

Interactions of natural and sexual selection: damsel­fish prioritize brood defense with male–male competition or courtship

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Summary

Natural and sexual selection often act in opposing directions, forcing individuals to prioritize activities necessary for survival with those required for reproduction. We examined the interaction of natural and sexual selection pressures on the behaviour of beaugregory damselfish, *Stegastes leucostictus*, by presenting territorial males with an egg predator and either a male or female conspecific, requiring males to prioritize brood defense with either courtship or intra-sexual competition. By measuring the time spent near stimuli, we examined the influence of several factors, including stimuli type, variation in predator number, and the presence of eggs in a nest site. Generally, males spent more time with conspecific stimuli than egg predators, suggesting that the sexual selection pressures of deterring rivals and attracting mates outweigh the natural selection pressure to engage in brood defense. This decision was affected by the sex of the conspecific presented, the presence of eggs in a male's territory, and a number of interactions of these factors, indicating that male damselfish consider multiple factors before investing in certain types and intensities of behaviours. Furthermore, observations of behaviours associated with courtship and intrasexual aggression show that a natural selection pressure impacts intra- and inter-sexually selected behaviours differently in this system.

Keywords: beaugregory damselfish, *Stegastes leucostictus*, courtship, egg predation, male–male competition, sexual selection, *Thalassoma bifasciatum*.

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Introduction

Although occasionally categorized as a subset of natural selection, sexual selection is often viewed as a distinct evolutionary process (Darwin, 1859, 1871; reviewed in Andersson, 1994). While natural selection leads to the evolution of adaptations that increase survival, and thereby fitness, sexual selection is solely responsible for driving the evolution of characters that enhance reproductive success. Theoretically, the interaction between these two types of selective pressures can be synergistic, but much more often it appears that these mechanisms are diametrically opposed (Fisher, 1930; Andersson, 1994). For example, the exaggeration of male secondary sex characters is thought to be impeded by fitness costs, such as increased predation and slow growth rates (Clutton-Brock et al., 1985; Magnhagen, 1991; Promislow, 1992; Promislow et al., 1992).

This interaction of natural and sexual selection pressures becomes more complex when both forms of sexual selection are considered. The evolution of sexually selected traits can be driven by competition within a sex (intra-sexual competition), as well as by differential choice for members of the opposite sex (intersexual selection). Teasing these mechanisms apart is difficult in many systems because the same characters that are important for male–male competition may also play a role in female mate choice (Berglund et al., 1996; Qvarnström & Forsgren, 1998; Wong & Candolin, 2005; reviewed by Hunt et al., 2009).

Empirical studies that consider intra- and inter-sexual selection as discrete mechanisms generally focus on the exaggeration of physical traits. For example, large body size in males is selected for by both male–male competition as well as female mate choice in a variety of species (e.g., house crickets, *Acheta domesticus*, Savage et al., 2005; fiddler crabs, *Uca paradisumier*, Jaroensutasinee & Jaroensutasinee, 2003; zebrafish, *Danio rerio*, Pyron, 2003; tiger salamanders, *Ambystoma tigrinum tigrinum*, Howard et al., 1997). Other traits showing a similar pattern of selection include coloration, fin length, body weight, and head shape (Hunt et al., 2009). Studies on these physical characters allow for easy characterization and quantifiable measurements of these traits. Much less attention is paid to the behavioural aspects of an animal's phenotype. Natural selection drives the evolution of behaviour that increases survival, such as increased vigilance and protection of young from potential predators. Sexual selection influences behaviour associated with obtaining mates, such as aggression toward rivals of the same

Table 1. Experimental design of double stimuli presentations.

Treatment	Conspecific bottle	Wrasse bottle
1	Male	1 wrasse
2	Male	3 wrasse
3	Female	1 wrasse
4	Female	3 wrasse

18 males were tested once in each of four treatments.

sex and courtship toward the opposite sex. A better understanding of the role of intra- and inter-sexual selection may be garnered from examination of these behaviours as they are usually performed exclusively in a given context, while physical traits are difficult to separate as a result of female choice or male–male aggression (see Table 1, Hunt et al., 2009).

