

Assessment and decision-making in a Caribbean damselfish: nest-site quality influences prioritization of courtship and brood defence

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In systems where territory quality varies, animals are expected to exhibit plasticity in behaviour in order to maximize fitness relative to their present territory quality. This requires assessment of territory quality followed by decision-making in relation to the priority of activities necessary for survival and reproduction. We examined how differences in territory quality of beaugregory damselfish (*Stegastes leucostictus*) influence the prioritization of courtship and egg defence by comparing behavioural responses of males defending artificial sites (high quality) with males defending natural sites (low quality) when presented with an egg predator, a conspecific female, and a simultaneous choice between both. A significant three-way interaction of territory quality, presentation type and stimulus was observed for time near stimuli. In paired presentations, males defending low-quality territories spent more time near a female and less near an egg predator; while males on high-quality territories spent more time near a predator than a female. Additionally, comparing single and paired presentations reveals that behaviours towards egg predators remain constant while behaviours towards females decrease with paired stimuli. These data suggest that territory quality and ecological context impact decision-making and the relative values of potential reproduction and/or past reproductive effort.

Keywords: beaugregory damselfish; courtship; decision-making; *Stegastes leucostictus*; territory quality

1. INTRODUCTION

For animals demonstrating territorial social systems, it is thought that the benefits of being territorial (access to resources, food and mates) outweigh the costs associated with defence (Brown 1964). Studies of these systems reveal that territoriality is not a rigidly fixed strategy, but rather a flexible state in which individuals demonstrate a constant process of assessment followed by appropriate levels of behaviours. Golden-winged sunbirds (*Nectarinia*

reichenowi) maximize foraging efficiency by adjusting territory size based on the caloric content of nectar in surrounding flowers (Gill & Wolf 1975). Similarly, funnel-web spiders (*Agelenopsis aperta*) are able to assess the value of a web based on food availability and escalate antagonistic encounters accordingly (Riechert 1979). When territory quality is increased for beaugregory damselfish (*Stegastes leucostictus*), males demonstrate higher levels of aggression towards conspecific intruders, as well as higher levels of courtship towards females (Itzkowitz & Haley 1999; Snekser *et al.* 2009). In these systems, as territory quality changes, individuals adjust their investment in territorial behaviours to maximize their relative fitness.

There are, however, many unique demands on individuals and animals do not simply invest in one behaviour at a time. Animals are forced to make decisions concerning the prioritization of behaviours based on internal and external stimuli (Blumstein & Bouskila 1996). When given a choice between feeding and reproduction, Syrian hamsters (*Mesocricetus auratus*) prioritize activities based on fuel availability and only reproduce when energy stores are high (Schneider *et al.* 2007). Ecological factors have been shown to cause changes in prioritization of foraging strategies, courtship behaviour and mate choice in invertebrates (Sih 1988), frogs (Ryan 1985) and fishes (Forsgren 1992). It seems likely that differences in territory quality also affect the choices that animals make in prioritizing behaviour.

We used male beaugregory damselfish to examine how territory quality influences the prioritization of two behaviours: courtship and egg defence. Both activities consist of energetically costly behaviours and cause territorial defenders to leave the safety of their spawning site, thereby exposing themselves to predation. These behaviours are mutually exclusive, as males cannot simultaneously engage in both. We hypothesized that males would adjust their prioritization of these activities in order to maximize fitness relative to their present territory quality. The quality of territories was artificially increased so that some males received higher levels of reproduction. We then presented males with single and paired stimuli to assess the effect of territory quality on the levels of behaviours across treatments. We predicted two possible outcomes. Males on high-quality territories could show higher levels of both types of behaviour, independent of single or paired presentations, implying that courtship and defence have a certain relative value and that investment in one behaviour does not preclude investment in the other. It is also possible that each behaviour has a different relative value in relation to the assessed territory quality, and, thus, the behaviours must be prioritized. In this case, we would expect to see an effect of territory quality on the prioritization of these activities.

2. MATERIAL AND METHODS

(a) Study organism and experimental design

Beaugregory damselfish are polygynous teleosts found along shallow Caribbean coral reefs. Reproductively mature males defend territories (1–2 m diameter) in rubble/sand habitat containing a nest site on which females deposit adhesive eggs. Females travel through territories inducing male courtship behaviour, referred to as 'dips'. After females spawn, the male is left to defend the eggs

from predation. Males also defend territories from conspecific and heterospecific intruders (Santangelo *et al.* 2002).

