattended clutches (Fig. 5A), no filial egg cannibalism event by

harem-owning males was observed (Fig. 7). Therefore, although harem-owning males are more prone to consume eggs when food availability is low, their behaviour of standing on unattended clutches is not related to egg cannibalistic attempts, which dismisses the foraging hypothesis.

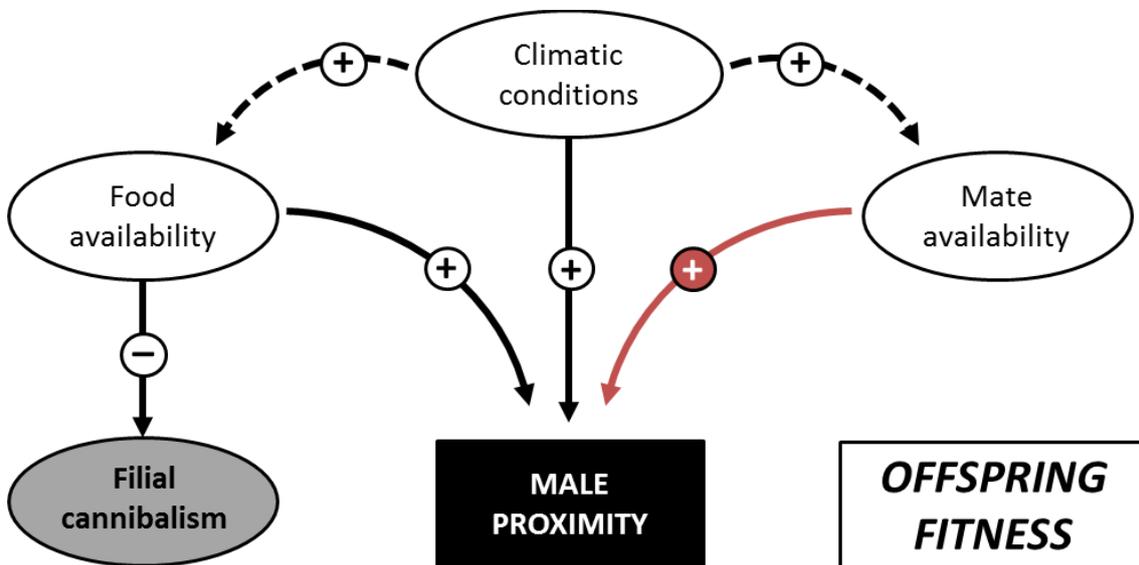


Figure 11. Observed effects of ecological factors on male proximity and filial cannibalism towards unattended clutches within harem-owning males' territories for the harvestman *Serracutisoma proximum*. Male proximity represents the proportion of observations that harem-owning males were in close proximity to the unattended clutch (≤ 20 cm), used as one of our proxies for potential flexible compensatory response. The arrows indicate the direction of positive (symbol "+") or negative (symbol "-") effects on male behaviour. Solid arrows represent direct effects while dashed arrows represent indirect effects. The red arrow indicates an effect in the opposite direction to expectation if male proximity consists in a compensatory parental behaviour (see Fig. 1). There is no ultimate effect of male proximity on offspring fitness.

Given that *S. proximum* harem-owning males behaviour towards unattended clutches has no effect on egg survival, females may compromise their current reproductive investment if they abandon the clutch or are forced to do so (e.g., by falling onto the river during agonistic interactions or strong rainstorms; SN and GSR, pers. obs.). In accordance, these abandonments are usually temporary (Buzatto et al. 2007) and females manage to return to their clutches within a few hours or days (SN and GSR, unpublished data). Given that females are generally promiscuous, accepting to mate with multiple males during the reproductive season, both sneakers and territorial invaders (Buzatto et al. 2011; GSR and SN, pers. obs.), they are likely to behave in the same way during the period of absence from their clutches. Particularly, if females still retain some mature and unfertilized eggs inside their reproductive tracts, extra-harem copulations increase the risks of sperm competition for the fertilization of such eggs experienced by harem-owning males. This is probably the case for our samples, since we

