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Interpopulational variation of the mating system in the peacock blenny *Salaria pavo*

João L. Saraiva · Giulia Pignolo · David Gonçalves · Rui F. Oliveira

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Abstract The ecology and mating system of two populations of the peacock blenny *Salaria pavo* that have been reported to differ in sexual behaviour were studied. In the Gulf of Trieste, a northern Adriatic Sea population lives in rocky shores, whilst in the Ria Formosa, an Atlantic population inhabits a coastal lagoon with sandy barrier islands. In the Gulf of Trieste, nest availability was found to be higher and nest aggregation lower than in Ria Formosa. Nesting males courted females more and in higher proportion, and inversely, females directed less courtship displays towards nest holders in the Gulf of Trieste than in Ria Formosa. The relative frequency of small female-like males that reproduce by parasitically fertilizing eggs in the larger males' nests was lower in the Gulf of Trieste population. This variation in the sexual behaviour of nesting males and females is likely to reflect a plastic behavioural response to the varying ecological conditions. The difference between populations in the relative frequency of parasitic males suggests that the male alternative reproductive tactics are condition-dependent.

Introduction

The spatial and temporal dispersion of mates, or the resources required to attract them, is thought to be a key issue in the environmental potential for polygamy (Emlen and Oring 1977). More recent studies have extensively confirmed this hypothesis and showed how the breeding strategies can be modulated according to resource dispersion and abundance (e.g. Kolhuru and Grether 2004; Weir and Grant 2004). Furthermore, theoretical models have demonstrated that mating systems are the outcome of the dynamics between both female and male strategies: Males and females can express adaptively flexible, choosy and indiscriminate behaviour so that they may change their behaviour—from moment to moment—to fit dynamically changing circumstances (Gowaty and Hubbell 2005). Flexible sex roles have been widely demonstrated in fish. For example, Forsgren et al. (2004) showed that along the spawning season of a Baltic population of the two spotted goby *Gobiusculus flavescens* (Fabricius, 1779), the operational sex ratio (OSR, the ratio of males in condition to reproduce to fertilisable females) shifts towards females and fish progressively change sex roles, with male courtship being predominant at the beginning of the breeding season and female courtship being predominant towards its end. Also in fish, a plastic response to resource availability has been demonstrated in cavity spawners with exclusive male parental care, a common reproductive mode in this class. In these species, the number of nesting sites can limit the

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J. L. Saraiva · D. Gonçalves · R. F. Oliveira
Instituto Superior de Psicologia Aplicada,
Rua Jardim do Tabaco 34,
1149-041 Lisbon, Portugal

J. L. Saraiva · D. Gonçalves (✉)
Centro de Ciências do Mar, Universidade do Algarve,
Campus de Gambelas,
8005-139 Faro, Portugal
e-mail: davidg@ispa.pt

G. Pignolo
Environmental Chemistry and Risk Assessment Research Unit,
Department of Chemical Sciences, University of Trieste,
via Giorgieri 1,
34100 Trieste, Italy

R. F. Oliveira
Instituto Gulbenkian de Ciência,
Champalimaud Neuroscience Programme,
Rua da Quinta Grande 6,
2780-156 Oeiras, Portugal

number of nest holder males, biasing the OSR towards females, thus limiting their fecundity (Kvarnemo and Ahnesjö 1996) and consequently increasing female competition for mates. The balance between the potential reproductive rates of each sex predicts the sex with the higher level of intrasexual competition (Ahnesjö et al. 2001; Clutton-Brock and Vincent 1991). As an example, Shibata and Kohda (2006) report for the blenny *Petroscirtes breviceps* (Valenciennes) a change in sex roles from typical (i.e. males court females) at the beginning of the breeding season to reversed (i.e. females court males) at the peak of the breeding period to typical again towards the end of the season. Together with the sex roles, so does the intrasexual competition shift from male–male to female–female to male–male. This is explained by a decrease in available nests along the season, reaching a critical point at the peak of the breeding season, and by a gradual increase in the number of available nests towards its end (Shibata and Kohda 2006).