Disparate intra- and inter-sexually selected behaviours are displayed by the beaugregory damselfish. When presented with conspecific stimuli in their natural environment, males show unique behavioural responses toward males and females (Santangelo et al., 2002; Snekser et al., 2009). Males approach other males and aggressively attack by biting and laterally displaying. In contrast, female conspecifics induce a courtship behaviour commonly referred to as a dip, as males rapidly swim up and down in the water column. These two behavioural responses are inherently mutually exclusive as a male that is attacking an intruder cannot simultaneously be performing dips and vice versa.

As is true of many systems, when male beaugregory damselfish are actively engaging in behaviour associated with reproduction (courtship or male–male competition), they leave themselves vulnerable to predation (personal observation), a natural selection pressure. A closely related species, the bicolor damselfish, *Stegastes partitus*, shows reduced levels of courtship behaviour in the presence of both fish and egg predators (Figueira & Lyman, 2007) and similar patterns are seen in the beaugregory damselfish (Leese et al., 2009). No study, however, has addressed how a natural selection pressure, like egg predation, might impact both intra- and inter-sexual competition simultaneously within this system. We utilized a common predator of damselfish eggs, the bluehead wrasse, *Thalassoma bifasciatum*, to investigate this relationship. While this species poses no direct threat to an adult damselfish,

they will swarm a nest site and feed on any eggs left unguarded (Itzkowitz, 1979). To deter wrasse from attacking their site, male bluegill damselfish will bite and chase heterospecific intruders and perform threat maneuvers (Haley & Müller, 2002; Leese et al., 2009).

Using the wrasse stimuli to represent the threat of egg predation as a proxy for a natural selection pressure, we examined the relationship between natural and intra- and inter-sexual selection and how these forces interact to determine the resultant behaviour of male damselfish. Males actively defending territories were simultaneously presented with two stimuli: one stimulus was a bluehead wrasse and the other was a conspecific male or female, allowing males to engage in either brood defense or one of the two types of sexual competition (i.e., male–male aggression or courtship).

We initially hypothesized that males would divide their time between both types of stimuli, and that the determining factor in choice of activity would be the perceived risk of egg predation as determined by the presence or absence of eggs in a territory. Males defend territories even when no brood is present, but there is evidence that this species assesses the presence (but not amount) of eggs in a nest site and adjust levels of defense accordingly (Haley & Müller, 2002; Leese et al., 2009). We expected that males with eggs would spend more time engaging in brood defense than in male–male competition or courtship. Males without eggs in their territory would experience no direct threat from an egg predator and would be more likely to spend time engaging with conspecific stimuli.

To further explore how individuals make decisions when presented with conflicting selection pressures, we also attempted to increase the threat of egg predation to focal individuals. Avian parents modify levels of nest guarding behaviours based on a number of external factors (Montgomerie & Weatherhead, 1988; Brunton, 1990; Lima & Dill, 1990; Whittam & Leonard, 2000) and we anticipated similar responses in this system. Ordinarily, bluehead wrasse will form shoals when a food source is identified (Itzkowitz, 1979). As the number of wrasse attempting to feed on a brood increases, there is the potential for a much greater reduction in clutch size. This swarming predation of the wrasse may influence the prioritization of behaviour. We manipulated the level of threat of egg predation by increasing the number of wrasse presented to territorial males. We expected that an increase in the number of egg predators would lead to increases in brood defense over

male–male competition or courtship, but only for males with eggs in their territories.

Finally, we predicted that the sex of the conspecific stimuli would influence the prioritization of behaviour. Male and female conspecifics represent very different potential impacts to an individual's fitness. Females present an opportunity to mate and gain eggs, thus increasing current reproductive success. Conversely, intruding males may prey upon eggs, intercept females, or usurp the territory, thereby representing potential decreases in both current and future reproductive success. Because of these differences, we would expect an overall effect of the sex of the conspecific stimulus on the prioritization of behaviour with brood defense, in addition to the influences of the brood predators and the presence or absence of eggs.

