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Bessa, Eduardo; Sabino, José

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Research Article

Territorial hypothesis predicts the trade-off between reproductive opportunities and parental care in three species of damselfishes (Pomacentridae: Actinopterygii)

Eduardo Bessa^{1,2} & José Sabino³

¹Laboratório de Ecologia Comportamental da Reprodução, Universidade do Estado de Mato Grosso Rod MT 358 km 7, Jd. Aeroporto, CEP 78300-000. Tangará da Serra-MT, Brazil

²Depto. de Zoologia e Botânica, UNESP, Instituto de Biologia, Letras e Ciências Exatas Programa de Pós-Graduação em Biologia Animal

³Universidade Anhanguera-Uniderp, Projeto Peixes de Bonito, 79037-280 Campo Grande, MS, Brazil

ABSTRACT. Paternal care is rare in most animals, but common in fishes, including Pomacentridae. One way of explaining it is through the territorial hypothesis, which predicts that paternal care may evolve when caring for a territory with eggs will not cost more than territories without eggs. Here we describe the reproductive behavior of three pomacentrids from São Paulo, Brazil, and evaluate if the territorial hypothesis explains their behavioral variation through five predictions. We checked if females have multiple spawns (prediction 1), if they forage more (prediction 2) and if territory defence demands more when eggs are present (prediction 3). We also described how visible eggs are (prediction 4) and how available nesting sites are (prediction 5). *Chromis multilineata* differed from *Abudefduf saxatilis* and *Stegastes fuscus* by not guarding the eggs, spending less time with territoriality and fanning eggs; and more time feeding and foraging. Females of the three species are iteroparous. Females' *A. saxatilis* and *S. fuscus* foraged more than males, which spent the same amount of time in territorial defence before and after eggs were delivered. These two species also have very conspicuous egg clutches on clean rock surfaces defended by them. On the other hand, males and females of *C. multilineata* spent the same time foraging, while territoriality took more effort after eggs were present and it spawns cryptic eggs amid *Sargassum*, a common and disperse micro-environment in São Paulo rocky shores. Territorial hypothesis explains why paternal care by *A. saxatilis* and *S. fuscus* lasts longer than by *C. multilineata*.

Keywords: reproductive behavior, resource defence, rocky reef fish, behavioral ecology, sex role reversal, southwestern Atlantic.

La hipótesis territorial predice la compensación entre las oportunidades reproductivas y el cuidado parental en tres especies de peces damisela (Pomacentridae: Actinopterygii)

RESUMEN. El cuidado paterno es raro en la mayoría de los animales, pero común en los peces, incluyendo los Pomacentridae. Una forma de explicar este fenómeno es la hipótesis territorial, que predice que el cuidado paterno puede evolucionar cuando la protección de un territorio con huevos no cuesta más que la de territorios sin huevos. Aquí se describe el comportamiento reproductivo de tres pomacentrídeos de São Paulo, Brasil, y se evalúa si la hipótesis territorial explica la variación de su comportamiento a través de cinco predicciones. Se analizó si las hembras tienen múltiples desoves (predicción 1), si forrajean más (predicción 2) y si la defensa del territorio es mayor cuando los huevos están presentes (predicción 3). También se evaluó si los huevos eran visibles (predicción 4) y cuán disponibles eran los sitios de anidación (predicción 5). *Chromis multilineata* difería de *Abudefduf saxatilis* y *Stegastes fuscus* por no proteger a sus huevos, dedicar menos tiempo a la territorialidad y ventilación de sus huevos, y más tiempo para la alimentación y forrajeo. Las hembras de las tres especies son iteróparas. Las hembras de *A. saxatilis* y *S. fuscus* forrajean más que los machos, que gastan la misma cantidad de tiempo en la defensa territorial antes y después de liberar los huevos. Estas dos especies también defienden a desoves muy conspicuos adheridos en superficies de roca limpia. Por otra parte, las hembras y machos de *C. multilineata* pasaron el mismo tiempo forrajeando, mientras la territorialidad tomó

más esfuerzo después, con los huevos presentes, y los desoves estaban escondidos en medio de *Sargassum*, un ambiente común y disperso en micro-ambientes de las costas rocosas de São Paulo. La hipótesis territorial explica el motivo por el cual el cuidado paterno de *A. saxatilis* y *S. fuscus* es más prolongado que el de *C. multilineata*.

