



Flexible compensation of uniparental care in an arachnid species: things are not always what they seem

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Flexible compensatory parental care takes place when one parent increases its parental effort in response to its mate's reduction or absence. Although this behavioural response is well known in species with biparental care, the few cases attributed to species with uniparental care are usually based on descriptive observations of apparent compensation without a proper examination of its effects on offspring fitness. In the 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 experimentally investigated under field conditions whether this behaviour constitutes an example of true parental compensation. We evaluated the effects of ecological and life history factors on males' proximity to unattended clutches. We also presented egg predators to the harem-owning males and parental females when they were standing on their clutches and compared their aggressive responses. Finally, we compared egg survival between three manipulation groups: in the absence of both adults; in the presence of only the harem-owning males; and in the presence of the parental females. We observed that males spent considerably less time standing on clutches than parental females, rarely attacked potential egg predators (in contrast to parental females which commonly exhibited aggressive behaviours) and, ultimately, had no effect on offspring survival. Our results do not support the existence of paternal compensation in *S. proximum*. Instead, we hypothesize that males' behaviour comprises a tactic that increases: (1) fertilization success of unfertilized eggs retained by egg-tending females that temporarily abandon the clutch; and/or (2) mating success with newcomer mates that trade copulations for the opportunity to cannibalize the unattended offspring. This study demonstrates that it is imperative to formally test adaptive assumptions before deriving conclusions on the evolution of complex traits and their implications, as an apparently adaptive behaviour is not always what it seems.

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Although parental care enhances offspring fitness and ultimately the fitness of parents (Alonso-Alvarez & Velando, 2012; Santos, Bueno, Gilbert, & Machado, 2016), it may also impose great costs on the caregivers (Alonso-Alvarez & Velando, 2012; Gross & Sargent, 1985). Because both parents share the benefits of care but each pays the costs individually, sexual conflict over care can easily emerge, in which one parent benefits from getting rid of the costs at the expense of its mate's efforts (Houston, Székely, & McNamara, 2005). When a caregiver alters its investment in care, by behavioural adjustments or offspring abandonment, its mate may adaptively respond by changing its own parental behaviour.

For instance, theoretical models predict that a decrease in parental effort by one caregiver should favour compensation by its mate increasing care, as long as the benefits in terms of improvement in offspring fitness outweigh the costs of care (e.g. Johnstone, 2011; McNamara, Houston, Barta, & Osorno, 2003).

Compensatory responses over care have been widely reported in species with biparental care (e.g. Harrison, Barta, Cuthill, & Székely, 2009; Lehtonen, Wong, Svensson, & Meyer, 2011; Smiseth & Moore, 2004) and in cooperative breeders (e.g. Wright & Dingemanse, 1999; Zöttl, Fischer, & Taborsky, 2013). In contrast, known cases in species with uniparental care are scarce. In such cases, when the caregiver dies or deserts the whole brood, compensation for its absence is expressed by the remaining parent exhibiting parental behaviours ('flexible compensation of uniparental care', sensu Ringler et al., 2015; also called 'facultative' or 'amphisexual' care, sensu Simon, 1983). For example, in frogs with male-only care, the

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absence of a parental male results in females performing critical transport of tadpoles to water (*Allobates femoralis*, Ringler et al., 2015; Ringler, Pašukonis, Ringler, & Huber, 2016) or repelling egg predators and preventing egg desiccation and fungal propagation as efficiently as their mates (*Eleutherodactylus johnstonei*, Bourne, 1998). In at least two arthropod species, individuals of one of the sexes aggressively guard the offspring (males in the case of the assassin bug *Rhynocoris tristis*, and females in the case of the spider *Manogea porracea*), but in their absence, their mates behave likewise against egg predators, increasing offspring survival compared to unattended clutches (respectively, Beal & Tallamy, 2006; Moura, Vasconcellos-Neto, & de Oliveira Gonzaga, 2017). 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 these behaviours have probably become evolutionarily constrained to one sex (Klug, Alonzo, & Bonsall, 2012). This may explain, at least in part, the rarity of reported cases of flexible compensation of uniparental care in the literature.

Shifting from a nonparental to a parental state usually involves performing activities that are not regularly present in the behavioural repertoire of the parent that compensates. Therefore, the costs associated with parental care (Alonso-Alvarez & Velando, 2012; Gross & Sargent, 1985) may be even more severe for the compensating individual. Consuming part of its own brood (i.e. 'partial filial cannibalism') in these cases may constitute an adaptive counterstrategy that alleviates the energetic costs of compensatory care, given that the individual is likely to reallocate the nutrients obtained to providing care towards the remaining offspring (reviews in Klug & Bonsall, 2007; Manica, 2002) or other competing activities. Partial filial cannibalism may increase generally when food availability is low (Klug & Bonsall, 2007; Manica, 2002) or only in large broods, owing to lower relative costs of sacrificing a few eggs (e.g. Fitzgerald, 1992; Manica, 2002). Thus, given that partial filial cannibalism co-occurs with parental care, a more comprehensive understanding of flexible compensatory decisions should take their association into account.