Fieldwork was completed in the backreef of Discovery Bay Marine Lab of Jamaica during June 2007. Twenty male beaugregory damselfish actively defending territories were selected and their territories were tagged and numbered for repeated observations (territories are rarely usurped (Itzkowitz *et al.* 1995) and tagging territories eliminates any stress caused by handling the fish). Each male was arbitrarily assigned to one of two treatment groups: natural sites or artificial sites. Ten males received only a tag (natural sites). Each of the remaining 10 males was given an artificial breeding site (for photograph and description, see Itzkowitz & Haley 1999). Artificial sites are considered 'high quality' because males on artificial sites receive more eggs than males on natural sites (Itzkowitz 1991), and thus have higher reproductive success. A two-week acclimation period to artificial sites ensured adequate time for egg deposition, although behavioural differences are observed within 48 h of territory manipulation (Snekser *et al.* 2009), suggesting that territory assessment is based on an increase in present as well as future reproductive success. Area of egg coverage (cm^2) on artificial sites was recorded daily.

(b) Behavioural observations

Males were presented stimuli in clear plastic bottles (165 mm \times 240 mm) placed approximately 20 cm from the centre of the territory. Males were tested in three separate behavioural tests: (i) a yellow-phase bluehead wrasse (*Thalassoma bifasciatum*), a predator of damselfish eggs (Itzkowitz & Makie 1986), (ii) a female beaugregory, and (iii) a simultaneous two-bottle presentation of both stimuli. Stimulus fishes were caught in an area separate from the study site, used immediately after capture, presented to all subjects, and released the same day.

Each male was observed for three separate trials for each of the three tests and the order of tests was randomized. Over a 3 min period, time spent within one body length of a bottle was recorded, as well as aggression towards the wrasse (number of bites) and courtship towards the female (number of dips).

(c) Statistical analysis

Behaviours were averaged from the three separate trials for each test. All data were normally distributed with the exception of dips performed during paired presentations. Time near a stimulus was compared using a mixed-model $2 \times 2 \times 2$ factorial ANOVA with presentation type (single/paired) and territory quality (natural/artificial) as between-subject factors and stimulus type (wrasse/female) as a within-subject factor. Bites and dips were compared between presentation type and territory quality with a 2×2 factorial ANOVA for wrasse and female presentations, respectively. For artificial sites, all behaviours were correlated with the average area of egg coverage using Pearson product moment correlation coefficients. Statistics were conducted with SPSS 12.0.

3. RESULTS

There was a significant three-way interaction of presentation type, territory quality and stimulus on the time spent near stimuli ($F_{1,18} = 4.81$, $p = 0.041$). For paired presentations, males on artificial sites spent more time with a wrasse than a female, while males on natural sites spent more time with a female than a wrasse. Males on artificial sites also spent more time with stimuli (main effect: $F_{1,18} = 8.59$, $p = 0.009$) and there was a significant two-way interaction of territory quality and presentation type ($F_{1,18} = 12.21$, $p = 0.003$), with males on artificial sites spending more time than males on natural sites near stimuli when presented singly, while equivalent amounts of time were spent with paired stimuli. For all males, the decrease in time near females from single to paired presentations is greater than the decrease in time near wrasse (stimulus \times presentation type ($F_{1,18} = 14.20$, $p = 0.001$)). There was not a significant main effect of stimulus ($F_{1,18} = 1.399$, $p = 0.252$); however, males on artificial sites spent more time with wrasse than females, and males on natural sites spent

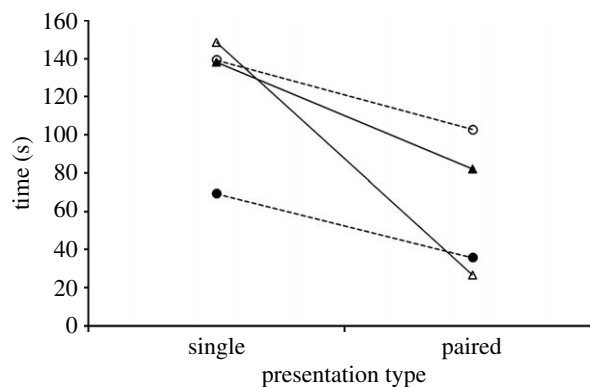


Figure 1. Mean time spent with female (triangles) or wrasse (circles) by males defending natural (filled symbols) or artificial (open symbols) sites compared between single and paired presentations.

more time with females than wrasse (stimulus \times territory quality ($F_{1,18} = 19.57$, $p < 0.001$; figure 1).

Territory quality did not influence dips ($F_{1,18} = 1.19$, $p = 0.289$); all males showed lower levels of courtship during simultaneous presentations compared with single presentations ($F_{1,18} = 30.17$, $p < 0.001$; figure 2a). Males on artificial sites performed more bites than males on natural sites towards a wrasse ($F_{1,18} = 27.30$, $p < 0.001$), regardless of the presentation type ($F_{1,18} = 3.50$, $p = 0.078$; figure 2b).