Palabras clave: comportamiento reproductivo, defensa de recursos, peces de costa rocosa, comportamiento ecológico, reversión del papel sexual, Atlántico suroccidental.

Corresponding author: Eduardo Bessa (prof.bessa@yahoo.com.br)

INTRODUCTION

Reproduction is the final target of any organism. It is through reproduction that the organism passes away its genetic information to keep present in the gene pool of its population. Despite of that, to reproduce is useless if the offspring itself does not reach the reproductive age, what may demand parental care. This behavior brings many costs and a trade-off between reproducing and taking care of the offspring is expected (Clutton-Brock, 1991). Parental care is usually accomplished by females, since they benefit more from the energy invested in the offspring than males (Queller, 1997), although, in many cases males exert this (Ridley, 1978).

There are various explanations for why males care for their offspring (Wright, 1998). Williams (1975) provided one of the most convincing explanations. He suggests that prolonged paternal care will evolve when males already defend territories including a rare spawning site to attract females as a resource defence polygyny (Emlem & Oring, 1977). The presence of eggs is also supposed to attract more females (Manica, 2010). Birds and fishes are especially prone to paternal care (Ridley, 1978); among them coral reef damselfishes are known to be devote fathers (Breder & Rosen, 1966).

The Pomacentridae family (damselfishes) belongs to suborder Labroidei, Perciformes, Actinopterygii (Nelson, 1994). They are divided in 28 genera and 384 species (Froese & Pauly, 2011) distributed through all the tropical oceans. Restricted to shallow regions with hard substrate, their main region of diversity is the South Pacific Ocean. In Brazil four genera and 14 species are known (Moura & Menezes, 2003). These species are explored for aquarium trade, from January 1995 to November 2000 a total of 6.800 individuals were traded in Ceará state (Monteiro-Neto *et al.*, 2003). The present study focused three of the most frequent species in São Paulo State northern coast (Menezes & Figueiredo, 1985): *Abudefduf saxatilis*, *Stegastes fuscus* and *Chromis multilineata*. These species form territories in at least part of the

reproductive season; males court females, fecundate the eggs and guard them. How long the paternal care lasts, what is guarded in the territory and what kind of substrate is used for spawning varies between species (Emery, 1973).

Although Williams (1975) explains most of the parental care in fishes, it is not known to explain the variation in paternal effort in pomacentrids. This paper aims to compare *A. saxatilis*, *S. fuscus* and *C. multilineata*, and then define what aspects of their biology may explain how much males care for their offspring. For that we test the following predictions drawn from territorial hypothesis: (1) female should be iteroparous, (2) females should forage and feed more than guarding males, (3) time budget dedicated to territoriality should not change from territorial to parental males, (4) egg-clutches should be easily spotted, (5) egg-clutches should be placed on rare defendable resources.

Iteroparity is expected since females will not benefit from paternal males if they cannot, ecologically or physiologically, lay multiple clutches per breeding season (Tallamy, 2000). The second prediction is based on the idea that, by feeding more, females will increase their fecundities; this was reviewed by Armstrong & Witthames (2011). If taking care of an empty territory or one filled with eggs takes the same amount of time and offspring survival is greatly enhanced by parental care, then, we may expect that paternal care will occur, what takes us to prediction three. The fourth prediction that clutches will be easily seen has two consequences; it may be easily seen and evaluated by a female searching for a good father to deliver her eggs to (Sikkel, 1995), albeit it may also result in being easily spotted by a visual oriented egg predator, common on reefs (Lowe-McConnell, 1999). Finally, territoriality will only occur when a resource for which animals would compete has an aggregated pattern of distribution (Wilson, 2000), thus, a territorial explanation for paternal care requires first that the parents are territorials.

