



Intra- and interspecific aggression do not modulate androgen levels in dusky gregories, yet male aggression is reduced by an androgen blocker



Philippe Vulliou^{a,b}, Redouan Bshary^b, Albert Frank Huascar Ros^{b,*}

^a Department of Zoology, University of Cambridge, Cambridge, UK

^b University of Neuchâtel, Institute of Biology, Neuchâtel, Switzerland

ARTICLE INFO

Article history:

Received 24 February 2013

Revised 26 June 2013

Accepted 26 June 2013

Available online 6 July 2013

Keywords:

Testosterone

11-ketotestosterone

Flutamide

Teleost

Simulated resident–intruder test

Year-round territoriality

Aggression

ABSTRACT

Discussions about social behavior are generally limited to fitness effects of interactions occurring between conspecifics. However, many fitness relevant interactions take place between individuals belonging to different species. Our detailed knowledge about the role of hormones in intraspecific interactions provides a starting point to investigate how far interspecific interactions are governed by the same physiological mechanisms. Here, we carried out standardized resident–intruder (sRI) tests in the laboratory to investigate the relationship between androgens and both intra- and interspecific aggression in a year-round territorial coral reef fish, the dusky gregory, *Stegastes nigricans*. This damselfish species fiercely defend cultivated algal crops, used as a food source, against a broad array of species, mainly food competitors, and thus represent an ideal model system for comparisons of intra- and interspecific territorial aggression. In a first experiment, resident *S. nigricans* showed elevated territorial aggression against intra- and interspecific intruders, yet neither elicited a significant increase in androgen levels. However, in a second experiment where we treated residents with flutamide, an androgen receptor blocker, males but not females showed decreased aggression, both towards intra- and interspecific intruders. Thus androgens appear to affect aggression in a broader territorial context where species identity of the intruder appears to play no role. This supports the idea that the same hormonal mechanism may be relevant in intra- and interspecific interactions. We further propose that in such a case, where physiological mechanisms of behavioral responses are found to be context dependent, interspecific territorial aggression should be considered a social behavior.

© 2013 Elsevier Inc. All rights reserved.

Introduction

A behavior is considered social if it has fitness effects on both its actor and receiver (West et al., 2007). Scientists discussing social behavior typically refer to intraspecific interactions (Blumstein et al., 2010), and as an example, a recent textbook on the topic did not mention a single case of interspecific interactions (Székely et al., 2010). This omission may look surprising since organisms are sometimes embedded in a heterogeneous network where interspecific interactions are frequent and exert profound effects on fitness (Bshary, 2001; Peiman and Robinson, 2007). In addition, intra- and interspecific behaviors can be classified largely along the same line depending on their effect on the direct reproductive fitness of the different partners. At the exception of altruism which is not expected in interspecific interactions, behaviors directed towards con- or heterospecific individuals can be mutually beneficial, selfish or spiteful. From a modeling perspective, the main difference is that interaction partners belong to different gene pools in interspecific interactions, which causes mainly quantitative adjustments (Bergström et al., 2003; Doebeli and Knowlton, 1998). Thus, the question arises

whether a distinction between intra- and interspecific interactions is useful or whether it hinders a better integration of concepts.

A classical argument for a distinction between intra- and interspecific behaviors originates from studies of aggression. Intraspecific aggression shown during escalated fighting is generally restricted to the reproductive season, sex specific and facilitated by androgen hormones such as testosterone (T) (Borg, 1994; Liley and Stacey, 1983; Wingfield et al., 2006). In contrast, aggression directed against heterospecifics, like killing of prey, may be shown by both sexes and unrelated to T (Bernard, 1976; Gammie et al., 2003; Giammanco et al., 2005). This argument takes a general behavior (aggression) as the starting point for the distinction. At the proximal level though, it was postulated early on that it would be more appropriate to explore the causation of intra- and interspecific behaviors in a specific context, rather than as a function of against whom it is directed (Huntingford, 1976). In order to do so we studied the relationship between hormonal correlates with intra- and interspecific aggression in the context of territoriality. In this context, the immediate consequences of an aggressive act by the territory holder on intra- or interspecific intruders are comparable, and according to Huntingford (1976) in such a situation the aggressive response would be best brought about by a shared physiological factor. We selected androgens as a candidate physiological factor, because castration and