restricted clutches to only those with recently laid eggs, as well as for previous results on *S. proximum* male' behaviour towards unattended clutches (Alissa et al. 2017; see Supplementary Material S3). In this sense, we argue that such behaviour may be a mating activity that consists of waiting for the parental female to return to an easily predictable location and promptly copulating and inseminating her. This behavioural strategy is expected to be especially relevant if the last male to mate fertilizes most of the eggs, which is probably the case, given that males exhibit mate-guarding behaviour (Buzatto et al. 2011), a tactic that efficiently reduces sperm competition (Simmons 2001) and is more likely to evolve under the condition of last-male sperm precedence (Harts & Kokko 2013). In fact, harem owning-males attempted to copulate immediately with conspecific females during the predator exposure experiment, regardless of whether or not they were the original parental females of the unattended clutches. Moreover, the fact that sneaker males and territorial males from different harems adopt the same behaviour of standing on unattended clutches gives additional support to this hypothesis.

The increase in harem-owning males' filial cannibalism observed over the course of the breeding season is also in line with the interpretation of males' behaviour of standing on unattended clutches as mating activity of waiting the return of parental females. Although the benefits of protecting the offspring against egg predators are expected to decrease in reduced clutches (Coleman et al. 1985; Lazarus & Inglis 1986; Clutton-Brock 1991), the costs of care are unlikely to change with clutch size in *S. proximum*, making less worthwhile for females to provide care for reduced clutches (Eadie & Lyon 1998). Moreover, in species with seasonal breeding, the chances of females being able to invest in successful future reproduction may decline as the breeding season progresses due to energetic demands being compromised by previous and current investment (e.g., translated into deteriorated physical condition) (Trivers 1972; Carlisle 1982), or because of the season's temporal limitations over future parental investment by the end of it (Montgomerie & Weatherhead 1988). Consequently, females should be more prone to abandon less valuable offspring at the beginning or during the peak of the breeding season than at the end of the season. In one anecdotal observation conducted in January, a parental female of *S. proximum* that returned to a massively reduced clutch (ca. less than 20% of the original eggs), instead of resuming parental activities, simply fed upon all the remaining eggs and left, laying another clutch inside the same harem about two months later. From a male's perspective, if he does not control his egg consumption on unattended clutches, he may increase the chances for the returning female to desert, thus affecting his own reproductive success. Therefore, males' egg consumption may not only change according to the difficulty of finding food resources, but may also adaptively respond to the probability of

whole-brood desertion by parental females. Future experimental manipulations are still needed to discern if egg cannibalism by harem-owning males is influenced only by changes in food availability, or if males independently respond to changes on desertion decisions of parental females over the course of the breeding season.

One additional and non-mutually exclusive explanation for *S. proximum* males' behaviour of standing on unattended clutches is that they may gain additional mating opportunities, even if parental females have died or are unable to return to the offspring, by allowing other females to feed upon the clutch. Indeed, males have been frequently seen copulating with unfamiliar ovigerous females on unattended clutches, allowing them to prey upon eggs and nymphs while mate-guarding them (see Alissa et al. 2017 and *Results*; Fig. 8b). Given that offspring survival is the same whether or not a male is standing on the unattended clutch, we argue that *S. proximum* males may better improve their fitness by trading sex with ovigerous females for access to food resources, represented by eggs and nymphs. This coincides with observations in January during a pilot study when a harem-owning male allowed and guarded simultaneously several females while they were consuming almost all eggs from an unattended clutch. Moreover, about a month later, one of these females returned and oviposited within the male's territory. Therefore, standing on unattended clutches seems to be beneficial not just for harem-owning males, but also for any other male who comes across unattended offspring and waits for females. By controlling the rate of egg consumption on unattended clutches any male will be increasing its mating opportunities, and this may explain the rarity of egg cannibalism by males in general. For all the arguments presented above, we suggest that the behaviour of adult males towards unattended clutches constitutes a form of mating effort rather than a parental behaviour.