MATERIALS AND METHODS

Study site

The present study was carried out in São Sebastião and Ilhabela, northern shore of São Paulo, Brazil (23°49'S, 45°25'W). The region is characterized by the presence of São Sebastião Channel and by its predominantly rocky shore, most of which is covered with algae, soft corals and sponges. São Sebastião Island represents an obstacle for winds and more energetic events, with less turbulent water inside the channel.

Collects and fecundity analysis

Seventeen mature *Abudefduf saxatilis* females were collected with hook and bait and killed with benzocaine at 100 ppm for 20 min, animals were then injected with formalin at 10%. They were dissected and gonads were submitted to histology. We used haematoxylin-eosin (HE) method with the gonads included in paraffin and cut in 5 µm slices. Only one female of *Stegastes fuscus* and no *Chromis multilineata* were collected. The same treatment given to *A. saxatilis* was done to *S. fuscus* but further data for *C. multilineata* and *S. fuscus* iteroparity were taken from literature (Myrberg *et al.*, 1967; Souza *et al.*, 2007). Observing how distended the visiting females' abdomens were after they left the nest, as commonly used in aquaculture (Woynarovich, 1989), offered an indirect and complementary approach to the presence of iteroparous females in the study area.

Observation

We did 114 h of SCUBA diving in a mean depth of 4 m during day time from November 2002 to February 2003, including finding individuals, nest marking, acclimatation period, evaluating algae coverage and egg location (for *C. multilineata*). Observed individuals were standardized for size (*A. saxatilis* ~150 mm, *S. fuscus* ~130, *C. multilineata* ~110 mm). Observations started after a 5 min acclimation interval.

We began by doing an ethogram listing and describing all the behaviors of interest with *ad libitum* method (Martin & Bateson, 2007). Meanwhile we also checked where eggs were placed and how easily seen they were. Nests were marked with a coloured buoy anchored to the bottom by a fishing weight and accompanied four times a day to evaluate parent desertion and egg hatching.

We then did 15 min sessions using focal animal with instant samples every 30 s (Martin & Bateson, 2007) measuring the frequency of each behavior.

Underwater notes were taken with soft pencils on polyethylene waterproof sheets with tables printed in laser printers. Focal animals were identified by species, life stage (with or without eggs) and sex.

Abudefduf saxatilis may be sexed by its color and behavior (males are bluish and guard a territory). Male and female *Stegastes fuscus* were identified by accompanying a marked nest previously filled with eggs (Since only males guard the eggs; Souza *et al.*, 2007) or by their courting behavior. *Chromis multilineata* could be sexed by the presence of a swallowed genital papilla in females (Myrberg *et al.*, 1967; Swerdloff, 1970).

Data analysis

An analysis of similarity using Euclidian distance (ANOSIM) (Costa *et al.*, 2010) was used to compare the behaviors of the three species with 1000 permutations. A principal component analysis (PCA) was used to order the sampled individuals by the number of observations of each behavior (Manly, 2008). A Mann-Whitney sum of ranks test (Zar, 1999) checked the difference in the time spent foraging between males and females within each species due to the heterocedastic nature of the data. Following, a t-test (Zar, 1999) compared the time dedicated to territoriality between males guarding territories with or without eggs, since these data were normally distributed. Type I error tolerance was $\alpha = 0.05$.