The occurrence of male alternative reproductive tactics (ART; Taborsky 1998) can also be driven by male intrasexual competition for limited reproductive resources. When resources are limiting and defendable, some males invest in territorial defence and female attraction (bourgeois males, sensu Taborsky 1997) whilst others parasitically exploit reproductive resources (parasitic males, sensu Taborsky 1997). Bourgeois males may invest in the differentiation of morphological ornaments, the expression of courtship signals and/or the defence of a breeding territory (Taborsky 1994, 1997, 2001). Parasitic males use female mimicry, sneaking behaviour or cooperation with bourgeois males in order to get access to the spawning area and to reproductive resources defended by the bourgeois male (Taborsky 1994, 1997, 1998, 2001).

We investigated the variation in male and female sexual behaviour and in the occurrence of male ART between two populations of the peacock blenny *Salaria pavo* (Risso) that differ in their ecological conditions. The peacock blenny is a small intertidal fish occurring in the Mediterranean and adjacent Atlantic coasts (Zander 1986). The species is sexually dimorphic, with males being larger than females and presenting several conspicuous secondary sexual characters (SSC) such as a head crest and an anal gland in the first two rays of the anal fin (Fishelson 1963; Papaconstantinou 1979; Patzner et al. 1986). Males are territorial, defending nests in crevices or holes in the rock, and present exclusive male parental care of the clutch (Patzner et al. 1986). In Mediterranean rocky shore populations, parental males are reported to actively court females (Fishelson 1963; Patzner et al. 1986). However, in a natural population of *S. pavo* living in the Ria Formosa coastal lagoon (Algarve, Southern Portugal), where the very few adequate nesting substrates are provided by artificial materials that delimit clam culture fields, courtship is almost entirely initiated by females, and both male and female intrasexual competition occurs (Almada et al. 1995). The aggregation of nests in this population has a clear impact on the dynamics of the sex roles as nest aggregation seems to further bias the OSR towards females (Saraiva et al. 2009). In addition, alternative reproductive male phenotypes have been described in two lagoon populations, one at the Gulf of Lion, France (Ruchon et al. 1995), and the other also at Ria Formosa (Gonçalves et al. 1996). In these two areas, the shortage and aggregation of hard substrates that provide nest sites seems to promote a strong male–male competition for nests, with small males being unable to acquire nests and adopting an alternative reproductive tactic. This tactic has been characterized in some detail at the Ria Formosa population. Small males reproduce parasitically by mimicking the females' courtship behaviour and morphology in order to approach nesting males and fertilize eggs during spawning events (Gonçalves et al. 1996, 2005). Some males do not breed in their first year (T. Fagundes, J. Saraiva, D. Gonçalves and R.F. Oliveira, unpublished data), suggesting a condition-dependent tactic for small males that can either reproduce as parasitic males or postpone reproduction to subsequent breeding seasons (Oliveira et al. 2005). A long-term mark-recapture study shows that parasitic males switch into the nesting tactic after their first breeding season (T. Fagundes, J. Saraiva, D. Gonçalves and R.F. Oliveira, unpublished data). Parasitic males have not been described for the Mediterranean populations where nest sites are widely available (Fishelson 1963; Patzner et al. 1986). Although the observed differences have been attributed to phenotypic plasticity, divergence in sexual traits between populations may also result from genetic effects such as drift, adaptation to environmental conditions, or sexual selection (Panhuis et al. 2001; Coyne and Orr 2004).

In this study, the hypothesis that variation in nest site availability correlates with both sex roles and the occurrence of alternative reproductive phenotypes was tested. For this purpose, the reproductive behaviour of the peacock blenny in the Gulf of Trieste and Ria Formosa was compared. The ecological conditions were characterized, the reproductive behaviour in the field was observed, and the occurrence of ART was assessed. We predicted that *S. pavo* inhabiting areas with abundant nest sites should present typical sex roles (i.e. with predominant male courtship behaviour and male–male competition) and absence or low frequency of parasitic males, whilst in areas with a scarcity of nest sites, the sex roles should be reversed (i.e. with predominant female courtship behaviour and female–female competition) and the frequency of parasitic males should be high.

