

DEFENSE OF A MULTI FUNCTIONAL TERRITORY AGAINST INTERSPECIFIC INTRUDERS BY THE DAMSELFISH *STEGASTES NIGRICANS* (PISCES, POMACENTRIDAE)

ALEXANDRA M. HAMB

Integrative Biology, University of California, Berkeley, California 94720 USA

Abstract. Animals exhibit territorial behavior to defend essential resources such as food or offspring. Interspecific aggression is linked with territoriality and this behavior has been observed between species with overlapping ecology. This behavioral study complements existing research on interspecific aggression in vertebrates, specifically reef fish. It examines the possible functions of territoriality and motivations for aggression towards heterospecifics without ecological overlap. The territorial damselfish, *Stegastes nigricans* is an algae farmer that defends an individual territory used for a food supply, a breeding site, and shelter. Territorial interactions between *S. nigricans* and other fish species were examined through behavioral observations in Mo'orea, French Polynesia. Aggressive interactions between *S. nigricans* and intruding fish were analyzed based on four main factors: intruder species, diet, activity, and location in *S. nigricans* colony. The effect of *S. nigricans* colony size on the exclusion of intruders was also examined. *Stegastes nigricans* exhibited the most aggression towards two groups of intruders: non-algae eaters feeding in the interior of the colony and algae eaters swimming in the interior of the colony. It was found that large colonies of *S. nigricans* were not more effective at excluding intruders than small colonies. The three factors that were the most indicative of whether *S. nigricans* reacted aggressively towards an intruder were intruder species, diet, and location in the colony. Two common themes of interspecific aggression were found to be the defense of a food resource and the protection of reproductive assets.

Key words: reef fish; *Stegastes nigricans*; Pomacentridae; interspecific aggression; Mo'orea, French Polynesia; territoriality

INTRODUCTION

Territoriality can be defined as any behavior on the part of an animal, which tends to confine the movements of that animal to a particular locality (Etkin 1964). The emergence of territoriality can be related to essential life processes such as resource acquisition and the need to exclude other members from the area where these activities occur (Etkin 1964). Because of this, territorial behavior is intricately linked with agonism and animals maintaining territorial boundaries do so via aggressive actions (Etkin 1964).

Interspecific aggression is an important aspect of territorial behavior in birds, fish and mammals (Thresher 1976). Interspecific interactions occur when two non-related species compete over a resource such as food or shelter (Thresher 1976). This type of behavior has been observed in species with overlapping ecology and the result of this interaction is the exclusion of one of the species by the other (Simmons 1951).

It is thought that the primary function of interspecific territoriality is the protection of

food resources from heterospecific competitors (Ebersole 1977). One ecological factor, such as the maintenance of a reliable food supply, can act as a selective force leading to the evolution of interspecific territoriality (Orians and Willson 1964, Low 1971). This theory can account for the positive correlation between increases in aggression and increases in diet overlap between species (Low 1971, Hixon and Brostoff 1983, Harrington and Losey 1990, Letourneur *et al.* 1997, Bay *et al.* 2001, Gochfeld 2010).

Previous studies on reef fish have examined interspecific aggression by territorial species on non-territorial species (Losey 1982). The amount of time and energy spent engaged in interspecific defense demonstrates its importance in the ecology of fish (Low 1971, Myrberg and Thresher 1974). In contrast to birds, where interspecific aggression can be a case of mistaken identity, territorial fish are defending a residence against species with similar food or space requirements or against species that threaten their spawn (Losey 1982).

Defense against species without any ecological requirement overlap implies other functions of territoriality (Thresher 1976). Interspecific aggression by damselfish is not limited to herbivorous fish but includes carnivorous fish and grazing invertebrates such as sea urchins and starfish (Hixon and Brostoff 1983, Letourneur *et al.* 1997, Gochfeld 2010). Mapstone *et al.* (2007) showed that *Stegastes nigricans* (Pomacentridae) chased away grunts (Haemulidae) and wrasses (Labridae), both of which are carnivorous. The exclusion of angelfish (Pomacanthidae) and butterflyfish (Chaetodontidae) species by the damselfish *Eupomacentrus planifrons* (Pomacentridae) could be in defense of the shelter space, not food resources or spawn (Thresher 1976). When sea urchins were experimentally exposed in *S. nigricans*' territories, immediate eviction occurred via chasing or physical removal by *S. nigricans* (Hata and Kato 2004, Mapstone *et al.* 2007).