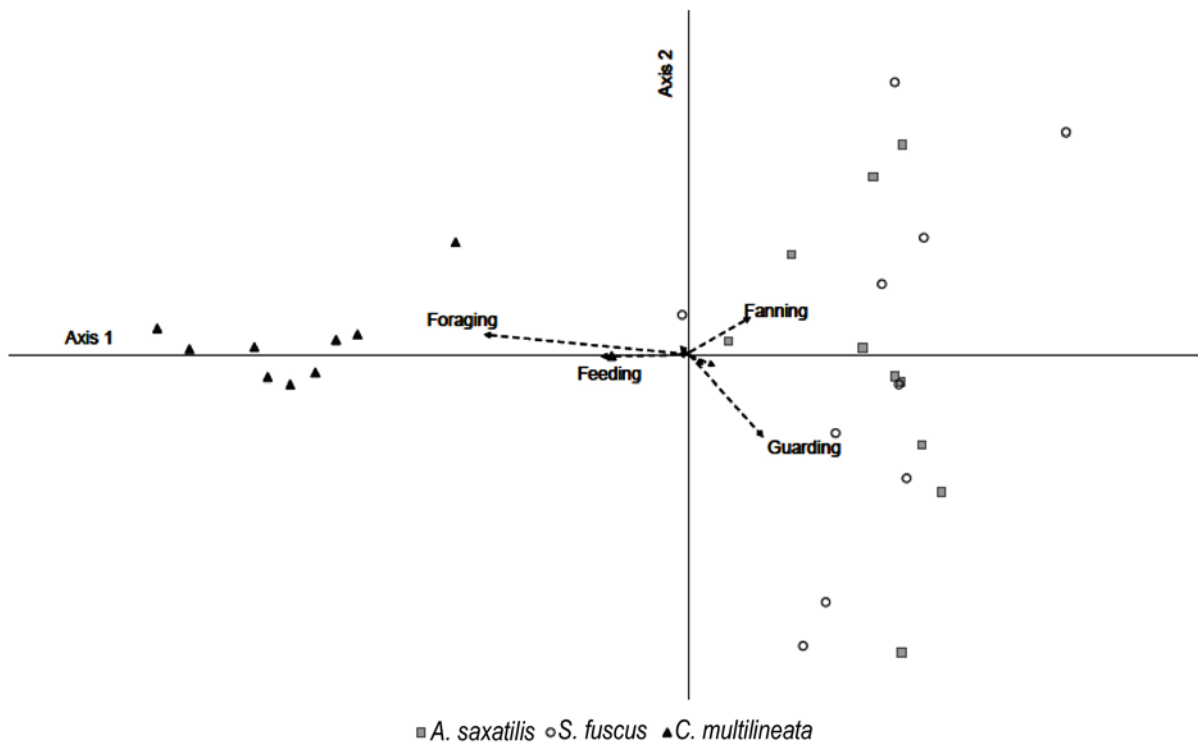
RESULTS

Fourteen behaviors were observed (Table 1), although, they varied greatly among the three species (ANOSIM = 0.6248; N = 300; $P < 0.001$). *Abudefduf saxatilis* and *Stegastes fuscus* behave more similarly than *Chromis multilineata*. This may be observed both in the PCA (Fig. 1), where these two species overlay while *C. multilineata* is concentrated on the left of axis 2, and in the barplot (Fig. 2), where the frequency of the main behaviors are similar for *A. saxatilis* and *S. fuscus*, but differ from *C. multilineata*. The PCA pointed that the vectors 'guarding' and 'fanning' ordered *A. saxatilis* and *S. fuscus*, while 'feeding' and 'foraging' influenced *C. multilineata* (Fig. 1). The first and second axis explained 80.2% of the data dispersal.

Female *Abudefduf saxatilis* presented multiple spawning with oocytes ready to be delivered and atretic follicles in their ovaries in the 17 collected females. The single mature female of *Stegastes fuscus* collected also presented atretic follicles and mature eggs, suggesting multiple spawnings. Furthermore, the remaining turgid abdomens seen on females leaving

Table 1. Behavioral repertoire of the pomacentrids from São Paulo northern shore.**Tabla 1.** Repertorio comportamental de los pomacentrídeos de la costa norte de São Paulo.