Materials and methods

Breeding ecology

At Ria Formosa, the only adequate nesting sites are found in artificial reefs that delimit clam culture fields in muddy intertidal flats. These reefs are made of bricks, stones, tiles and other debris, and nesting males use brick holes as nests (Almada et al. 1994). Artificial reefs made of 25 bricks, laid in three separate groups of 5, 14 and 6 bricks, were inspected during the breeding season. Bricks were located at regular intervals of approximately 50 cm in the intertidal zone. Individuals that sheltered or nested inside the brick holes were inspected during low tide. The fish were lightly anaesthetized with MS222 (Sigma, Germany), carefully removed from their holes, and morphometric measurements were performed in situ. The following measures were taken using a calliper: standard length (SL), head height (HH), body height (BH) and crest height (CH). The fish were then returned to their original brick hole. Every unobstructed brick hole was considered a potentially available nest.

In the Gulf of Trieste, transects were carried out in the rocky shore during the breeding season. Each transect covered 25 m^2 of substrate, with quadrats of 1 m^2 placed alternately left and right of a 25-m line parallel to the shoreline, at approximately 1–1.5 m deep. The number of nests occupied and potentially available (see below for definition) was registered in each quadrat. A total of 18 transects were performed, covering 450 m^2 of substrate. Nest holder males were attracted out of the nest with food (usually an open mussel) inside a transparent plastic bag, which was opened around the nest entrance. Once the male was out of the nest and inside the bag, the opening was sealed. Morphometric measurements were performed in situ with the male inside the bag and SL, HH, BH and CH measured using a calliper. Both morphometric measurement methods were calibrated. Whilst the male was still in the plastic bag, the following nest measurements were taken: nest height (NH), nest width (NW) and nest depth (ND). NH was the maximum height of the nest entrance in which the nest holder would fit. NW was the maximum width of the nest entrance, perpendicular to NH, in which the nest holder would fit. ND was the longest straight distance to the inside of the nest, measured from the plane defined by NH and NW. All measures were performed to the nearest 0.1 mm. At the end of these measurements, the male was returned to the nest. In subsequent observations, no case of nest rejection was registered.

The operational a priori criteria to classify cavities as potential nests was that their NH, NW and ND would have to be within the limits defined by the mean±1 standard deviation of the NH, NW and ND of 46 occupied nests previously measured.

Behavioural observations

Focal behavioural observations to nesting males were carried out in both populations whilst snorkelling. The frequency of the different behaviours was registered in underwater slates with previously drawn behavioural grids. The following behaviours were registered: frequency of exits from the nest, frequency of male courtship, frequency of male intra- and intersexual aggression, frequency of visits to the nest by other males, frequency of female visits to the nest, frequency of female courtship displays towards the nest holder, frequency of parasitic male visits to the nest and frequency of parasitic male courtship displays towards the nest holder. Observations lasted for 20 min and were repeated on three different days, except in cases where the male had meanwhile abandoned the nest. Qualitative traits of the nest holder (such as body marks and secondary sexual characters development) were registered to assure its identity in subsequent observations. After the last observation period and whenever possible, both the nest and the nest holder male were measured following the procedure described above. In the Gulf of Trieste, 31 males were observed during the breeding seasons (May to July) of 2004 and 2005, whilst at Ria Formosa 36 males were observed during the breeding season (June–July) of 1996.

Occurrence of ARTs

In order to assess the relative frequency of the two male morphotypes in both populations, two types of sampling were performed in June 2004: In the Gulf of Trieste, a food trap as described above was used, placed in an open area and left open so that several animals could enter. Once one or more animals entered, the trap was closed and the fish were placed in an opaque container underwater. The trap would then be placed again successively until there were no more fish in sight.

In the same month, the population from Ria Formosa was sampled using the technique described in Gonçalves et al. (2003): During low tide, a transect of 80 bricks was inspected, and animals that sheltered or nested in the brick holes were sexed.

Males are easily distinguishable from females upon inspection of the genital papillae. Nest holder males express conspicuous secondary sex characters (a head crest and an anal gland), whilst males that do not express secondary sex characters can be either immature or parasitic males. Since parasitic males have mature gonads and release sperm upon gentle pressure of the ventral lateral surface of the abdomen (Gonçalves et al. 1996), we have used sperm release as a criteria for distinguishing between these two male types.

Statistical analyses

The statistical analyses were performed using the software SPSS 13.0 for Mac OSX. All tests were two-tailed and the significance level set at $\alpha=0.05$. Because assumptions for parametric tests were generally not met, non-parametric tests were used.