* Corresponding author at: University of Neuchâtel, Department of Behavioural Ecology, Rue Émile-Argand 11, 2009 Neuchâtel, Switzerland. Fax: +41 327183001.

replacement studies have demonstrated a central role of these steroid hormones in the causation of aggressive behavior (Adkins-Regan, 2005). For intraspecific territorial aggression a two-way causal relationship has been described, where social challenges stimulate the release of androgens, which in turn facilitate territorial aggression towards intruders (Hau, 2007; Oliveira, 2004; Ros et al., 2002, 2004; Wingfield et al., 1990). This relationship has been mostly investigated during the reproductive period, and has generally been shown to vary with the degree of social instability associated with parenting style, and mating system (Goymann, 2009; Hirschenhauser and Oliveira, 2006; Wingfield et al., 1990, 2006). Indeed, it has been shown that socially induced increases in androgen levels, in particular in testosterone (T), can be induced experimentally by simulating a territorial intrusion using decoys (Desjardins et al., 2006; Gleason et al., 2009; Goymann, 2009; Hay and Pankhurst, 2005; Hirschenhauser et al., 2004; Ramenofsky, 1984).

In coral reefs, niche overlaps between species may lead to both intra- and interspecific competition for shelter or food (Holbrook and Schmitt, 2002; Muñoz and Motta, 2000; Myrberg and Thresher, 1974). This is particularly evident in some species of damselfish that are called 'gardeners' as they grow and harvest algae as a food source (Ceccarelli, 2007; Karino and Nakazono, 1993), and defend these in a permanent territory against a broad array of potential competitors throughout the year (Di Paola et al., 2012; Ebersole, 1977; Hata and Kato, 2002, 2003, 2006; Hata et al., 2010). Our study species, the dusky gregory, *Stegastes nigricans*, forms colonies where each individual solitary defends its algal crop (Karino and Kuwamura, 1997). Here we address two main issues. We first ask whether the relationship between androgens and intraspecific territorial aggression, as observed in reproductively active territorial fish (Desjardins et al., 2006; Hirschenhauser et al., 2004; Ros et al., 2004), hold outside of the reproductive period. We then question whether this relationship found for intraspecific territoriality would be similar when territorial aggression is directed against heterospecific intruders.

In our first experiment, we measured the effects of both intra- and interspecific territorial aggression on plasma levels of androgens, focusing on T and 11-ketotestosterone (KT). These two androgens are behaviorally the most relevant in teleosts (Borg, 1994; Kime, 1993). In a second experiment, we investigated any causal effect of androgens on territorial aggression by treating the residents with slow-release implants of flutamide, an androgen receptor blocker (Sebire et al., 2008), or castor oil as a control. We compared territorial aggression towards conspecific and heterospecific intruders to test whether androgens might act as a common causal factor for both types of responses. As a heterospecific intruder we selected another year round territorial damselfish, the herbivore *Plectroglyphidodon lacrymatus*. Under natural conditions, *P. lacrymatus* are often found on the edges of *S. nigricans* colonies and competition might occur over vacant territories which also represent a food resource (Hata and Kato, 2006). Occasional aggressive interactions have indeed been observed between free living individuals of the two species (Vulliou, personal observation). Because the endocrine system varies with sex, we tested for possible sex-specific effects of androgens on territorial behaviors by including both males and females in our study.

Materials and methods

Animals, handling and housing

S. nigricans is a monomorphic damselfish species, whose small colonies are found on shallow coral reef patches (Karino and Kuwamura, 1997). Its territory has multiple purposes as it supplies algae to feed on, shelter between the coral, and substrate for breeding. During the reproductive period, which is restricted to summer months (see Galzin, 1987; Jan et al., 2003; Karino and Nakazono, 1993), females temporarily leave their territory to spawn in the territories

of males (Karino, 1999; Karino and Nakazono, 1993). Gonads are regressed in non-reproductively active *S. nigricans* (Karino, 1999), and seasonal variation in gonad size has been described at low to intermediate levels in the winter period (Galzin, 1987). The experiment measuring the behavioral and androgen responses of residents *S. nigricans* exposed to standardized resident–intruder (sRI) tests (experiment 1) was conducted from June to September 2010 at the Lizard Island Research Station (Southern hemisphere: –14.696, 145.455). The experiment determining the flutamide effects on behavioral response towards intra- and interspecific sRI (experiment 2) was carried out from September to November 2011 at the Dahab Marine Research Centre (DMRC, DiveIn) in Dahab, Egypt (Northern hemisphere: 28.470, 34.508).