Territorial behavior can foster social aggregation in otherwise solitary animals (Manning 1972). Moreover, the presence of territoriality can indicate social organization in reef fish (Myrberg and Thresher 1974). The effect of holding territory can create neighborhoods of solitary individuals that are bound to each other socially (Getty 1989). Although neighbors are in constant competition with each other, they share common enemies and mutual interests that can result in incidental cooperation (Getty 1989). Damselfish, although highly territorial and aggressive, can occur in large colonies. Cooperative defense between colony members provides the opportunity to exclude mutual predators more efficiently and decrease the cost of defense for each member (Gochfeld 2010).

The territorial, algae farming damselfish, *Stegastes nigricans* defends a multi functional territory utilized as a food source, a residence, and for males, a breeding site (Thresher 1976). Because of its territorial behavior, *S. nigricans* is considered a keystone species in coral reef communities (Williams 1980, Hixon and Brostoff 1983, Gochfeld 2010). *Stegastes nigricans* limit herbivory in their territories through intensive algal farming and territorial behavior (Gochfeld 2010). Colonies of *S. nigricans* play a crucial role in the structure of local reef communities and promote coral (Gochfeld 2010) and algal diversity (Williams 1980, Hixon and Brostoff 1983).

My research focused on territorial interactions between *Stegastes nigricans* and

other reef fish and grazing invertebrates. I observed *S. nigricans* colony size, the presence and type of aggressive behavior towards intruders, and participation in aggressive behavior by more than one *S. nigricans* towards an intruder. I looked at intruder species, diet, and location in the *S. nigricans* colony as well as intruder activity. Additionally, I looked at the presence of aggression by *S. nigricans* towards invertebrate intruders to compare this behavior to *S. nigricans*' interactions with vertebrate intruders.

I hypothesized that larger colonies of *S. nigricans* would be more effective at excluding intruders than smaller colonies. I also predicted *S. nigricans* would show the most aggression towards three groups of intruders. I hypothesized that high diet overlap between *S. nigricans* and herbivorous intruders would result in increased aggression. I believed an intruder in the interior of an *S. nigricans* colony would threaten more individual territories than an intruder located at the periphery, therefore eliciting a greater aggressive response. Lastly, I predicted *S. nigricans* would act aggressively towards intruders that were actively feeding on or near their algal mats.

METHODS

Study site

I conducted my study between September and November, 2011 in Mo'orea, French Polynesia (17°32'19.84"S, 149°49'46.28"W). I chose the three study locations based the presence of large populations of the study organism, *Stegastes nigricans*. The first location was the lagoon and reef crest at Temae Public Beach (17°29'50.45"S, 149°45'28.09"W) (Fig.1). The second location was the lagoon at the Hilton Mo'orea Lagoon Resort (17°29'6.02"S, 149°50'42.68"W) (Fig. 1). The final location was the lagoon at Faimano Public Beach (17°29'9.65"S, 149°50'48.58"W) (Fig. 1).



FIG. 1. Distribution of study locations in tropical lagoons in Mo'orea, French Polynesia

Study organism

Stegastes nigricans Lacépède 1802 (Dusky Gregory damselfish) are territorial algae farmers and are often found with *Acropora* coral. Coloration varies from light to dark gray-brown with a distinct black spot at the rear base of the dorsal fin and individuals can grow to 14 centimeters. During the breeding season, the males have a wide, vertical white stripe in the middle of the body (Randall 2005).

