



## ECOSYSTEMS

# Different environment, different reproductive strategies? Unexpected field observations in the harvestmen *Discocyrtus prospicuus* (Laniatores: Gonyleptidae)

PATRICIA P. IGLESIAS, MARTÍN O. PEREYRA, ESTEFANÍA STANLEY, CARLOS A. TOSCANO-GADEA & ABEL PÉREZ-GONZÁLEZ

**Abstract:** The evolution of reproductive strategies depends on the relative balance between current benefits and future costs. Geographic variation in demographic and ecological factors has the potential to affect reproductive strategies by altering this optimal cost-benefit balance. Here, we studied a population of the harvestmen *Discocyrtus prospicuus* inhabiting an environment never studied before in this context: a tidal freshwater wetland. We made monthly observations of male-female interactions and their association with egg clutches during a two-year field survey. Our results do not match the expected pattern for this species, consisting of males deserting females immediately after copulation, and females laying isolated eggs and abandoning them after oviposition. Conversely, we show for the first-time pairs *D. prospicuus*, formed by a female and a male, resting together before and after oviposition. Females of this wetland population lay the eggs in small clutches and some of the clutches had eggs in more than one stage of development. Also, we found many females alone over or near the egg clutch in the typical resting position. These findings markedly widen the behavioral specter previously reported for this species and set the stage for future research to determine the causes of these variations.

**Key words:** Egg number, embryonic stages, mating pairs, mate guarding, maternal care, temporary brood desertion.

## INTRODUCTION

Mate guarding and parental care are strategies that enhance reproductive success. Mate guarding has generally been interpreted as a male tactic to avoid extrapair copulations and to ensure paternity, while females may benefit through experiencing reduced predation (Rodríguez-Muñoz et al. 2011). On the other hand, parental care increases the average number of surviving offspring (Smiseth et al. 2012). However, both strategies impose substantial costs, as they consume time that could be spent searching for other mates, foraging or sheltering, and may

increase risks of injury and death (Alcock 1994, Fontaine & Martin 2006, Kokko & Jennions 2008, Requena et al. 2014). Thus, the evolution of these behaviors should depend on the relative balance between current benefits and future costs.

Geographic variation in demographic and ecological factors such as the stress induced by the physical environment, food availability, intraspecific competition, sex ratio, and natural enemies has the potential to affect reproductive strategies by altering this optimal cost-benefit balance (Emlen & Oring 1977, Mobley & Jones 2009, Scordato 2017). Therefore, to understand

the mating systems of a species, it is necessary to study populations occupying contrasting environments and even the same population at different times of the year/season (Schulte & Lötters 2013). The assessment of intraspecific variation is also crucial to a better understanding of the evolution of reproductive strategies between species in comparative-phylogenetic studies (Caetano & Machado 2013, Gilbert & Manica 2015).

In harvestmen, post-copulatory interactions show considerable variation at the interspecific level, including the maintenance of the reproductive couple after sperm transfer, and grasping or remaining close until or during oviposition (Machado et al. 2015, Machado & Macías-Ordóñez 2007). A mating pair may remain together until the female abandons the clutch under the male's protection (i.e. paternal care; Requena & Machado 2014), until the male abandons the clutch, leaving the eggs under female's protection (i.e. maternal care; Machado & Oliveira 1998, Buzatto & Machado 2008), or until both abandon the clutch after copulation or oviposition (i.e. no parental care; see table 12.1 Machado & Ordóñez 2007, Stanley 2011). Since parental care may be costly to guarding adults, unable to forage or take shelter, temporary brood desertion has been reported as a strategy to minimize the costs related to parental care (Machado et al. 2004, Chelini & Machado 2012). In these cases, guarding adults may reduce the costs related to egg loss during periods of temporary parental absence by additional defenses such as egg hiding (Machado & Raimundo 2001), egg camouflage against the substrate (Machado & Raimundo 2001) or egg coating with mucous (e.g. Requena et al. 2009, Chelini & Machado 2014). Physical and chemical egg protections are also usually observed in species without parental care (Machado & Macías-Ordóñez 2007).