This study demonstrates that it is not sufficient to assume that a parental behaviour is adopted by the sex that normally does not provide care when its partner deserts or dies by simply observing what it seems to be, it is necessary to evaluate its effects on offspring fitness. We recommend investigating this in other species in which flexible compensation of uniparental care is largely presumed, mainly in harvestmen and some frogs. Assuming the existence of flexible compensation of uniparental care can lead to erroneous interpretations when testing predictions about the expression and intensity of compensatory responses. Further, we argue that what seems to be a parental behaviour at first may represent a mating tactic, a hypothesis that still needs to be tested in *S. proximum* and other species, taking into account the multidimensional scenario of mating behaviours, which may include activities that cannot be performed simultaneously, such as territory patrolling and defence, female guarding and waiting for females on unattended clutches.

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SUPPLEMENTARY MATERIAL

S1. FLUCTUATION IN EGG PREDATION PRESSURE

Table S1 shows the results of a model selection analysis where candidate models include one relating the number of eggs lost over four days to the sampled months for data of clutches where both harem-owning males and parental females were absent ('no adult' group), and the no effect model. The best supported model was the null effect model, indicating that there is no empirical evidence to support temporal variation in egg predation pressure over the sampled period, and therefore we decided to exclude this potential predictor from our analyses (Fig. 1).

Table S1. Summary of candidate models ranked by the Akaike Information Criterion corrected for small samples (AIC_c) relating the number of eggs lost over four days to the sampled months in the manipulation group where harem-owning males and parental females were absent.

| Candidate models | Coefficients' estimates | | | | K | AIC_c | ΔAIC_c | w_i |
|--------------------------|-------------------------|-------|-------|-------------------------|----------|--------------|----------------|-------------|
| | I | March | April | Θ | | | | |
| Null effect model | 3.31[†] | – | – | 0.60[†] | 2 | 242.0 | 0.0 | 0.84 |
| Month | 3.64 [†] | -0.11 | -0.68 | 0.63 [†] | 4 | 245.4 | 3.4 | 0.16 |

Best model based on AIC_c in bold ($\Delta AIC_c \leq 2$). The “[†]” symbol indicates parameters whose 95% confidence intervals do not include zero. February was chosen as the reference category for month. Coefficients: I represents the intercept; Θ represents the shape parameter of the negative binomial distribution of the errors. K : number of estimated parameters; ΔAIC_c : difference in AIC_c between each model and the model with the lowest AIC_c ; w_i : Akaike weights. Sample size for all models is 29 clutches (11 clutches sampled in February, 3 in March and 15 in April).

S2. MULTICOLLINEARITY ANALYSES FOR PREDICTOR VARIABLES

Due to significant correlations between our predictor variables (Table S2), we used ‘tolerance’ as an indicator of multicollinearity problems, estimated as $1 - R^2$, where R^2 is calculated by regressing each predictor variable onto the remaining predictors in a multiple regression analysis. The strongest correlation was between our variables mean precipitation and mate availability, coinciding with small values of ‘tolerance’ (≤ 0.4 ; Table S3), indicating potential multicollinearity problems if both variables are included into a same model (Allison 1999). Although there were other significant pairwise correlations between our predictor variables (Table S2), we did not find strong linear dependencies between predictor variables that would lead to multicollinearity problems if either mean precipitation or mate availability but not both were included together with all the rest of our predictor variables (tolerance values > 0.4 ; Table S3).

Table S2: Pearson's correlation coefficients between all our ecological and life-history predictor variables

| | Mean precipitation | Mate availability | Harem size |
|-------------------|--------------------|-------------------|------------|
| Mate availability | 1.00*** | - | - |
| Harem size | 0.29** | 0.29** | - |
| Clutch size | 0.57*** | 0.56*** | 0.06 |

Note: *** $p < 0.001$; ** $p < 0.01$.