Pattern	Category	Act	Description
Self-preservation	Feeding	Foraging	Searching for food
		Feeding	Grabbing food
		Filial cannibalism	Feeding on its own eggs
	Stationary	Resting	Stopped by the bottom
		Intraspecific	Escaping co-specific chasers
		Interspecific	Escaping heterospecific chasers
Territoriality	Escaping	Flashing	Snapping the bottom with the flank in territory or not
		Guarding	Staying in the territory on guard for invaders
	Chasing	Intraspecific	Swimming behind co-specifics
		Interspecific	Swimming behind heterospecifics
Reproductive	Sexual reproduction	Courtship	Attracting females
		Mating	Releasing gametes
Parental care	Shared effort	Fanning	Making water flow over the eggs with pectoral fins
		Nest cleaning	Picking debris from nest with the mouth

**Figure 1.** Principal component analysis (PCA) of the behaviors of *Abudedefduf saxatilis*, *Stegastes fuscus* and *Chromis multilineata*. Arrows represent the behaviors that most affect each species. Notice how *A. saxatilis* and *S. fuscus* overlay and are distinct of *C. multilineata*.**Figura 1.** Análisis de componentes principales (PCA) de los comportamientos de *Abudedefduf saxatilis*, *Stegastes fuscus* y *Chromis multilineata*. Las flechas representan los comportamientos que afectan más a cada especie. Notar que *A. saxatilis* y *S. fuscus* se sobrepone y son distintos de *C. multilineata*.

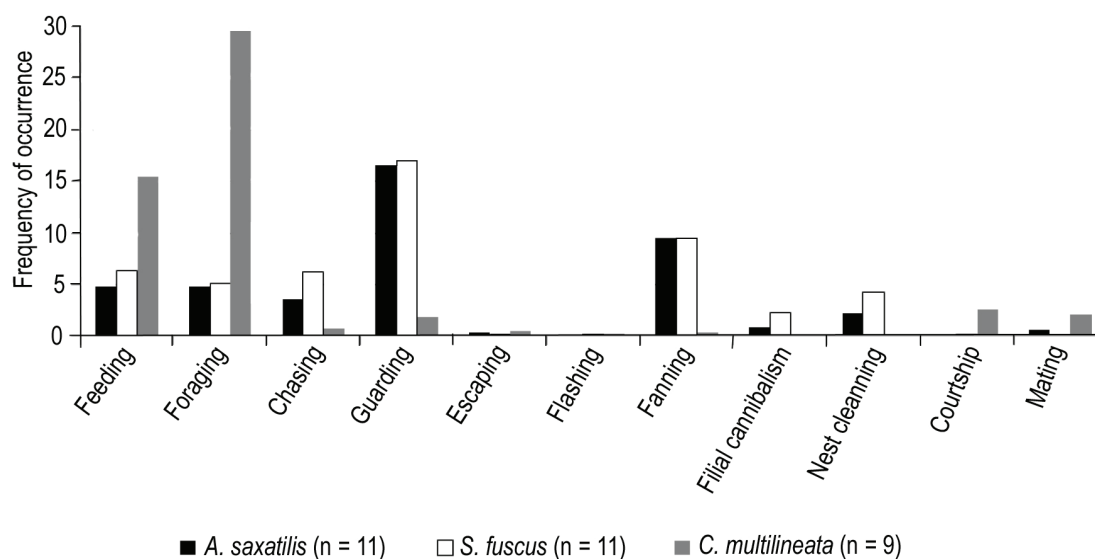


Figure 2. Frequency of the main behaviors executed by the damselfishes stressing the difference between the paternal species (*Abudefduf saxatilis* and *Stegastes fuscus*) and the less territorial one (*Chromis multilineata*).