Although some studies have demonstrated defense or care of the egg clutches, parental care in harvestmen has generally been based on field observations of females or males found on the eggs in a typical resting position, or on observations under unnatural conditions (Machado & Macías-Ordóñez 2007, Caetano & Machado 2013, and references therein). Observations of egg clutches instead of isolated eggs were also used as further evidence supporting parental care. This situation is particularly the case of species that uses the underside of rocks and fallen logs as oviposition sites where it is impossible to observe individuals without disturbing them and their environment (Machado & Macías-Ordóñez 2007).

The harvestman *Discocyrtus prospicius* (Holmberg, 1876) (Laniatores: Gonyleptidae) is found primarily in shady forests of temperate environments in central and northern regions from Argentina and Uruguay (Acosta & Guerrero 2011, Simó et al. 2014), and uses the underside of rocks and fallen logs as oviposition sites (Iglesias & Pereyra 2020). Based on the available literature, this species has been considered as without mate guarding after copulation (i.e. the male immediately deserts the female after copulation and does not remain while she oviposits), and without maternal care (see states of characters 19 and 21 in Caetano & Machado 2013, Canals 1936, Toscano-Gadea 2011, Stanley 2011). Therefore, other associated characteristics such as mate-guarding behavior and temporary brood desertion are automatically ruled out (see characters 20 and 22 in Caetano & Machado 2013). All these studies were carried out either in laboratory conditions or in continental areas. Here, we studied a population inhabiting a contrasting environment, a tidal freshwater wetland exposed to unpredictable floods, and show evidence suggesting a differentiation in the reproductive strategy of *Discocyrtus prospicius*.

## MATERIALS AND METHODS

During August 2012 to July 2014, while studying the population dynamics and reproductive phenology of *D. prospicuus* in a freshwater wetland of Argentina (34°22'55" S, 58°34'38" W; ~8 m above sea level; see Iglesias & Pereyra 2020), we made monthly observations of male-female interactions and their association with egg clutches. Observations were made between 10:00 AM and 1/1:30 PM. The study area is exposed to predictable tides and unpredictable floods produced by south to southeastern winds (Kandus & Malvárez 2004). However, when the tide level is high, even though the study area is not flooded, the soil is drenched (see Iglesias & Pereyra 2020, for a detailed description of the study area).

The sampling method was based on inspecting all fallen logs in the study area (2,500 m<sup>2</sup>, more details in Iglesias & Pereyra 2020). We were unable to mark and track each log individually since unpredictable floods change the location and the number of fallen logs. From each fallen log in the sampled area, we recorded: the presence of mating pairs and egg clutches, the number of eggs per clutch, and the number and sex of individuals in a typical resting position near (less than 5 cm) or over the eggs. Mating pairs consisted of motionless male and female in the typical resting position with legs in contact or at less than 1 cm.