Experimental design

At each of my three study locations I chose five variably sized colonies of *S. nigricans*. I marked the location with a waypoint using a Global Positioning System (GPS) and also flagged each site with an assigned number (1-15). I measured the depth from the bottom and from the top of the coral head to the water surface. I also measured the dimensions (length and width) of the coral head. I estimated the number of individuals in each colony in order to determine the density of *S. nigricans* on the coral head. I categorized *S. nigricans* colonies as small (1-15 individuals), medium (15-30 individuals), or large (30-45). I recorded sex and body size (small, medium, large) of the individuals in each colony to account for their possibility as confounding variables. In addition, I recorded the number of *Diadema* sp. and *Echinometra* sp. urchins on the coral head. To account for any bias caused by abiotic factors, I recorded water and air temperature, presence or absence of wind and time of day. Lastly, I photographed each coral head from several different angles.

Behavioral observations

In order to conduct my behavioral observations I first had to create an ethogram identifying the different behaviors of *S. nigricans* (Table 1). Following preliminary observations, I constructed my ethogram consisting of four aggressive behaviors (Posing 2, Lunging, Chasing, Biting) and four non-aggressive behaviors (Posing 1, Hiding, Farming, Retreating). Three fellow researchers tested my ethogram in the field to ensure the behaviors I defined were replicable and objective.

I conducted ten-minute behavioral observations on all fifteen colonies and replicated each colony three times controlling for the time of day. *Stegastes nigricans* actively feed in the early afternoon so I conducted my observations between 9:00 and 13:00 (Letourneur *et al.* 1997). I positioned an underwater camera on a flexible tripod on the coral head to videotape the behavior of *S. nigricans*. After positioning the camera and turning it on, I allowed for a one-minute adjustment period for the fish to recover from the disturbance caused by the camera and my presence. During the ten-minute observation, the total number of non-aggressive behaviors (Posing 1, Hiding, Farming, Retreating) and one aggressive behavior (Posing 2) were tallied. Three of the aggressive behaviors (Lunging, Chasing, Biting) were recorded in combination with information about the territorial interactions between resident *S. nigricans* and any intruders. I collected the following information: intruder species, intruder location in the colony (interior or periphery), intruder activity (feeding or swimming) and total number of *S. nigricans*

TABLE 1. Ethogram of *Stegastes nigricans* behavior

Behavior	Description
Posing (P)	Facing intruder, backpedaling with pectoral fins with body still and pointed upwards at an angle of 45° 1. Dorsal fin relaxed 2. Dorsal fin erect
Lunging (L)	Lunge towards intruder with tail flick
Chasing (C)	Leaves territory to pursue intruder
Biting (B)	Biting motion directed towards intruder with or without physical contact
Hiding (H)	Taking cover underneath overhanging coral or between crevices
Farming (F)	Removing unwanted algae from territory or eating algae
Retreating (R)	Retain relaxed posing position and backpedal with pectoral fins to move

participating in the aggressive behavior towards the intruder. I added intruder diet to my data after the behavioral observations were conducted using Randall's (2005) reef fish identification guide.

Field manipulation

In order to look at interactions between *S. nigricans* and invertebrate intruders, I collected five *Echinometra* sp. sea urchins from the bay in front of the UC Berkeley Gump Station (17°29'24.30"S, 149°49'33.59"W). I placed an *Echinometra* urchin in the interior of a *S. nigricans* colony, either on bare coral or on algae. I recorded the time of the first aggressive action by *S. nigricans* towards the urchin and the total time it took *S. nigricans* to remove the urchin from the colony. I conducted five replicates for each of the five colonies at the Hilton Mo'orea Lagoon Resort, for a total of 25 trials.

Statistical Analysis

For my data analysis, I used the statistics software program JMP (JMP, Version 9). I used a logistic regression model to look at the relationship between *S. nigricans* density and the presence of aggressive behavior towards intruders. I performed Pearson's Chi-square tests to determine if the differences in *S. nigricans* aggressive and non-aggressive behaviors were due to the four main factors I examined: intruder diet, intruder location, intruder activity and intruder species. I used a one-way ANOVA to look at *S. nigricans* efficiency at removing *Echinometra* sp. Finally I used a linear regression model to look at the relationship between *S. nigricans* density and *Echinometra* sp. density.