Figura 2. Frecuencia de los principales comportamientos hechos por los pomacentridios marcando las diferencias mientras las especies paternas (*Abudefduf saxatilis* y *Stegastes fuscus*) y la poco territorial (*Chromis multilineata*).

the nest site may be due to oocytes still available for future mates.

Females of *A. saxatilis* and *S. fuscus*, but not *C. multilineata*, spend more time foraging and feeding than males (Table 2). Males of *A. saxatilis* fed almost five times less than females, while *S. fuscus* males forage just about 39% less. This time budget is directed to other activities such as territoriality and parental care, while females certainly increase energy intake. *Chromis multilineata* males foraged just a little less than females (15%).

The same happened with time invested in territory defence before and after eggs were delivered to the territorial male. *A. saxatilis* and *S. fuscus* males spend the same time budget on territory defence with or without eggs (less than 40% increase for *A. saxatilis* and about 35% decrease for *S. fuscus*), but the investment in territory defence by *C. multilineata* raised significantly (more than 10-fold) for the short time these males held their territories (Table 3).

A. saxatilis and *S. fuscus* spawn on clear rock surfaces kept by their mates in the territory. *A. saxatilis* clutches are purple patches of eggs of around 250 cm² adhered to rocky surfaces in the territory of a male. The eggs of *S. fuscus* form white elliptic clutches of around 200 cm². Both these species have to build their nests clearing rock areas with their teeth. *C. multilineata* eggs are cryptic and disperse amid *Sargassum* tuffs (see Fig. 3 in Myrberg *et al.*, 1967).

Table 3. Do male territoriality stay the same after eggs are delivered? t-test confirms that territoriality does not take more effort from species like *Abudefduf saxatilis* and *Stegastes fuscus* with more devoted paternal care, but will cost more in species in which paternal care is less likely to last, like *Chromis multilineata*. t: statistics result, df: degree of freedom, P: associated probability. Critical value for P was $\alpha = 0.05$.

Tabla 3. ¿La territorialidad de los machos se mantiene después que él recibe huevos? El test-t comprueba que la territorialidad no resulta en más esfuerzo de especies como *Abudefduf saxatilis* y *Stegastes fuscus* con cuidado paternal más desarrollado, pero va a costar más en especies en las cuales el cuidado paternal es más corto, como *Chromis multilineata*. t: resultado de la estadística, df: grados de libertad, P: probabilidad asociada. El valor crítico de P fue $\alpha = 0.05$.

Species		Mean	t	df	P
<i>A. saxatilis</i>	without eggs	24.8	2.27	8	0.052
	with eggs	34.6			
<i>S. fuscus</i>	without eggs	41.1	1.800	7	0.097
	with eggs	30.7			
<i>C. multilineata</i>	without eggs	0.4	3.203	5	0.033
	with eggs	4.6			

This alga is abundant and widely spread on the rocky shores of São Paulo northern coast.

DISCUSSION

Pomacentrid males invest their time and energy in parental care. Parental care in *Abudefduf saxatilis* and *Stegastes fuscus* lasts until the larvae hatch, parents defend offspring from predators, fan and clean the eggs. These two species agree in every aspect with the general pattern suggested for pomacentrids by Breder & Rosen (1966) and Balon (1975). They present nuptial color (*A. saxatilis*) or no secondary sex character (*S. fuscus*), mate in pairs, spawn demersal adhesive eggs on rocks, which will be guarded and fanned by the male. Both are egg-guarders who belong to the nesting sub-guild and are lithophiles. On the other hand, *Chromis multilineata*, despite showing no colour dimorphism, mating in pairs and spawning demersal adhesive eggs, does not guard the eggs for more than a few hours, hiding them amid *Sargassum* banks in São Paulo coast, disagreeing markedly from previous classifications of Pomacentridae.