Methods

Animal model

The beaugregory damselfish is found in tropical marine waters throughout the Caribbean. Males defend territories (1–2 m diameter) in rubble and sand habitat containing a cave or crevice on which females deposit adhesive eggs. Males mate polygynously and a male's territory may include egg clutches from many different females simultaneously. As is common of polygynous systems, males show great variation in reproductive success. Levels of reproduction are higher, however, when males are given artificial breeding sites (Itzkowitz et al., 2001). Females are territorial as well, but each day travel widely in search of mates, visiting male territories and inducing male courtship behaviour (Horne & Itzkowitz, 1995). After finding a suitable mate, females deposit their eggs and leave the site and the male is left to guard the eggs. Courtship behaviour occurs year round, but spawning fluctuates with the lunar cycle (Itzkowitz, 1985). This study was conducted over a 4-day period (5–8 June 2008) to limit the influence of the lunar cycle on behaviour.

Experimental design

All field work was conducted in the back reef of Discovery Bay Marine Laboratory, located in Discovery Bay, Jamaica. At the onset of the study, 18 adult

male beaugregory damselfish actively defending territories were selected. Each male was given an artificial breeding site composed of four pieces of PVC tubing attached in a cross formation to a square plastic base measuring 30 cm² (for picture see Itzkowitz & Haley, 1999). The use of artificial sites allowed for the direct observation of eggs without manipulation of the territory. Artificial sites also served to equalize territory quality among males, as males typically adjust behavioural levels in accordance with the quality of the territory (Itzkowitz & Haley, 1999; Santangelo et al., 2002; Snekser et al., 2009). Each site was marked with a numbered tag for repeated observations and to avoid replication in data collection. Beaugregory males show a high level of territory fidelity and a previous study in which individuals were injected with non-toxic acrylic paint showed that sites are rarely usurped by other males (Itzkowitz et al., 1995). Males were given 14 days to adjust to the new sites prior to behavioural testing.

Stimuli fishes were caught in an area separate from the study site and kept in flow tanks for the duration of the study. For behavioural tests, males were presented with stimuli in two clear plastic bottles (165 mm diameter × 240 mm height) placed approx. 30 cm from the center of the artificial site. The bottles contained small holes on top, allowing for water flow and possible chemical communication. Each male was tested once with each of four treatments: (1) 1 wrasse and conspecific male; (2) 3 wrasse and conspecific male; (3) 1 wrasse and conspecific female; and (4) 3 wrasse and conspecific female (Table 1). The four treatments occurred on consecutive days with each male in the study being exposed to the same treatment on a given day. The same stimuli fishes were used within, but not between treatments.

The presence of eggs was monitored in each site daily. Haley & Müller (2002) found that male beaugregory damselfish adjusted aggression behaviour toward egg predators based on the presence or absence of eggs, but found no correlation between the amount of eggs or number of egg clutches and any type of behavioural measure. Thus, for analysis, males were either grouped as 'eggs' ($N = 8$) or 'no eggs' ($N = 7$) at the time of testing. Three males were omitted from statistical analysis as their egg status changed during the four day testing period.

Behavioural observations

After placement of the bottles containing stimuli fishes approx. 30 cm from the center of the artificial site, behaviour was observed for a three minute

period. As a measure of attention, the total time spent within 10 cm of either stimulus bottle was recorded. In addition, a number of stereotypic behaviours were monitored. Aggression behaviours toward wrasse included bites at the bottle as well as downhead threats. This behaviour has previously been used as a measurement of aggression toward heterospecifics (Haley & Müller, 2002) and could occur at the bottle or while the male was over his territory. Aggression toward male conspecifics consisted of the number of bites at the bottle as well as lateral displays, a threat behaviour demonstrated primarily in the presence of conspecifics (Santangelo et al., 2002; Snekser et al., 2009). Lateral displays occurred exclusively at the bottle when the males were side by side. Courtship toward a female was measured by counting the number of dips that occurred. Dips occurred both near and away from the bottle.