Results

Breeding ecology

The distance to the nearest neighbour at Ria Formosa was found to be significantly shorter than in the Gulf of Trieste (mean±SEM: Ria Formosa=32.57±12.34 cm, Gulf of Trieste=116.55±49.51 cm; $N_{\mathrm{RIA\ FORMOSA}}=36$, $N_{\mathrm{GULF\ OF\ TRIESTE}}=27$, Mann–Whitney *U* test, $U=154.0$, $P<0.001$). Males occupied a significantly higher proportion of available potential nests at Ria Formosa than at Gulf of Trieste (RF=36 out of 96, Gulf of Trieste=66 out of 838; $\chi^2=77.7$, $df=1$, $P<0.001$).

Behaviour

There was a higher frequency of both male and female visits to the nests in Ria Formosa (male visits: $U=318.0$, $P<0.01$, Fig. 1a; female visits: $U=112.5$, $P<0.001$, Fig. 1b).

When comparing between populations and correcting for female visits to the nest in each population, males courted more in the Gulf of Trieste than in Ria Formosa ($U=224.0$, $P<0.001$, Fig. 2a), whilst females courted more in Ria Formosa than in the Gulf of Trieste ($U=355.0$, $P<0.01$, Fig. 2b).

Males attacked females more frequently in the Gulf of Trieste than in Ria Formosa ($U=393.0$, $P<0.01$, Fig. 3a), but the frequency of male–male aggressive interactions was similar when corrected for the frequency of other males approaching the nest ($U=487.0$, $P>0.05$, Fig 3b). Nest holders left the nest less often at Ria Formosa (Ria Formosa=0.41±0.19 exits/20 min, Gulf of Trieste=1.87±0.37 exits/20 min, $N_{\mathrm{RIA\ FORMOSA}}=36$, $N_{\mathrm{GULF\ OF\ TRIESTE}}=31$, $U=230.0$, $P<0.001$).

Alternative reproductive tactics

At Ria Formosa, 16 out of the 40 males sampled (40%) were identified as parasitic males, whilst in the Gulf of Trieste only 4 parasitic males out of the 30 males sampled (13.3%) were detected. Therefore, the incidence of the alternative tactic was significantly higher at Ria Formosa ($\chi^2=6.0$, $df=1$, $P<0.05$). In the Gulf of Trieste, female-

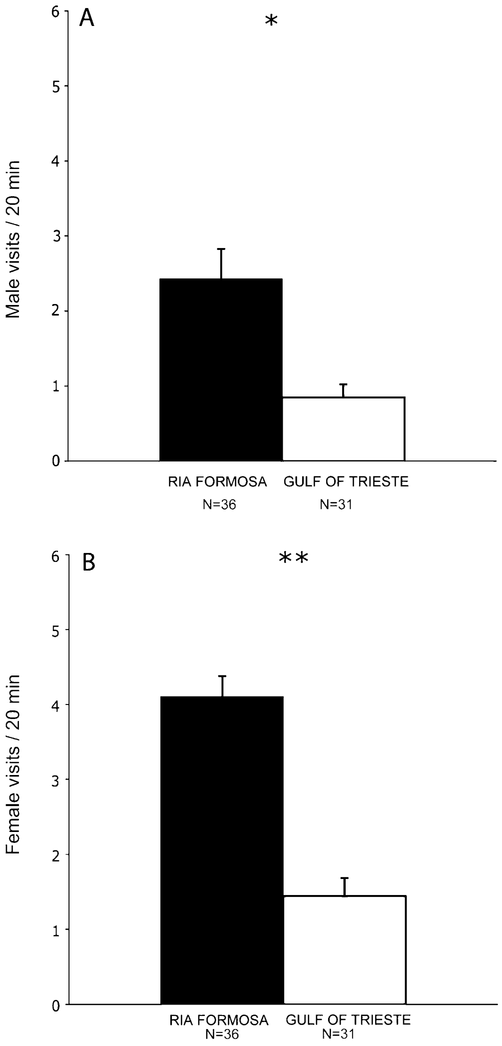

Fig. 1 Male (**a**) and female (**b**) visits to the nest per 20 min in the Ria Formosa and Gulf of Trieste populations. *$P<0.01$; **$P<0.001$. Values are presented as the mean+1 standard error of the mean