Table S3: Tolerance values for each of our predictor variables.

| Predictor variables | First step | Second step | |
|---------------------|-------------------|-------------------|-------------------|
| Mean precipitation | 0.01 | excluded | 0.61 [†] |
| Mate availability | 0.01 | 0.62 [†] | excluded |
| Harem size | 0.90 [†] | 0.90 [†] | 0.90 [†] |
| Clutch size | 0.65 [†] | 0.67 [†] | 0.66 [†] |

In the first step, we included all candidate predictor variables, and in the second step we excluded the variables that presented multicollinearity problems (tolerance ≤ 0.4) in the first step, one at a time. “†” represents tolerance > 0.4 .

S3. RE-ANALYSIS OF DATA FROM ALISSA ET AL. 2017

Due to some inconsistencies between our findings and the results reported in Alissa et al. (2017), we re-run the statistical analyses reported in the published paper. Although the data is not yet publicly available, we contacted the authors and had access to the files used to conduct their analyses. Below, we briefly describe their methodological procedure (please see details in the original paper; Alissa et al. 2017), our concerns with their statistical analyses and the results of our own analyses on their data.

They conducted fieldwork in February 2013, with the same population and at the same location we conducted our study on the harvestman *Serracutisoma proximum* (i.e., transect 2 depicted in Fig. 2 of the main text). They searched for egg-tending females in the first two days, and conducted naturalistic observations in the harems in the subsequent 10 days, when they quantified the number of females laying new clutches (called 'newcomer females'), the number and age of eggs in each clutch (called 'clutch size' and 'clutch age', respectively) and estimated the distance between harem-owning males and females, calculating the proportion of observations in which each harem-owning male was in close proximity of a female within his territory (i.e., $\leq 15\text{cm}$; called 'frequency of mate guarding'). They, then, experimentally removed one parental female from each harem and conducted observations on the harem-owning males' behaviour for four days, quantifying the proportion of observations in which these males were in close proximity of unattended clutches within their territories (i.e., $\leq 15\text{cm}$, equivalent to our proxy for 'male proximity') and the number of eggs per clutch at the beginning and at the end of the observation period. They used a model selection approach based on the Akaike Information Criterion corrected for small samples AIC_c (Burnham & Anderson 2002) to compare different generalized linear models representing the isolated and additive effects of clutch size, clutch age, number of newcomer females and frequency of mate guarding on male proximity, assuming a binomial distribution of the errors.

Observational count data are known to be overdispersed with respect to best-fitting models, a problem that can increase type I errors, resulting in selection of complex models over more simple formats and, consequently, misleading interpretations from reported results (see Richards 2008). Unfortunately, this is the case for the analyses in Alissa et al. (2017), given that the ratio of the residual deviance over degrees of freedom in the full-additive model is $(322.67 / 30) \approx 10.75$, when the binomial distribution of the errors assume it to be close to 1. The use of compound probability distributions, such as the beta-binomial, is an effective way to address overdispersion in count and proportion data (Bolker 2008; Richards 2008). In fact, comparing the adjustment of the full-additive model using a binomial distribution of the errors with an equivalent model assuming a beta-binomial distribution shows extremely greater

support in favour of the model addressing the overdispersion of the data, with direct impacts on the estimates of the relative relevance of each predictor variable (Table S4). Therefore, we re-analysed the data from Alissa et al. (2017) using models that consider a beta-binomial distribution of the errors.

Table S4. Summary of full models ranked by the Akaike Information Criterion corrected for small samples (AIC_c) relating *Serracutisoma proximum* males' proximity to ecological variables, using two different distributions for the errors.

| Candidate models | Distribution of errors | Coefficients' estimates | | | | | | K | AIC_c | ΔAIC_c | w_i |
|--------------------------|------------------------|--------------------------|--------------------------|-------------|--------------------|-------------------------|-------------------------|----------|--------------|----------------|-------------|
| | | I | CS | CA | NF | MG | ϕ | | | | |
| CS + CA + NF + MG | Beta-binomial | -1.79[†] | -0.37[†] | 0.07 | -0.26 | 0.68[†] | 3.08[†] | 6 | 198.7 | 0.0 | 1.00 |
| CS + CA + NF + MG | Binomial | -1.71 [†] | 0.13 [†] | 0.03 | -0.43 [†] | 0.54 [†] | – | 5 | 413.7 | 215.0 | <0.001 |