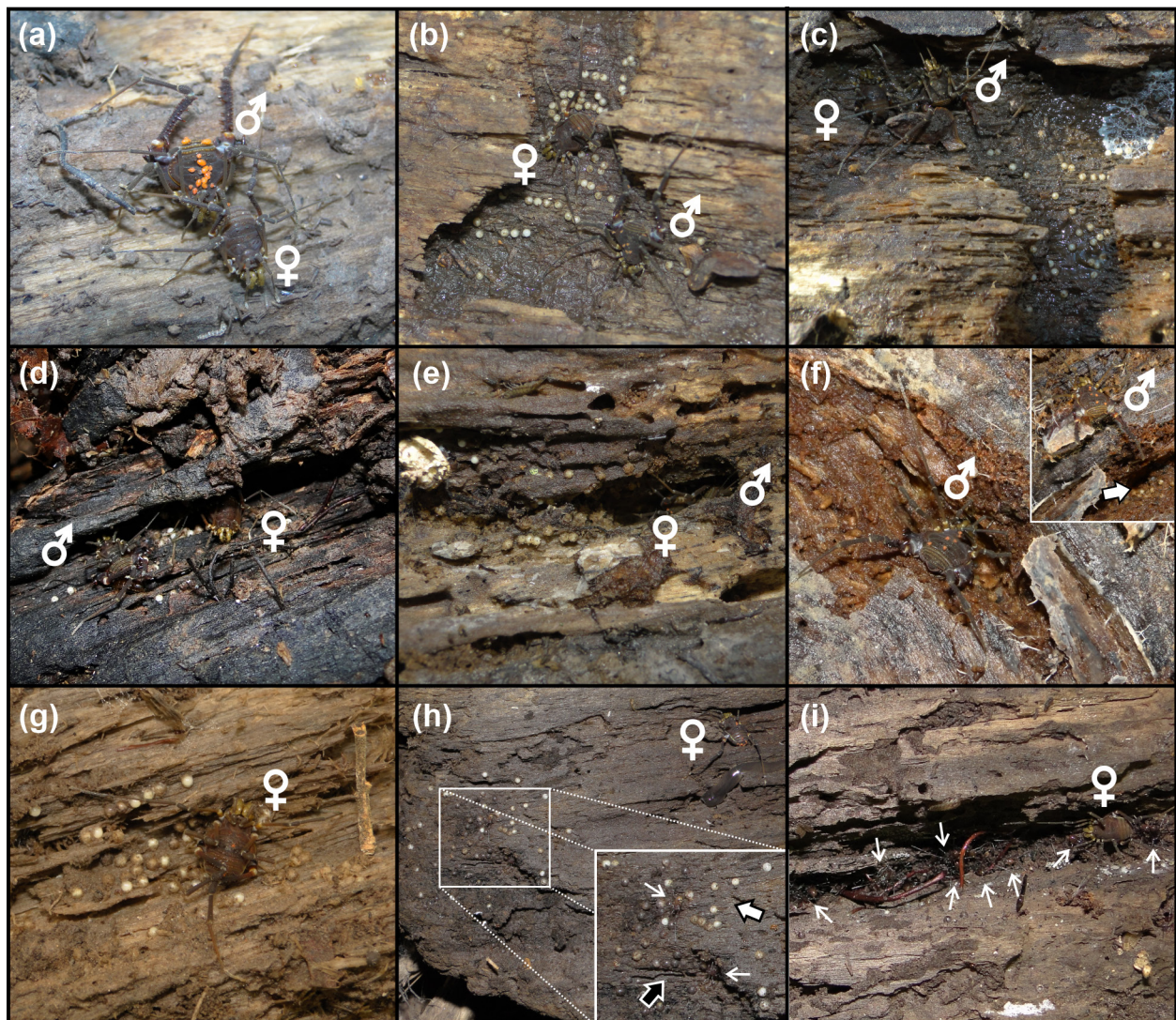
To evaluate whether the number of eggs per clutch (response variable) was associated with the number and sex of the individual/s found nearby (i.e. female, male, pair, or none), we used a GLM with a Poisson distribution of errors and Tukey contrasts. Analyses were run in R 3.5.2 using the packages *car* (Fox et al. 2012) and *multcomp* (Hothorn et al. 2016).

## RESULTS

Pairs in a typical resting position (Figure 1a-e) were seen throughout the year except in August 2012, and January and December 2013. The number of pairs recorded had a peak in April 2013 and July 2014 (Figure 2a). We detected two periods in which none of the mating pairs were found with an egg clutch, from April to June 2013 and from January to April 2014 (Figure 2a). These periods were followed by periods in which the number of mating pairs found with an egg clutch increased.

However, we found egg clutches almost throughout the whole year (except in January and December 2013, and January 2014; Iglesias & Pereyra 2020). Eggs were always covered with debris. Most of them were in the same stage of embryonic development, but we also found some large clutches with eggs in at least two embryonic stages (Figure 1h) and even newly hatched juveniles (Figure 1i). A total of 108 egg clutches were found throughout the study, 35 of them were found unattended, but in the remaining clutches, we observed a female (n = 27; Figure 1g), a male (n = 6; Figure 1f), or a pair of adult female and male (n = 39; Figure 1b-e), either sitting on the eggs or remaining next to the clutch (see Figure 2b).

The mean number of eggs per clutch was 27.6(±19) when were unattended, and 28.8(±19), 27.8(±10) and 22.8(±20) when were guarded by a female, a male, or a pair, respectively. No significant differences were detected in the number of eggs when a pair or only a male was found nearby (Tukey test:  $Z = -2.36$ ,  $p = 0.079$ ). However, clutches had fewer eggs when they were found with a pair or only a male nearby than when they were found guarded by a female (Tukey test:  $Z = -4.67$ ,  $p < 0.001$ ) or unguarded (Tukey test:  $Z = 4$ ,  $p < 0.001$ ).