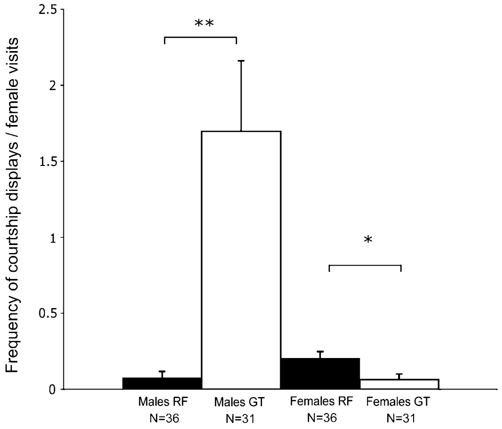

Fig. 2 Frequency of male and female courtship displays in the Ria Formosa (*RF*) and Gulf of Trieste (*GT*) populations, corrected for the frequency of female visits to the nest. *$P<0.01$; **$P<0.001$. Values are presented as the mean+1 standard error of the mean

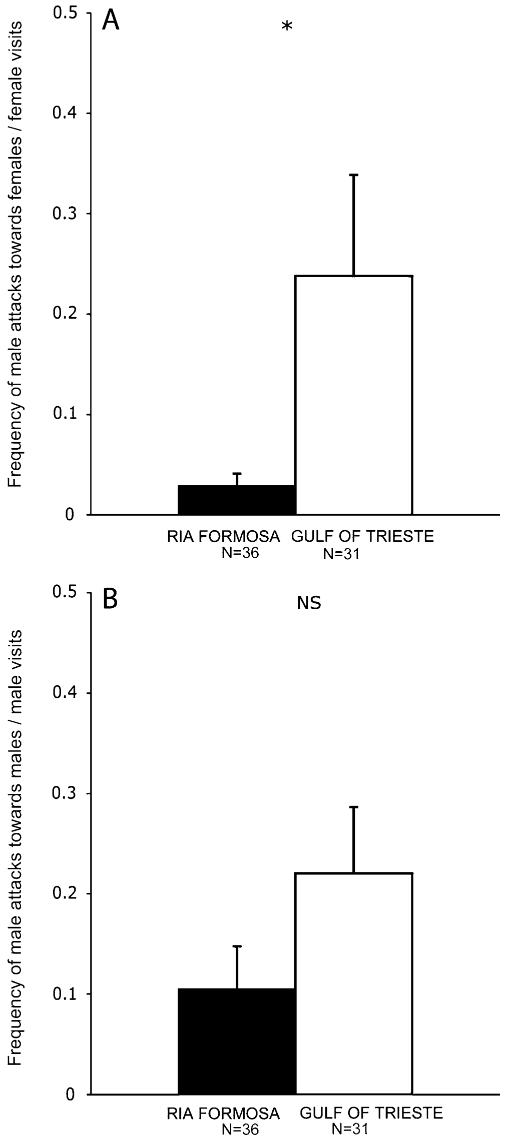

Fig. 3 Frequency of male attacks towards females corrected for the frequency of female visits (**a**) and frequency of male–male agonistic interactions corrected for the frequency of male intrusions (**b**) in the Ria Formosa and Gulf of Trieste populations. $^*P<0.01$; NS, $P>0.05$. Values are presented as the mean+1 standard error of the mean

mimicry behaviour (i.e. courting nest holders using female-like displays) from smaller males lacking secondary sex characters were never observed, whilst in Ria Formosa the frequency of this behaviour was 0.630±0.232 acts/20 min.