RESULTS

Over the course of my behavioral observations, a total of 648 intruders were observed from 30 different fish species and nine different families. The three most abundant intruders were *Thalassoma hardwicke* (n=191), *Ctenochaetus striatus* (n=96) and *Dascyllus aruanus* (n=64). The most common fish families observed were consistent with the three most abundant intruders: Labridae (n=227), Acanthuridae (n=157) and Pomacentridae (n=132). I recorded an average number of 12 intruders and 24 aggressive interactions per observation period.

Colony size and behavior

The density of *Stegastes nigricans* did not seem to influence whether *S. nigricans* responded aggressively to an intruder. For example, the relationship between *S. nigricans* density and the presence of aggressive behavior towards intruders was not statistically significant (logistic regression, $R^2=0.0004$, $P=0.61$). Furthermore, colony size was not a factor in determining the presence of aggressive behavior towards an intruder (logistic regression, $R^2=0.0001$, $P=0.81$).

Intruder diet

Intruder diet did not affect the presence of aggression towards intruders by *S. nigricans* (Pearson's Chi-square Test, $\chi^2=3.71$, $df=1$, $P=0.05$) (Fig. 2). However, *S. nigricans* were aggressive 56% of the time to non-algae eaters, but only 48% of the time to algae eaters. The overall trend showed about an equal probability of *S. nigricans* acting aggressively towards algae and non-algae eaters.

There were differences in aggressive behavior towards algae and non-algae consuming fish when broken down into three specific behaviors: lunge, chase and bite. When partitioned by diet, aggressive behavior by *S. nigricans* proved to be significant (Pearson's Chi-square Test, $\chi^2=11.47$, $df=2$, $P=0.003$) (Fig. 2). For example, *S. nigricans* bit algae eaters 11% of the time, but only bit non-algae eaters 2% of the time. *S. nigricans* lunged at algae eaters 49% of the time and chased non-algae eaters 52% of the time.

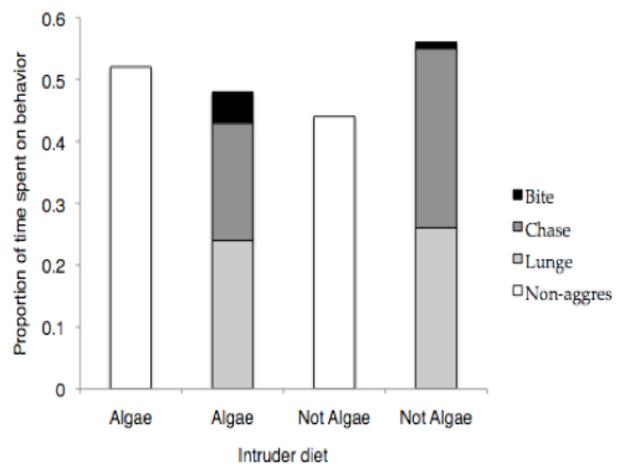


FIG. 2. The effect of intruder diet on the proportion of time spent exhibiting aggressive and non-aggressive behaviors by *S. nigricans*

Intruder location in colony

There was a higher probability of *S. nigricans* reacting aggressively when an intruder was located in the interior of the colony than at the periphery (Pearson's Chi-square Test, $\chi^2=8.74$, $df=1$, $P=0.003$) (Fig. 3). However, the specific aggressive behaviors (lunge, chase, bite) of *S. nigricans* towards intruders in the interior versus the periphery of the colony were not significant (Pearson's Chi-square Test, $\chi^2=0.6$, $df=2$, $P=0.74$). For example, once *S. nigricans* reacted aggressively towards an intruder, the probability of the fish demonstrating one aggressive behavior over another was low regardless of the location of the intruder in the colony.