There were no significant correlations between the average area of egg coverage for males on artificial sites and any of the behavioural measures in the single wrasse presentations (bites, $r = 0.236$, $p = 0.511$; time, $r = 0.020$, $p = 0.956$), single female presentations (dips, $r = -0.275$, $p = 0.443$; time, $r = 0.385$, $p = 0.271$) or in paired presentations (bites, $r = 0.528$, $p = 0.117$; time with wrasse, $r = 0.357$, $p = 0.312$; dips, $r = -0.079$, $p = 0.827$; time with female, $r = -0.063$, $p = 0.863$).

4. DISCUSSION

Male damselfish appear to assess their present territory quality and adjust behavioural levels accordingly. It is clear that this assessment is based on multiple cues. Here, territory quality, the context in which a stimulus appeared and stimulus type all influenced the time that males spent away from their territory. When provided with a choice, males on natural sites spent more time near a female than a wrasse and males on artificial sites spent more time near a wrasse than a female. Measurements of aggression, but not courtship, also support this difference in prioritization.

There are several possible causes for males on different quality territories to have different priorities. Territory quality probably affects the potential threat of an egg predator. Males on low-quality territories have fewer eggs than males on high-quality territories and therefore the wrasse poses little threat. While males defending artificial sites spent more time with and performed more bites towards the wrasse, these behaviours occurred independent of the amount of eggs present. It is also possible that the open structure of artificial sites increased egg vulnerability. An increase in the present reproductive success coupled with a potential increase in vulnerability may account for the observed differences between territory types.

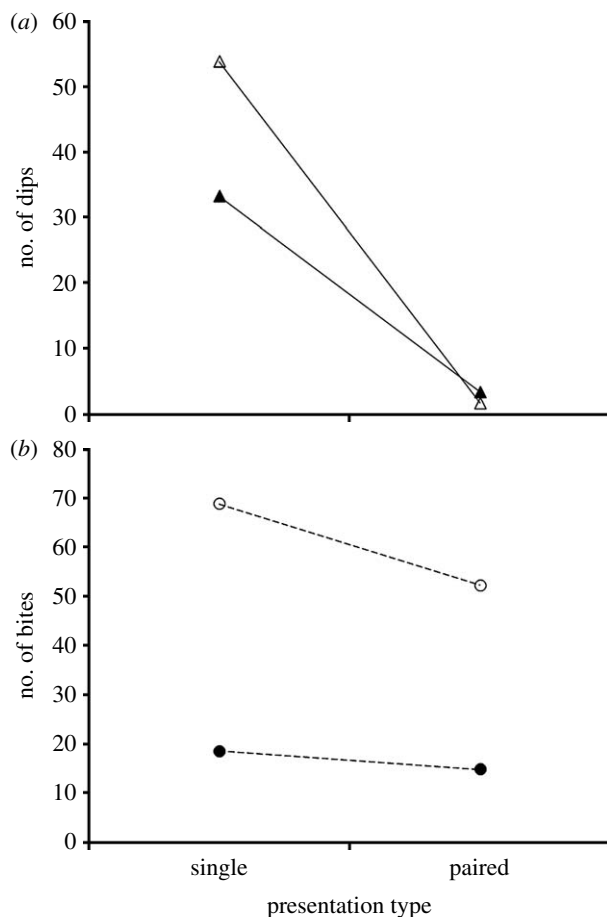


Figure 2. Mean number of (a) dips towards a female and (b) bites towards a wrasse by males defending natural (filled symbols) or artificial (open symbols) sites compared between single and paired presentations.

In either case, the threat of the wrasse appears to remain constant as the presentation context (single/paired) had no effect on aggression.

By contrast, time spent near a female differed between territory qualities in paired, but not single presentations. In polygynous systems, such as beaugregory damselfish, most males infrequently receive reproduction (Bateman 1948; Howard 1978) and, therefore, any individual female is highly valued as a source of eggs. Thus, when the female is presented alone, all males spent most of their time courting. In paired presentations, however, the high level of egg defence by males on artificial sites precluded them from spending time near the female. Males on natural sites spent less time with the wrasse, and thus were able to maintain similar amounts of time near females.

While males on natural sites spent relatively more time near females, this investment was not reflected in courtship behaviour. When the female was paired with a wrasse, males on natural sites performed a lower number of dips than that in single presentations. It appears that, while investment in the female is still high (in terms of time), the behaviour of courting may be too risky to be performed in the presence of an egg predator, indicating that males modify not simply time investment, but also levels of specific behaviours based on the context of the presented stimuli.

Taken together, the influences of territory quality, stimulus type and context on behavioural prioritization demonstrate a role for complex decision-making in territorial teleosts.

All experimental methodologies were conducted in accordance with procedural guidelines of the DBML, University of the West Indies, Jamaica.

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