Discussion

Finding and choosing the right nest is crucial for reproduction. An adequate cavity that fits the size of the nest holder may prevent intrusion whilst still enabling females to enter because they are smaller than males (Kotrschal 1988). At Ria Formosa, however, nearly 100% of nesting males nest in bricks (Almada et al. 1994). Due to the shape of brick holes, the choice of an adequate nest is a difficult task in this population. There seems to be a preference for holes with one of the openings obstructed and the other narrowed by concrete, sand or other debris (Almada et al. 1994; personal observation). Facing this scarcity of adequate cavities, nests become an extremely valuable resource, and only the largest and more competitive males can occupy a nest (Almada et al. 1994; Saraiva et al. 2010), even if it is very close to a neighbour. This excludes many mature males from reproduction, which keep on searching for nests, so nest holders probably restrain from leaving the nest as a mechanism to prevent nest takeovers (Almada et al. 1995). Interestingly, this does not seem to compromise their ability to attract females since nest holders from Ria Formosa display their large crest (larger than those from Gulf of Trieste; Saraiva et al. 2010) whilst they lay at the entrance of the nest with their head protruding (Almada et al. 1995). As there are many more females searching for spawning opportunities in Ria Formosa than in the Gulf of Trieste and they rely on visual cues to assess male quality (Gonçalves et al. 2002), nest holders from Ria Formosa do not need to exit the nest to attract females. Males from the Gulf of Trieste, however, cannot rely only on their SSC because nests are dispersed, and probably as a consequence, females do not visit males as often as in Ria Formosa. Consequently, males display courtship behaviours in and outside of the nest more frequently in order to invite females into the nest to spawn. These differences in the expression of male courtship behaviours most probably reflect a female-biased OSR in Ria Formosa: Assuming an equal ratio of males to females in both populations, the number of males qualified to mate (Kvarnemo et al. 2001) is greatly reduced at Ria Formosa due to the scarcity and aggregation of adequate nesting substrate (Saraiva et al. 2009). Whilst this enhances the nest holders' resource holding potential, it should also limit females' potential reproductive rate and drive females into actively courting males (Ahnesjö et al. 2001). Conversely, in the Gulf of Trieste, there are cavities in excess and even very small males can acquire nests and develop SSC (Saraiva et al. 2010). But as males leave the nest to court, they face a high risk of other males stealing fertilizations of their clutch. This higher sperm competition regime is reflected on the higher gonadosomatic index (gonad weight/body weight) found among males in the Gulf of Trieste relatively to the Ria Formosa (Saraiva et al. 2010). Even females, which are reported to practise egg cannibalism (Gonçalves and Almada 1997), may present a risk to the clutch whilst the male is away. This would explain why there are more male–female attacks in the Gulf of Trieste population. Interestingly, the observed patterns fit in the theoretical model proposed by Gowaty and Hubbell (2005), which explains that behavioural plasticity allows individuals to be simultaneously competitive and choosy if it enhances their fitness.

Besides having an effect on sex roles, the scarcity of nest sites in Ria Formosa also seems to promote male ARTs. As only the largest males can acquire and secure nests, the only reproductive option for lower size class males is to reproduce parasitically (Taborsky 1998; Saraiva et al. 2010). In fact, there is a clear separation of sizes among Ria Formosa males, with parasitic males being much smaller than nest holders (Gonçalves et al. 1996, 2008). Interestingly, the size of these female-like males overlaps the size of the smallest nest holders in the Gulf of Trieste (Saraiva et al. 2010). This raises the question about their presence (although in a reduced frequency) at the Gulf of Trieste, an area where nest sites are abundant. A possible explanation may be that these males mature too late in the breeding season to grow SSC and directly compete for females. As size does not seem to be an issue for males to find a nest and even males in the lowest size classes can do it, a possible reason for a male to assume a parasitic tactic may be an incomplete maturation state at the onset of the breeding season. At this point, only a much reduced percentage of males find themselves caught in an inappropriate time window to fully develop the bourgeois male secondary sexual characters (Saraiva et al. 2010). Nevertheless, although the large testes development of parasitic males at the Gulf of Trieste strongly suggests that they are reproductively active, their reproductive tactic is not clear as we failed to observe any attempt to parasitically fertilize eggs or any female-like displays by these males. Whilst in Ria Formosa the parasitic males rely on their female-like appearance and behaviour to approach nests and court nest holders (Gonçalves et al. 1996, 2005), parasitic males from Trieste do not have such a female-like behavioural pattern to follow as females rarely court. Instead, parasitic males may rely on invitations by nest holders to enter the nest as this is the typical mating sequence in this population, but further investigation is needed to clarify this subject.

An experimental approach using long-term common garden experiments (i.e. allowing individuals from the two populations to grow in either nest abundant or nest scarce environments) should help confirm the hypothesis of environmental modulation of sexual behaviour and male ART in *S. pavo*. These populations represent a rare case where the assumptions for ecological modulation of behavioural plasticity can be tested at a large scale.

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