Statistical analysis

To analyze the effects of all factors on the time that each male spent near a bottled stimulus, a $2 \times 2 \times 2 \times 2$ repeated measures factorial ANOVA was performed. Three within subjects factors were considered with two levels of each variable: stimulus type (conspecific/wrasse), sex of conspecific (male/female) and wrasse number (1/3). A between subjects factor of egg status was analyzed with males being grouped as either 'eggs' or 'no eggs'.

Since the specific behaviours directed at the wrasse and those directed at the conspecific stimuli were not equivalent to each other (e.g., bites toward a wrasse are not the same as dips toward a female), these could not be analyzed using the same repeated measures ANOVA. Behaviours directed toward wrasse (bites and downhead threats) were compared using a $2 \times 2 \times 2$ repeated measures factorial ANOVA. Within subjects factors were sex of conspecific (male/female) and wrasse number (1/3), with egg status (eggs/no eggs) as a between subjects factor. A 2×2 repeated measures factorial ANOVA was performed for behaviours directed toward conspecific males (bites and lateral displays) and conspecific females (dips) with wrasse number (1/3) a within subjects factor and egg status (eggs/no eggs) as a between subjects factor. Results were considered significant at $p \leq 0.05$.

Results

Time spent near stimuli

The amount of time spent near a given stimuli was affected by nearly all factors examined. Statistical results of the repeated measures ANOVA ($df = 1, 13$) are presented in Table 2. Across all treatments, males spent significantly more time near bottles containing conspecifics than wrasse. There was also a main effect of the sex of conspecific with males spending more time near stimuli when a conspecific male was presented rather than when a conspecific female was presented. There was not a significant effect of wrasse number as the time males spent near stimuli was not different between presentations with 1 or 3 wrasse. There was a significant main effect of the between subjects factor, egg status, as males with eggs spent less time near stimuli than males without eggs. A number of significant interactions of these factors were revealed as well, including stimulus type \times sex of conspecific, stimulus type \times wrasse number, stimulus type \times egg status, sex of conspecific \times wrasse number, sex of conspecific \times egg status, and a three-

Table 2. Statistical results for repeated measures $2 \times 2 \times 2 \times 2$ factorial ANOVA on time spent near bottled stimuli.

Effect	<i>F</i>	<i>p</i>
Stimulus type	120.688	<0.001*
Sex of conspecific	28.188	<0.001*
Wrasse number	2.788	0.119
Egg status	16.704	0.001*
Stimulus type \times sex of conspecific	44.280	<0.001*
Stimulus type \times wrasse number	5.761	0.032*
Stimulus type \times egg status	13.133	0.003*
Sex of conspecific \times wrasse number	7.535	0.017*
Sex of conspecific \times egg status	5.511	0.035*
Wrasse number \times egg status	0.980	0.340
Stimulus type \times sex of conspecific \times wrasse number	7.756	0.015*
Stimulus type \times sex of conspecific \times egg status	0.729	0.409
Stimulus type \times wrasse number \times egg status	0.002	0.963
Sex of conspecific \times wrasse number \times egg status	0.131	0.723
Stimulus type \times sex of conspecific \times wrasse number \times egg status	1.211	0.291

There were two levels of three within subject factors: stimulus type (consppecific/wrasse), sex of conspecific (male/female) and wrasse number (1/3), and two levels of a between subject factor: egg status (eggs/no eggs). *Significant *p* value (≤ 0.05).