With the exception of a few studies (e.g. Beal & Tallamy, 2006; Bourne, 1998; Moura et al., 2017; Ringler et al., 2015), flexible compensation of uniparental care has usually been assumed simply by the behaviour of the remaining parent, which usually does not provide care, towards the abandoned offspring (frogs: Bickford, 2004; Simon, 1983; harvestmen: Buzatto & Machado, 2009; Machado & Oliveira, 1998; Willemart & Gnaspini, 2004). Although frogs and harvestmen are promising study models for understanding the evolution and maintenance of parental care and compensatory behaviours, the assumption that this apparent parental behaviour is adaptive needs formal testing. This assumption should be supported by robust evidence of the effect of the adult's behaviour on the improvement in offspring fitness. The neotropical harvestman *Serracutisoma proximum* (Arachnida: Opiliones) is one example in which flexible compensation of uniparental care has been largely assumed but is far from being confirmed. In this species, territorial males monopolize oviposition sites, which can attract several females to each male's territory, forming a harem-based system (Buzatto & Machado, 2008). These males guard females for a few days during oviposition, which prevents extrapair copulations with males that furtively seek mating opportunities (Buzatto, Requena, Lourenço, Munguía-Steyer, & Machado, 2011). Each female remains on its clutch and improves offspring survival by aggressively repelling egg predators (Buzatto, Requena, Martins, & Machado, 2007). When a female dies or temporarily deserts the clutch, territorial males may stand on the unattended eggs, an activity that competes with patrolling and defending the territory and guarding other females in the harem (Buzatto & Machado, 2008). This behaviour has been interpreted as

flexible compensation of uniparental care (Buzatto & Machado, 2009), although males vary considerably in the time spent with the clutch, with no detectable effect on offspring survival (Alissa, Muniz, & Machado, 2017).

Here, we experimentally investigated under field conditions whether the behaviours exhibited by *S. proximum* males indeed constitute flexible compensation of uniparental care. We hypothesized that males should exhibit similar responses against egg predators as parental females and, ultimately, improve offspring survival. We also evaluated how males' behaviours are affected by ecological and life history factors. We expected the expression of compensatory behaviours to decrease in response to unfavourable climatic conditions, owing to increases in stressful physiological conditions (e.g. Chelini & Machado, 2012; Santos, 2007) and/or reductions in food availability (e.g. Barve & La Sorte, 2016; Lavery & Kieffer, 1994). We also expected males to intensify compensation towards large clutches due to the direct benefits of large clutch size on males' reproductive success (e.g. Coleman & Fischer, 1991; Koskela, Juutistenaho, Mappes, & Oksanen, 2000). Moreover, the expression of compensatory behaviours should take the existence of trade-offs between different components of fitness into account. Given that standing on unattended clutches competes with patrolling and defending the territory, and with guarding other females in *S. proximum* (Buzatto & Machado, 2008), we expected the temporal trade-off between mating and parental effort to be resolved in favour of compensatory parental behaviours when the chances of mating are relatively low (Stiver & Alonzo, 2009). Finally, we expected unfavourable climatic conditions to reduce the availability of food resources and, hence, increase the payoffs of engaging in partial filial cannibalism. Therefore, by sacrificing some eggs, males would gain energy to sustain care for the remaining offspring, particularly in large clutches, where the relative costs of sacrificing a few eggs are diminished (Fitzgerald, 1992; Manica, 2002).

METHODS

Study Site

We carried out fieldwork in an Atlantic Forest fragment at Intervales State Park (24°14'S, 48°04'W; 800 m above sea level), located in the state of São Paulo, southeastern Brazil. We collected the data in February, March and April 2016, a period comprising the second half of the breeding season of *S. proximum* (Buzatto & Machado, 2008). Mean daily precipitation declined during the sampling period (Fig. A1a) and ranged from 0.4 to 3.4 mm, while the average temperature ranged from 20 to 22 °C (data from station F-5-046 at Intervales State Park).

We conducted behavioural observations and experimental manipulations for 8 days each month 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. Because the reproductive activity of *S. proximum* decreases from February to April (see Buzatto & Machado, 2008), the density of reproductively active adults, both territorial males and parental and ovigerous females (Fig. A1b), decreased throughout the sampled months. Therefore, to sustain reasonable sample sizes, we progressively increased the sampling effort over time by extending our sampled area downstream, with the total sampled area varying between months (Fig. A2).

Behavioural Observations

In every sampled month, we started by conducting an intensive 2-day search for *S. proximum* clutches in the sampled area. To avoid

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