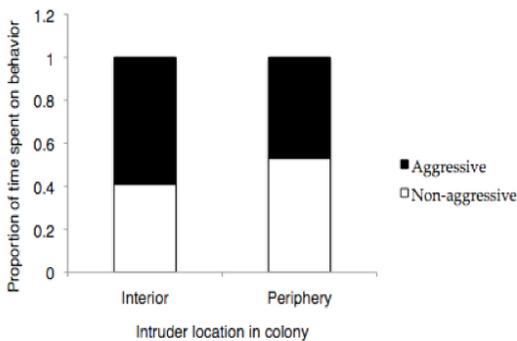


FIG. 3. The effect of intruder location on the proportion of time spent exhibiting aggressive and non-aggressive behavior by *S. nigricans*

Species of intruding fish

There was a difference in the presence of aggressive behavior towards *Thalassoma hardwicke*, *Ctenochaetus striatus*, and *Dascyllus aruanus* (Pearson's Chi-square Test, $\chi^2=37.06$, $df=2$, $P<.0001$) (Fig. 4). *Stegastes nigricans* demonstrated aggression towards *T. hardwicke* 61% of the time but only 36% and 20% of the time towards *C. striatus* and *D. aruanus* respectively.

The difference between specific aggressive behaviors shown by *S. nigricans* towards *T. hardwicke*, *C. striatus*, and *D. aruanus* is statistically significant (Pearson's Chi-square Test, $\chi^2=10.25$, $df=4$, $P=0.036$). For example, *S. nigricans* chased *T. hardwicke* 54% of the time and lunged at *C. striatus* 69% of the time. The sample size for *D. aruanus* ($n=13$) was small however, the proportion of time spent by *S.*

nigricans chasing (54%) versus lunging (46%) at *D. aruanus* was almost equal.

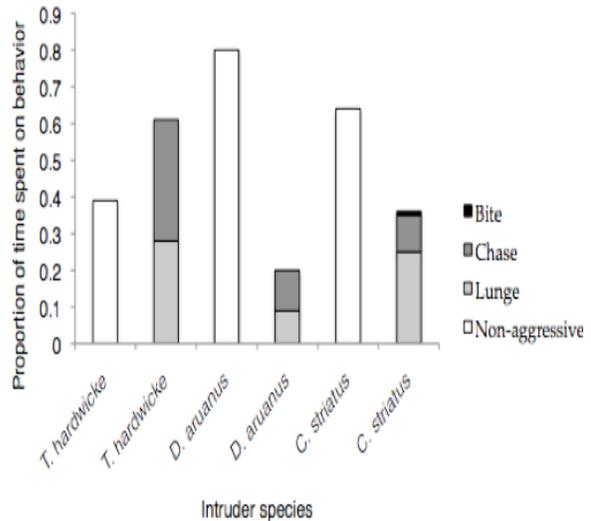


FIG. 4. The effect of intruder species on the proportion of time spent exhibiting aggressive and non-aggressive behaviors by *S. nigricans*

Intruder activity

Stegastes nigricans was not more likely to exhibit aggression with intruder activity (feeding or swimming) (Pearson's Chi-square test, $\chi^2=3.24$, $df=1$, $P=0.07$). It was not more likely that *S. nigricans* would show aggressive behavior towards a swimming intruder than a feeding intruder or vice versa.

When *S. nigricans* responded aggressively towards an intruder the probability of *S. nigricans* lunging, chasing, or biting the intruder did not differ between swimming and feeding intruders (Pearson's Chi-square Test, $\chi^2=4.54$, $df=2$, $P=0.10$).

Echinometra sp. manipulation

I observed aggressive behavior by *S. nigricans* towards *Echinometra* sp. in all 25 trials. In 24 out of 25 trials, *S. nigricans* physically removed the sea urchin from the colony. The average length of time for complete removal of the sea urchin was 69 seconds with a minimum of 14 seconds and a maximum of 240 seconds. During all trials, the intruder was effectively removed in a comparable amount of time (one-way ANOVA, $F_1=0.027$, $P=0.87$). Moreover, there

was no relationship between *S. nigricans* density and *Echinometra* sp. density (linear regression, $R^2=-0.03$, $P=0.87$). Colony size was not a factor in the presence of invertebrate intruders.