Best models based on AIC_c in bold. The symbol “+” between covariates represents additive effects models, and the “†” symbol indicates coefficient estimates whose 95% confidence intervals do not included zero. Coefficients: I represents the intercept; CS represents clutch size; CA represents clutch age; NF represents the number of newcomer females; MG represents the proportion of the observations where a harem-owning male guarded the parental female of the focal unattended clutch, at up to 15 cm; and ϕ represents the over–dispersion parameter of the beta-binomial distribution of the errors. K : number of estimated parameters; ΔAIC_c : difference between the AIC_c of each model and the one with the lowest AIC_c ; w_i : AIC_c weight for each model. Sample size for all models is 35 harem-owning males.

Similar to our study, Alissa et al. (2017) did not manipulate any of the predictor variables, but just explored their natural variation, and their data may incur in multicollinearity problems. We used ‘tolerance’ as an indicator of multicollinearity problems, estimated as $1 - R^2$, where R^2 is calculated by regressing each predictor variable onto the remaining predictors in a multiple regression analysis. The tolerance for each predictor variable is greater than 0.4 (Table S5), a threshold usually accepted as the minimum value to interpret as no strong linear dependencies between variables that would lead to multicollinearity problems (Allison 1999). Nevertheless, clutch age is correlated to both the number of newcomer females and frequency of mate guarding (Table S5, Fig. S1), a fact that deserves special attention for the biological interpretation of the correlative association with male proximity.

Table S5: Pearson's correlation coefficients between all ecological predictor variables and tolerance.

| | Clutch size | Clutch age | Newcomer females | Tolerance |
|-------------------------|-------------|------------|------------------|-----------|
| Clutch size | – | – | – | 0.94 |
| Clutch age | 0.07 | – | – | 0.62 |
| Newcomer females | 0.12 | -0.52** | – | 0.71 |
| Mate guarding | -0.18 | -0.43* | 0.20 | 0.79 |

Note: * $p < 0.05$; ** $p < 0.01$.