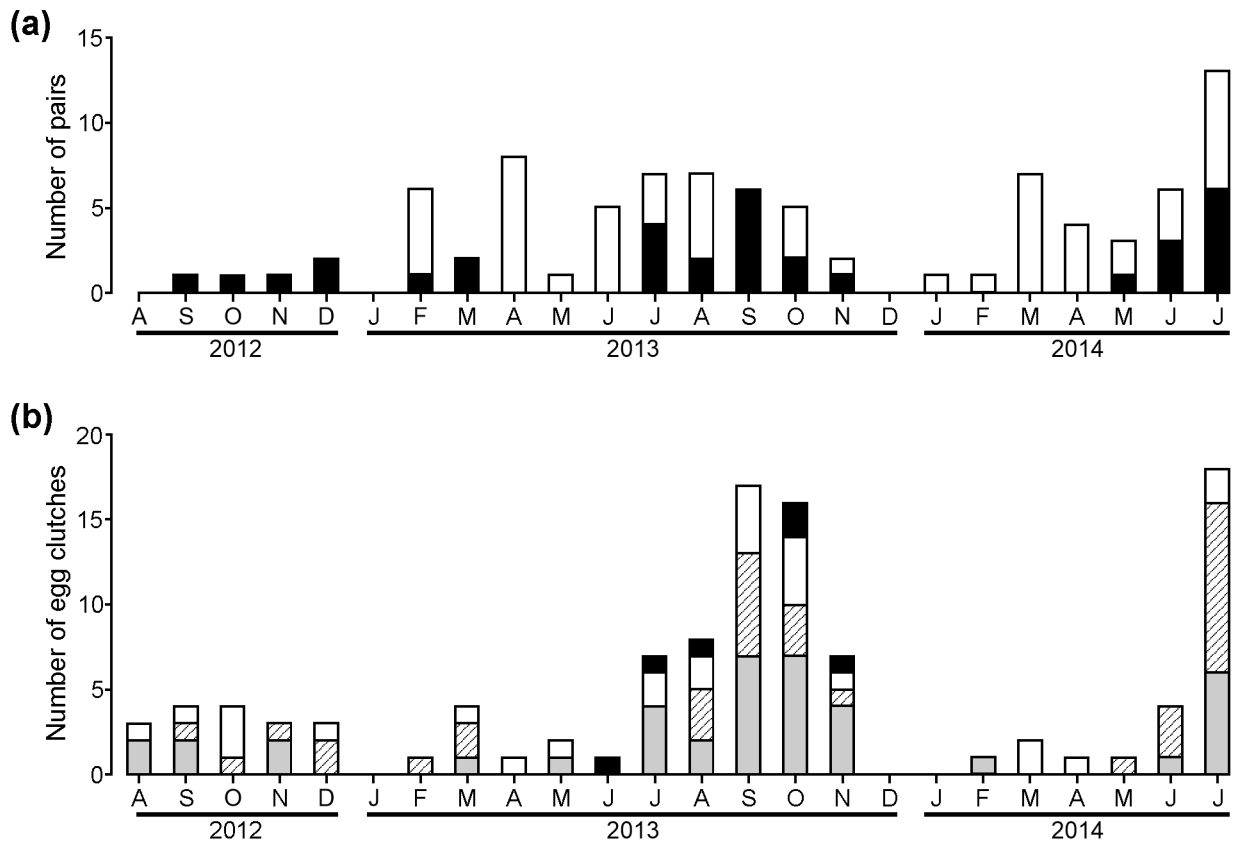
**Figure 1.** Reproductive behavior of *D. prospicius*. (a) Pair resting together on the underside of a fallen log. (b-e) Mating pairs with eggs. (f) Male guarding a clutch of eggs (the arrow points out the previously hidden eggs). (g) Female taking care of eggs. (h) Eggs in different embryonic stages (thick arrows) and newly hatched nymphs (thin white arrows). (i) Female and newly hatched nymphs (arrows). Some individuals moved slightly from the resting position during the time it took to obtain the photo.

## DISCUSSION

Our field observations show for the first-time pairs *D. prospicius*, formed by a female and a male, resting together before and after oviposition. As we only considered adults in the typical resting position and also considering that harvestmen usually move at night hours (and we did fieldwork at noon), the chances that the

individuals sampled were potential predators or vagrants were minimized.