DISCUSSION

The territorial, algae farming damselfish *Stegastes nigricans* excluded fish and invertebrate intruders from their territory via aggressive behavior. *Stegastes nigricans* reacted in varying levels of aggression (lunging, chasing, biting) depending on the threat presented by the intruder. The time and energy *S. nigricans* devoted to aggressive behaviors accentuates the importance of interspecific territorial defense in their behavior and ecology (Low 1971, Harrington and Losey 1990).

My results indicated that larger colonies of *S. nigricans* (30-45 individuals) were not more effective at excluding fish intruders than smaller colonies (1-15 individuals). Furthermore, evidence from my field manipulations with *Echinometra* sp. showed that *S. nigricans* density did not confer an advantage to excluding invertebrates. In other systems, group size has been a factor in effective predator exclusion (Elliot 1985, Burger and Gochfeld 1992, Hass and Valenzuela 2002) but for *S. nigricans*, although colony size and fish density did not seem to be a factor in aggressive interactions between *S. nigricans* and intruders, it still may provide other advantages that I did not examine. For example, Karino (1993) found that group size in *S. nigricans* could be beneficial in regards to reproductive potential. Larger colonies have more potential mates to choose from and this could also reduce predation by minimizing the distance a fish has to travel to reproduce (Karino 1993). However, *S. nigricans* group size and density could simply be a result of coral head size; essentially the larger coral heads have a greater capacity to hold more *S. nigricans* territories, therefore the larger the coral head, the more *S. nigricans* present.

Initially I hypothesized that *S. nigricans* would act aggressively more often towards algae consuming fish than non-algae consuming fish. However, *S. nigricans* demonstrated aggressive behavior to both herbivores and carnivores in equal occurrence. Because my observations took place at the end of and following the breeding season (September-October), both algae eaters and non-algae eaters could be threats to *S.*

nigricans (Letourneur *et al.* 1997). *Stegastes nigricans* defends a multi functional territory used for both feeding and breeding, and therefore the food source and spawn are both vulnerable to predation during the breeding season and directly afterwards (Thresher 1976). Thresher (1976) found this behavior present in another pomacentrid fish, *Dascyllus trimaculatus*. *Dascyllus trimaculatus* defended against fish with no diet overlap suggesting the territory served additional purposes than a food resource. In particular, *D. trimaculatus* demonstrated increased aggression towards labrid fish, which are known egg eaters. *Stegastes nigricans* were aggressive towards labrid fish in 56% of my observations, particularly *Thalassoma hardwicke*, which is consistent with Thresher's findings.

Nest defense has been hypothesized to be a major contributor for the evolution of interspecific territoriality in birds (Howard 1920). Multiple authors have suggested that the theory of nest defense can be applied to pomacentrid fish (Albrecht 1969, Clarke 1970, Keenleyside 1972, Ebersole 1977). Though *S. nigricans*' aggressive interactions with labrid fish can be explained by overlap between intruder diet and the reproductive season, *S. nigricans* also demonstrated high rates of aggression towards scarid and chaetodontid fishes. Chaetodontid fish and *S. nigricans* do not occupy the same ecological niche nor do they consume eggs. A possible explanation for the high levels of aggression towards chaetodontid fish could be the protection of a shelter or the physical territory of an individual *S. nigricans*. It has been hypothesized that chaetodontid fish have the ability to usurp *S. nigricans*' territories and utilize them as a shelter from predators (Thresher 1976). However, I did not observe any territory stealing attempts by chaetodontid fish therefore, I cannot comment on this. In contrast, scarid fish and *S. nigricans* share similar feeding preferences so the aggressive behavior demonstrated by *S. nigricans* can be attributed to defense of individual algal mats. In addition, scarid fish are coral predators and *S. nigricans* colonies are often located within *Acropora* thickets or on *Porites* coral heads. By consuming the underlying structure on which *S. nigricans*' territories are located, scarid fish could elicit aggressive responses from *S. nigricans* in order to protect their residence.