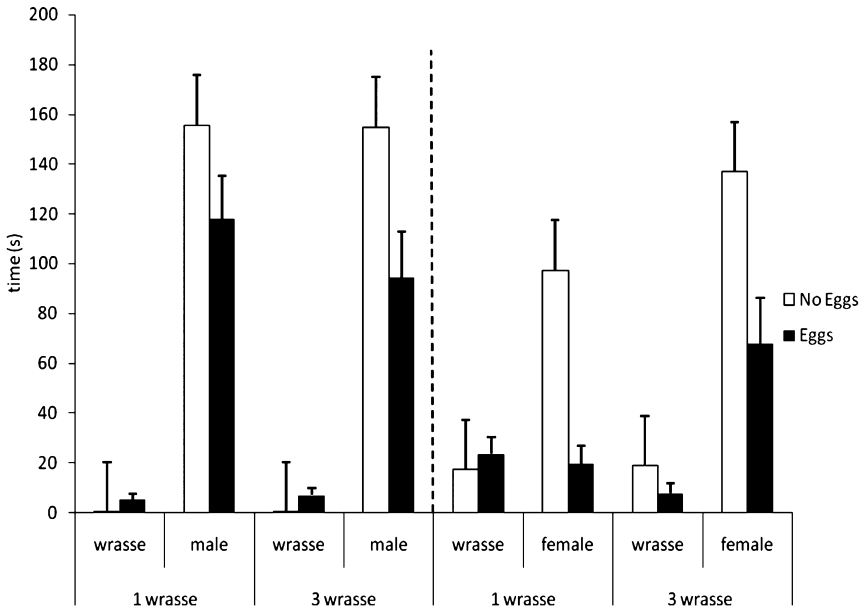


Figure 1. Mean + SE time(s) spent near bottled stimuli by territorial males with eggs (solid bars) and without eggs (open bars) for the four separate treatments.

way interaction of stimulus type \times sex of conspecific \times wrasse number. Despite the lack of a significant main effect of wrasse number, this factor did affect the time males spent near stimuli in conjunction with the influence of several other variables (Table 2, Figure 1).

Brood defense behaviour

Behaviour directed at the wrasse was also affected by various factors (ANOVA results Table 4). There were significant main effects of the sex of conspecific and egg presence on the number of downhead threats performed. When presented with a conspecific female and a wrasse, males performed an average of 5.23 threats per 3-min observation period compared to only 2.91 threats when wrasse were presented alongside a conspecific male. Males with eggs in their territory were nearly three times as likely to perform downhead threats as males without eggs (Table 3). There was also a significant interaction of sex of conspecific and wrasse number on the number of threats performed. The number of bites that male damselfish exhibited toward bottles containing wrasse, however, was not affected by the sex of

Table 3. Mean \pm SE of behaviours associated with brood defense, intrasexual aggression and courtship.

	1 wrasse		3 wrasse	
	No eggs	Eggs	No eggs	Eggs
Brood defense behaviour				
With conspecific male				
Bites at wrasse	0.43 \pm 0.43	3.50 \pm 1.59	0	3.38 \pm 1.46
Downhead threats	0.71 \pm 0.47	4.00 \pm 1.56	1.43 \pm 0.72	5.50 \pm 1.81
With conspecific female				
Bites at wrasse	4.71 \pm 4.08	8.38 \pm 3.07	5.42 \pm 4.94	3.63 \pm 2.06
Downhead threats	3.00 \pm 0.78	9.13 \pm 1.63	2.29 \pm 0.89	6.50 \pm 2.15
Intrasexual behaviour				
Bites at male	70.86 \pm 13.62	68.13 \pm 14.85	81.86 \pm 11.97	72.50 \pm 14.00
Lateral displays	12.29 \pm 1.87	12.25 \pm 3.09	8.14 \pm 1.51	5.88 \pm 1.65
Intersexual behaviour				
Dips	0	4.50 \pm 4.02	0.14 \pm 0.14	12.50 \pm 11.65

the conspecific in the other bottle, the number of wrasse, nor the presence or absence of eggs in a territory.