Since parental care is probably a characteristic inherited from their sister-group, Cichlidae, and *C. multilineata* is a derived taxon within Pomacentridae (Cooper *et al.*, 2009), its lack of paternal behavior is probably a secondary loss within Pomacentridae. If so, what are the possible causes for this loss? The predictions drawn from the classic book of Williams (1975) have pointed us some cues.

The first prediction suggested that, for paternal care to evolve, females should be iteroparous, so that they may benefit from guarding males (Tallamy, 2000). Results confirmed iteroparity in *A. saxatilis* and *S. fuscus* (presence of atretic follicles in fertile females), while abdominal turgidity suggested the same for all the three species. This was already expected from other studies (Myrberg *et al.*, 1967 for *C. multilineata*; Bessa *et al.*, 2007 for *A. saxatilis*; and Souza *et al.*, 2007 for *S. fuscus*); what confirms the first prediction for all the three species.

Our second prediction, that females were expected to forage and feed more than males, was proven only for the two paternal species. Males of *C. multilineata* forage as much as females. This extra feeding time females have may be converted in more numerous or larger eggs (Tsadik & Bart, 2007), increasing both the fitness of females and males that reproduced with them through indirect fitness (Donelson *et al.*, 2008).

Time invested in territory defence did not increase for *A. saxatilis* and *S. fuscus* (prediction 3), but rose significantly for *C. multilineata*. Both sexes of the

latter species can forage equally because neither spends time on territory defence. This will only change when males start courting females, moment when their territorial behavior increases. Other species from the genus *Chromis* have been described as territorials and paternal (Fishelson, 1970; Tzioumis & Kingsford, 1999). Even *C. multilineata*, in reefs where *Sargassum* were less abundant, defended algae tufts and guarded them after spawning (Myrberg *et al.*, 1967). It is important to mention that *S. fuscus* territoriality is similar to *A. saxatilis* during the reproductive period only. This species will stay guarding a territory for its feeding value (algae garden) in the cold months of the year, while male *A. saxatilis* have left their territories and spend the time foraging in the water column.

The easily seen eggs of *A. saxatilis* and *S. fuscus* confirmed prediction four. This will allow females to use it to choose partners. Clutches were much more conspicuous in the two former species and egg condition is known to be a cue for male quality (Sikkel, 1995; Manica, 2010). In *C. multilineata* a series of female visits to a male nest were described to happen one after the other in a short interval (Myrberg *et al.*, 1967), what we also observed in São Paulo. Therefore, eggs are probably not used by females to choose partners and paternal care is less interesting in terms of sexual selection. *C. Chromis multilineata* females probably use more cues from the male than from eggs he would be guarding.

The same conspicuous clutches that attract females can be spotted by visually oriented predators, increasing the need for nest protection. Some common visually oriented egg predators found in São Paulo rocky shores are *Abudefduf saxatilis*, *Chaetodon striatus* and *Diplodus argenteus* (Randall, 1967), amid many others.

Rare nest sites distributed in patches are a defendable resource to be guarded in territories (Maher & Lott, 1995). Our last prediction suggests that paternal males are supposed to be territorials since before reproductive period. Territorial males will have to spend time guarding a territory as much as they will spend on defending its offspring, reducing the costs of paternal care and, thus, explaining the evolution of this kind of sex role reversal. As long as *A. saxatilis* has to guard the clear rock nest he built and *S. fuscus* has the nest and an algae garden to guard in its territory, the extra cost driven to parental care is paid by the benefits of enhancing offspring survival. Since in rocky shores with large *Sargassum* banks covering up to 80% of the substrate, a common situation in São Paulo coast (Paula & Oliveira-Filho, 1980), algae tufts are not a rare resource distributed in patches. It is less

likely that *C. multilineata* will develop territoriality for guarding this nest site, augmenting the costs of parental care by the male.

We conclude that the variation in male parental care in the pomacentrids of São Paulo northern coast is explained by the territorial hypothesis, mainly in accordance to the availability of nest sites and the need to guard it as a scarce resource.

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