On one hand, the high proportion of pairs without an egg clutch found simultaneously may indicate that females take a relatively long time after mating to begin oviposition (i.e. several days instead of hours), and the male might not leave the female immediately after copulation. Alternatively, males could rest next to the females before copulation, probably



**Figure 2.** Male-female interactions in *D. prospicius* and their association with egg clutches. (a) Number of mating pairs with (black) and without (white) egg clutches found throughout the field survey. (b) Number of egg clutches found alone (gray) or with a mating pair (crosshatched), a female (white) or a male (black) in a typical resting position.

waiting for the females to become receptive (i.e. precopulatory mate guarding; e.g. Bel-Venner & Venner 2006, Parker & Vahed 2010).

On the other hand, the high number of pairs found with eggs after periods of pairs without eggs could be compatible with the hypothesis that mating pairs remain together from copulation to oviposition. Furthermore, the males may only leave the clutch after oviposition is finished. Possible evidence of this behavior is that the clutches with a male present had fewer eggs than the clutches without males, and the males were there waiting for further oviposition events. For instance, in the related species, *Neosadocus maximus*, females keep adding eggs to their clutches for a period of up

to 3 weeks after the first oviposition; (Chelini & Machado 2012). Also, females *N. maximus* show variation in the number of eggs added in a single day (between 2 and 73) and in the interval between two oviposition events (between 1 and 20; Chelini & Machado 2012). However, since we did not tag and follow these individuals, we cannot rule out that the males found near the females before and after oviposition were not the same individual. So if there are different males, and considering all males were recorded resting next to the egg clutches, there are two possible interpretations when a pair with eggs was found: 1) the new male has already copulated with the female and is waiting for oviposition (postcopulatory mate guarding),

or 2) the new male has not yet copulated, but the female allows the male to rest next to the eggs because she could copulate with him later (precopulatory mate guarding). Pairs of adult female and male associated with egg clutches have been previously reported in other harvestmen species (Gnaspini 1995, Manzanilla & Machado 2011). When females provide parental care, it has been suggested that males remain near the females to copulate again with her (e.g. *Goniosoma spelaeum*; Gnaspini 1995, Machado et al. 2009). Long-term studies involving tagging, capture, and recapture are necessary to better understand the behavior observed in this species.

We also found many egg clutches unattended or with a female in a resting position. These clutches do not differ in the mean number of eggs nor the standard deviation. Thus, it may suggest that females remain close to the clutch while still adding to the debris cover, but they are no longer receptive, and then abandon the eggs. In such a case, the risk of predation of unguarded eggs would be low since no significant difference was detected in the number of eggs of those clutches. Alternatively, it may indicate that there is some sort of egg attendance, besides the debris coat. Maternal care is widely distributed within the Neotropical family Gonyleptidae (Machado & Raimundo 2001). Although a debris coat is usually associated with a no parental care strategy, it has also been observed in other species of harvestmen eggs with maternal care, for instance, the harvestmen *Pachylus quinamavidensis* and *Discocyrtanus oliverioi* (ex *Discocyrtus oliverioi*, Kury & Carvalho 2016, Machado & Raimundo 2001, Elpino-Campos et al. 2001). Females of the species *D. oliverioi* never leave their eggs unattended despite the presence of the debris coat (Elpino-Campos et al. 2001). Otherwise, females *P. quinamavidensis* leaves the egg-clutch just before hatching.

Moreover, females of the gonyleptid harvestment *N. maximus* abandon their clutches periodically and keep adding eggs to their clutches for some weeks (i.e. temporary brood desertion strategy; Chelini & Machado 2012). This last species also covers its eggs with a hygroscopic mucous coat, which seems to act as an additional line of egg defense during the periods of female absence (Chelini & Machado 2014). In our study, the facts that A) eggs were laid in small clutches, instead of isolated as was reported in mainland populations (Canals 1936), B) the mean number of eggs, and even standard deviation, do not differ between clutches unattended or with a female resting, and C) that we have observed females resting near or over clutches in at least two different stages of development (Figure 1h) and with newly hatched juveniles (Figure 1h, i), suggest that this population of *D. prospicius* has a caring strategy more similar to *N. maximus* (temporary female absence and an extended oviposition period) than with the hypothesis of clutch desertion after oviposition. Unfortunately, we did not systematically record the stage of development of the eggs found throughout the study, which could have been useful as evidence for this hypothesis. Unpredictable floods may also explain, in part, the observed number of egg clutches unattended. Additional studies that focus more particularly on marking and following both adult individuals and egg clutches are needed to a better understanding of these findings.