Intrasexual behaviour

There was little influence of egg status or the number of wrasse on the two types of intrasexual aggression behaviours directed toward a conspecific male (ANOVA results Table 4). There were no significant effects of wrasse number or egg status on the number of bites performed, but there was a significant main effect of wrasse number on the amount of lateral displays exhibited. Males presented with 3 wrasse were less likely to perform lateral displays to a conspecific male than when they were presented with a single wrasse (Table 3).

Intersexual behaviour

There were no significant effects of any factor on the number of dips performed toward conspecific females (ANOVA results Table 4). Most males did not perform any dip maneuvers and a great deal of variation was observed among males that did actively court (Table 3). These results align themselves with those of Figueira & Lyman (2007) observed in *S. partitus* and Leese et al. (2009) in *S. leucostictus* who observed low levels of courtship behaviour when damselfish were exposed to brood predators.

Table 4. Statistical results for repeated measures factorial ANOVA on behaviours associated with brood defense (bites and downhead threats), intrasexual aggression (bites and lateral displays), and courtship (dips).

	Effect	<i>F</i>	<i>p</i>
Brood defense behaviour			
Bites at wrasse	Sex of conspecific	2.390	0.146
	Wrasse number	1.799	0.203
	Egg status	0.596	0.454
	Sex of conspecific × wrasse number	0.842	0.375
	Sex of conspecific × egg status	0.229	0.641
	Wrasse number × egg status	2.274	0.155
	Sex of conspecific × wrasse number × egg status	2.311	0.152
Downhead threats	Sex of conspecific	6.300	0.026*
	Wrasse number	0.081	0.780
	Egg status	7.544	0.017*
	Sex of conspecific × wrasse number	7.614	0.016*
	Sex of conspecific × egg status	0.652	0.434
	Wrasse number × egg status	0.081	0.780
	Sex of conspecific × wrasse number × egg status	1.795	0.203
Intrasexual behaviour			
Bites at male	Wrasse number	0.337	0.572
	Egg status	0.152	0.703
	Wrasse number × egg status	0.063	0.806
Lateral displays	Wrasse number	5.090	0.042*
	Egg status	0.259	0.619
	Wrasse number × egg status	0.229	0.640
Intersexual behaviour			
Dips	Wrasse number	0.930	0.352
	Egg status	0.867	0.369
	Wrasse number × egg status	0.866	0.369

Behaviours associated with brood defense were conducted with a $2 \times 2 \times 2$ factorial design (sex of conspecific, wrasse number, egg status) and behaviours associated with intrasexual aggression and courtship utilized a 2×2 factorial design (wrasse number, egg status).

*Significant *p* value (≤ 0.05).

Discussion

In agreement with our original hypothesis, male beaugregory damselfish divided their time between both conspecific and wrasse stimuli, but spent overwhelmingly more time near bottles containing conspecific individuals than those containing brood predators. Thus, it appears that, for this behavioural measure of attention, sexually selected behaviours take priority over the nat-

urally selected behaviour of brood defense. Wrasse represent a potential decrease in current reproductive success and, therefore, it seems apparent that males should defend against them. However, the situation in which a wrasse appears is clearly important. In this study, time spent defending against the wrasse equates to time that cannot be allocated to competing with rival males or courting females. Brood defense may be an important activity to survival, but one that must be prioritized given the specific context.

Intruding conspecific males likely pose much more of an overall threat to fitness levels than wrasse. Some male damselfish cannibalize their own egg clutches (Payne et al., 2003), and it is possible that intruding males would prey upon another male's eggs, thus directly lowering current reproductive success in much the same manner as a wrasse would. In addition, intruding males can intercept potential female mates and reduce the future reproduction from these females, as well as potentially usurping the defending male's territory. This result would carry the greatest fitness cost to the defending individual, as all current and future reproduction gained from the site would be lost. Given these risks, the adaptive response of territorial males to engage in intrasexual competition over brood defense seems an optimal solution to maximize fitness. The caveat of these explanations is that the intrasexual aggression seen between damselfish males cannot be categorically described as the result of sexual selection, as this aggression may be a naturally selected behaviour as well.