In both experiments individuals were collected (at 2–10 m depth) by spraying a small amount of clove oil (20% clove oil diluted in 80% ethanol) in the territories, and capturing the slightly sedated individuals using a hand net. Subsequently, fish were placed in a sealed plastic bag with fresh seawater and quickly transported to laboratory facilities where they were sexed by microscopic examination of genital papillae (e.g. Fishelson, 1998; Thresher, 1984).

Fish were housed individually and prevented from any visual and chemical contact with other fish. Each tank was provided with continuously flowing seawater and shaded from direct sunlight to keep water temperature and light conditions similar to those on the reef. To provide shelter and provoke natural behavior, a PVC pipe was placed at the back of the tank as a substitute for the coral rubble with algae that *S. nigricans* defends in nature (see Glickman and Caldwell, 1994). Pilot experiments with *S. nigricans*, and experiments with the related damselfish *P. lacrymatus* (Di Paola et al., 2012), have shown that residents in a tank with a pipe display vigorous aggressive behavior during sRI tests, resembling territorial aggression in the field. Fish were daily fed with commercial flakes for tropical fishes. Before beginning the experiments, all individuals were allowed to recover and acclimatize to the new environment for at least one week. This is a standard procedure in studies on fish endocrinology to minimize the impact of possible variation in prior social experiences.

Experiment 1: androgen modulation and territorial aggression

The measurements were based on a common design to test modulation of steroid hormones in territorial animals, the simulated resident–intruder (sRI) test (Trainor et al., 2009; Wingfield et al., 1990): the territory holder or resident is temporarily exposed to an unknown opponent, the intruder, and subsequently captured for blood sampling. The effect of sRI tests on steroid hormone levels is expressed as the level measured after sRI test (challenge level) compared to the level measured after a control period. Our sRI test was carried out by placing a conspecific or a heterospecific (*P. lacrymatus*) intruder in a transparent tube (Plexiglas 13 cm × 10 cm × 35 cm, filled with sea water) opposite to the shelter of the resident. The tube was left in the aquarium for 15 min during which all the behaviors of the resident were recorded using a Dictaphone. After the test the tube was taken out of the aquarium, and after a small delay a blood sample was drawn (see below). Controls for sRI comprised all of the sRI procedures but in the absence of the intruder in the transparent tube: i.e. standardized resident–intruder control (sRI-c) test. sRI and sRI-c tests took place in the afternoon between 12:30 h and 16:50 h.

A total of 69 *S. nigricans* individuals (Fork Length, FL, mean = 11.01 cm; SE = 0.54 cm) were captured. Of these individuals 46 were assigned to be "residents" and the remaining 23 individuals were assigned to be the conspecific "intruders". Additionally, 21 *P. lacrymatus* (FL mean = 8.02 cm; SE = 0.53 cm) were captured to be used as heterospecific "intruders". This resulted in the following 11 male–male and 12 female–female resident–intruder dyads per intra- and interspecific sRI test. The allocation of individuals to each group was semi-random as we balanced each group for size differences. Each resident was tested

متن کامل مقاله

دریافت فوری ←

ISIArticles

مرجع مقالات تخصصی ایران

- ✓ امکان دانلود نسخه تمام متن مقالات انگلیسی
- ✓ امکان دانلود نسخه ترجمه شده مقالات
- ✓ پذیرش سفارش ترجمه تخصصی
- ✓ امکان جستجو در آرشیو جامعی از صدها موضوع و هزاران مقاله
- ✓ امکان دانلود رایگان ۲ صفحه اول هر مقاله
- ✓ امکان پرداخت اینترنتی با کلیه کارت های عضو شتاب
- ✓ دانلود فوری مقاله پس از پرداخت آنلاین
- ✓ پشتیبانی کامل خرید با بهره مندی از سیستم هوشمند رهگیری سفارشات