Species with wide distribution often express phenotypic variation in life history traits among populations determined by ecological and/or genetic factors (Stearns 1992). *Discocyrtus prospicius* is a widely distributed species that face very contrasting environments. Differences in the length of the reproductive period have been previously documented between populations inhabiting this wetland

and continental areas. A long breeding season was found in this wetland, from February to November/December (Iglesias & Pereyra 2020), which contrasts with results coming from a two-year pitfall trap study conducted in Marindia (34°46'49.9"S, 55°49'34.1"W), a coastal town along the Río de la Plata in Uruguay, showing that the phenology of *D. prospicuus* covered the months from October to May (E. Stanley & C.A. Toscano-Gadea, in preparation). However, 87% of the catches in Marindia were made in an even more limited period: November to January (E. Stanley & C.A. Toscano-Gadea, in preparation). Our current study also shows variation in another reproductive trait, the clutch size (we found small clutches instead of isolated eggs), which also vary among populations in other taxa (e.g. Cruz-Elizalde & Ramírez-Bautista 2016). Thus, it is not surprising that different selection pressures also affect other reproductive behaviors such as mate and egg guarding. Geographic variation in the presence or absence of post-copulatory female guarding and territory defense has also been recorded in populations of the harvestmen *Leiobunum vittatum* (Buzatto et al. 2013).

Reproductive behavioral studies involving individuals that live under fallen logs is very challenging since we always have to turn the fallen logs disturbing the individuals and their environment. Furthermore, the unpredictability of this wetland, which is affected by occasional floods, also makes it a challenging environment for long-term studies. However, our findings markedly widen the behavioral specter previously reported for *D. prospicuus* and set the stage for future research. Further studies formally comparing populations from areas with similar characteristics, such as the islands in the Río Uruguay where the presence of this species is known (Laborda et al. 2018, Laufer et al. 2019), and in continental areas, such as Marindia where the species has been expanding its range

of distribution (E. Stanley & C.A. Toscano-Gadea, in preparation), will help to understand if it is the environment (i.e. phenotypic plasticity), the genetic divergence, or both whose are responsible for the unexpected observations reported here.

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**PATRICIA P. IGLESIAS<sup>1</sup>**

<https://orcid.org/0000-0002-3979-4253>

**MARTÍN O. PEREYRA<sup>1</sup>**

<https://orcid.org/0000-0002-1998-0163>

**ESTEFANÍA STANLEY<sup>2</sup>**

<https://orcid.org/0000-0001-7614-8704>

**CARLOS A. TOSCANO-GADEA<sup>2</sup>**

<https://orcid.org/0000-0002-7380-1402>

**ABEL PÉREZ-GONZÁLEZ<sup>3</sup>**

<https://orcid.org/0000-0002-424>

<sup>1</sup>Laboratorio de Genética Evolutiva, Universidad Nacional de Misiones – CONICET, Felix de Azara 1552, N3300LQH, Misiones, Argentina

<sup>2</sup>Departamento de Ecología y Biología Evolutiva, Instituto de Investigaciones Biológicas Clemente Estable, Avenida Italia 3318, 11600, Montevideo, Uruguay

<sup>3</sup>División Aracnología, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” – CONICET, Av. Ángel Gallardo, 470, C1405DJR Buenos Aires, Argentina

Correspondence to: **Patricia Iglesias**  
E-mail: [patricia.p.iglesias@gmail.com](mailto:patricia.p.iglesias@gmail.com)

#### Author contributions

P.P.I, M.O.P and A.P.G conceived of the study. P.P.I and M.O.P carried out the fieldwork. P.P.I performed the analyses and wrote the original draft of the manuscript. P.P.I, M.O.P, E.S, C.A.T.G and A.P.G discussed the results. M.O.P, E.S, C.A.T.G and A.P.G provided critical comments on the manuscript. All the authors approved the final version for submission.