As compared to these intruding males, conspecific females do not appear to pose any threat to the current reproductive success of territorial males. Yet, when given a choice of an egg predator and a conspecific female, males chose to spend much more time near the female than the wrasse. This suggests that the potential fitness benefit of attracting a female may outweigh the costs associated with brood defense, if the males successfully court and receive eggs. Interestingly, while a large percentage of time was spent with females, very few courtship dips were observed: only 3 of 15 individuals performed any dips to females. Since males were not actively courting, it is difficult to determine the reason males showed a prioritization in time spent with conspecific females over wrasse. One possible explanation is that the specific act of courting (dips) is too risky to be performed in the presence of brood predators, and that males were attempting to attract females simply by proximity, rather than exaggerated swimming displays.

With these clear differences in what each sex represents to the territorial male, it is not surprising that there is a significant main effect of conspecific sex on the amount of time spent with stimuli. When considering the observed behaviours associated with these activities, it is interesting that while very few territorial males performed dips, all of them displayed and performed bites toward conspecific males. This observation and the significant interaction of stimulus type and the sex of the conspecific strongly suggest that the presence of an egg predator has a much more limiting effect on inter-sexually selected behaviour than on intra-sexually selected behaviour.

Perhaps due to this difference in the way in which intra- and inter-sexually selected behaviours are affected by wrasse presence, we found some influence of the number of wrasse on the prioritization of behaviour. Specifically, there was a significant interaction of wrasse number and the sex of the conspecific. That is, when females were presented to territorial males alongside wrasse, there was an influence of the wrasse number, yet male–male aggression was minimally influenced by wrasse number. We had originally predicted that increasing the number of wrasse from one to three would increase time spent with and behaviours directed toward wrasse, but, possibly due to the strong impetus to spend time with conspecifics, we saw no such effect of increases in wrasse number, independent of other factors.

As expected, prioritization in activities was also affected by egg presence. Males that had eggs within their territories spent less time with stimuli than males without eggs across all treatments, presumably because males with eggs are spending more time within and above their territories. While there was an overall decrease in the time that males with eggs spent near stimuli, it appears that the majority of this decrease is due to decreases in time with the conspecific and not with the wrasse. Males with eggs seem to spend more time with wrasse than males without eggs, but since the time with wrasse constituted such a small percentage of the total amount of observation time, the overall effect of eggs was to cause a decrease in the time spent near stimuli. Of course, it must also be considered that intra- and inter-sexually selected behaviours were affected differently. It seems that, again, the presence of an egg predator has a much more limiting effect on inter-sexually selected behaviour than on intra-sexually selected behaviour, especially for those males with eggs within their territories.

Each of the multiple factors explored here clearly had some impact on the decision of territorial males to prioritize sexually selected behaviours

with brood defense. This provides evidence for the importance of context-dependent decision making in a species that lives in a complex, multi-faceted environment, like a coral reef. Animals with a similar ecology are likely to encounter multiple conspecific and heterospecific stimuli simultaneously and must maintain some plasticity in behaviour in order to make decisions that maximize relative fitness. Species with a less diverse ecology and different life history may not be adapted for similar situations and may only invest in single types of behaviour at any one time, eliminating the need for prioritization of these types of behaviour. This difference can even exist between populations of the same species, as has been observed in guppies, *Poecilia reticulata*. Male guppies from high-predation sites engage in less anti-predator behaviour and spend more time pursuing females, than males from low risk sites (Magurran & Seghers, 1994).

Here, some risk to a brood appears to be tolerated by territorial male damselfish so as to engage in interactions with conspecifics. These interactions with conspecifics appear to be the mechanism which drives sexual selection, resulting in specific intra- and inter-sexually selected behaviours. By considering these two mechanisms separately, it becomes clear that the two forms of sexual selection can influence, and be influenced by, natural selection in different ways. The classic view that the exaggeration of sexually selected characters is eventually opposed by natural selection may well be supported, but this process could be quite disparate depending on the form of sexual selection considered.

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