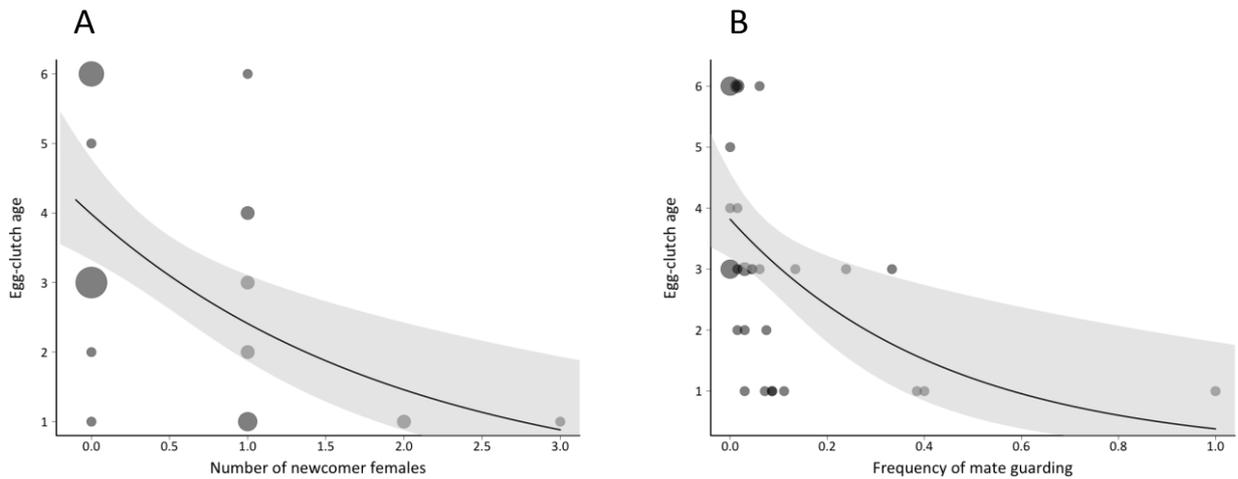


Figure S1. Correlations between predictor variables in data from Alissa et al. (2017). Association between egg-clutch age and (A) the number of females laying new clutches in each harem before the removal manipulation (i.e., ‘newcomer females’), and (B) the proportion of observations in which each harem-owning male was in close proximity of a female within his territory ($\leq 15\text{cm}$) before the removal manipulation (i.e., ‘frequency of mate guarding’). The size of the circles is proportional to the number of observations and the black lines represent the values predicted by the respective model, along with 95% confidence intervals (grey shadows).

We compared the adjustment of the alternative models to the observed data from Alissa et al. (2017) through a model selection approach based AIC_c (Burnham & Anderson 2002), using the in-built packages in the statistical environment R v.3.0.2 (R Development Core Team 2014), in addition to the packages ‘*bbmle*’ (Bolker & R Development Core Team 2016), ‘*aods3*’ (Lesnoff & Lancelot 2015) and ‘*glmmADMB*’ (Fournier et al. 2012). In order to derive direct comparison to the estimates provided in Alissa et al. (2017), we also centered and standardized all predictor variables prior to model fitting. The observed variation in male proximity to unattended clutches was better explained by a positive association with the frequency of mate guarding exhibited by harem-owning males towards parental females before the removal manipulation (Table S6; Fig. S2). Therefore, by considering explicitly a compound probability distribution of the error that addresses the overdispersion present in the observed count data, our model selection analysis favours a simple explanation with the isolated effect of only one predictor variable over more complex models. Although other competitive models are equally plausible to explain the proportion of observations in which each harem-owning male was in close proximity of the unattended clutch within his territory ($\Delta AIC_c \leq 2$), clutch size and the number of newcomer females have negligible effects on male proximity (Table S6) and are interpreted as uninformative parameters (*sensu* Arnold 2010). In this sense, we argue that the effects of both variables, reported and interpreted in Alissa et al. (2017), should be disregarded as biologically relevant in the studied context, as the evidence shows no support for such claim.

Table S6. Summary of candidate models ranked by Akaike Information Criterion corrected for small samples (AIC_c) relating the proportion of observations where the harem-owning males of the harvestman *Serracutisoma proximum* were found in close proximity (≤ 15 cm) to unattended clutches to ecological variables, including the null effect model (data from Alissa et al. 2017).

| Candidate models | Coefficients' estimates | | | | | | K | AIC_c | ΔAIC_c | w_i |
|-------------------|--------------------------|--------------------|-------------------|--------------|-------------------------|-------------------------|----------|--------------|----------------|--------------|
| | I | CS | CA | NF | MG | ϕ | | | | |
| MG | -1.72[†] | – | – | – | 0.52[†] | 2.80[†] | 3 | 193.6 | 0.0 | 0.291 |
| <i>CS + MG</i> | <i>-1.77[†]</i> | <i>0.32</i> | – | – | <i>0.58[†]</i> | <i>2.89[†]</i> | 4 | 194.5 | 0.9 | 0.182 |
| <i>NF + MG</i> | <i>-1.73[†]</i> | – | – | <i>-0.21</i> | <i>0.57[†]</i> | <i>2.91[†]</i> | 4 | 195.3 | 1.7 | 0.121 |
| CA + MG | -1.72 [†] | – | 0.17 | – | 0.60 [†] | 2.82 [†] | 4 | 195.7 | 2.1 | 0.100 |
| CS + NF + MG | -1.79 [†] | 0.37 | – | -0.28 | 0.65 [†] | 3.08 [†] | 5 | 195.9 | 2.3 | 0.093 |
| CS + CA + MG | -1.77 [†] | 0.33 [†] | 0.18 | – | 0.66 [†] | 2.91 [†] | 5 | 196.8 | 3.2 | 0.060 |
| Null effect model | -1.66 [†] | – | – | – | – | 2.30 [†] | 2 | 197.5 | 3.9 | 0.042 |
| CA + NF + MG | -1.73 [†] | – | 0.09 [†] | -0.18 | 0.60 [†] | 2.90 [†] | 5 | 198.0 | 4.4 | 0.032 |
| CS + CA + NF + MG | -1.79 [†] | -0.37 [†] | 0.07 | -0.26 | 0.68 [†] | 3.08 [†] | 6 | 198.7 | 5.1 | 0.022 |
| CS | -1.67 [†] | 0.15 | – | – | – | 2.30 [†] | 3 | 199.4 | 5.8 | 0.016 |
| CA | -1.67 [†] | – | -0.10 | – | – | 2.32 [†] | 3 | 199.7 | 6.1 | 0.014 |
| NF | -1.66 [†] | – | – | -0.06 | – | 2.31 [†] | 3 | 199.8 | 6.2 | 0.013 |
| CS + CA | -1.68 [†] | 0.16 | -0.11 | – | – | 2.32 [†] | 4 | 201.8 | 8.2 | 0.005 |
| CS + NF | -1.68 [†] | 0.16 | – | -0.09 | – | 2.32 [†] | 4 | 201.8 | 8.2 | 0.005 |
| CA + NF | -1.67 [†] | – | -0.18 | -0.14 | – | 2.36 [†] | 4 | 201.9 | 8.3 | 0.004 |

Best models based on AIC_c in bold and competitive models ($\Delta AIC_c \leq 2$) with uninformative additional parameters in italics. The symbol “+” between variables represents additive effects models, and the “†” symbol indicates coefficient estimates whose 95% confidence intervals do not include zero. Coefficients: I represents the intercept; CS represents clutch size; CA represents clutch age; NF represents the number of newcomer females; MG represents the proportion of the observations where a harem-owning male guarded the parental female of the focal unattended clutch, at up to 15 cm; and ϕ represents the over-dispersion parameter of the beta-binomial distribution of the errors. K : number of estimated parameters; ΔAIC_c : difference between the AIC_c of each model and the one with the lowest AIC_c ; w_i : AIC_c weight for each model. Sample size for all models is 35 harem-owning males.

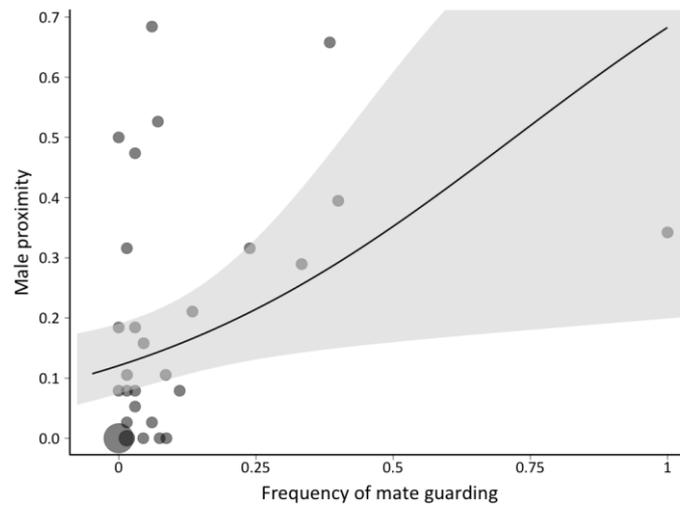


Figure S2. Association between harem-owning males' proximity and their frequency of mate guarding in the harvestman *Serracutisoma proximum*. Male proximity represents the proportion of observations that harem-owning males were in close proximity to the unattended clutch (≤ 15 cm) and mate guarding refers to the proportion of observations in which each harem-owning male was in close proximity of a female within his territory (≤ 15 cm) before the removal manipulation. The size of the circles is proportional to the number of observations and the black line represent the values predicted by the respective model, along with 95% confidence intervals (grey shadows).