Stegastes nigricans interacted aggressively with all three of the most abundant intruders however the perceived motivation for doing

so was different for each species. As mentioned previously, *Thalassoma harwicke*, a known egg eater, presented a threat to *S. nigricans*' spawn. *Ctenochaetus striatus* presented another major threat to *S. nigricans* ecology, competition for food resources. The hypothesis that one of the functions of territoriality is the defense of a food resource is consistent with the results of other scientists such as Low (1971) and Ebersole (1977). I infer that *S. nigricans* reacts aggressively towards herbivorous invaders year round because the maintenance of individual algal mats is a continuous process with no seasonal variation. *Stegastes nigricans*' interactions with *Dasycyllus aruanus* were non-aggressive the majority of the time. Both species are pomacentrid fish and have only diverged recently in the evolutionary timescale. Although there is high ecological niche overlap between *S. nigricans* and *D. aruanus*, *D. aruanus* may pose less of a threat to *S. nigricans*' territories. This is relevant to the concept of relative threat and how varying levels of aggression are shown towards different intruders based on the threat they pose (Myrberg and Thresher 1974). This is important in the partitioning of time and energy spent in interspecific interactions.

As predicted, *S. nigricans* showed more aggression towards intruders located in the interior than at the periphery of the colony. Residents were more likely to react to intruders in the interior of the colony than intruders on the periphery because the interior intruders were threatening a greater number of resident territories. The intruder was both a non-algae eater and located the interior of the territory for 6 of 10 instances where more than one *S. nigricans* reacted aggressively. This is consistent with the idea that protection of eggs is a high priority for *S. nigricans* during and directly after the breeding season (Thresher 1976).

The two groups of intruders that were subject to the most aggression by *S. nigricans* were algae eaters swimming in the interior and non-algae eaters feeding in the interior. The algae eater presented a threat to *S. nigricans*' food supply so an aggressive response to a swimming invader can be seen as preventative measures to deter future feeding. As mentioned previously, the non-algae eater could present a threat to *S. nigricans*' spawn or the territory as a shelter space. However, non-specific aggression towards nearby intruders that results in all intruding fish vacating the territory may be more energy efficient for *S. nigricans* than

assessing each intruder based on relative threat (Letourneur *et al.* 1997). It might also be beneficial for *S. nigricans* to allow some intruders into the territory in order to keep other species away (Gochfeld 2010). For example, the presence of a carnivorous species may dissuade algae eaters from intruding on *S. nigricans*' territories in search of food. However, this strategy could instead encourage potential intruders to encroach on *S. nigricans*' territories if a high number of intruders were already present in the territory and were not eliciting aggressive behavior from the resident fish.

My research showed that intruder species, diet and location in the colony were the three factors that were the most indicative of whether *S. nigricans* would react aggressively towards an intruder. However, the activity of the intruding fish did not seem to influence whether *S. nigricans* reacted aggressively. There were most likely other factors that I did not examine that were more important in excluding an intruder than what it was doing at the time of intrusion. I believe *S. nigricans* evaluates intruders on the potential threat they pose to each of the three main resources they defend: a food source, a breeding site and a shelter area. The activity of the intruder is probably supplemental to the threat the intruder poses.

Stegastes nigricans contributes to coral reef community stability by regulating the interactions between fish and invertebrate grazers and the algae and coral they feed upon. They enhance coral diversity by preventing the overgrowth of algae via farming and exclude coral predators such as parrotfish (Scaridae) (Hixon and Brostoff 1983, Gochfeld 2010). *Stegastes nigricans*' territories can serve as sanctuaries for corals from the predator, *Acanthaster planci* (Gochfeld 2010). Currently, there is an *A. planci* outbreak in Mo'orea, French Polynesia and the corals are vulnerable to severe decreases in density. *Stegastes nigricans* can help prevent the loss of coral biodiversity, which is considered the largest threat to the world's ecosystems (Stachowicz 2001). *Stegastes nigricans* also promotes algal diversity by limiting herbivory through interspecific territoriality (Gochfeld 2010). It is important to understand the motivations behind interspecific territoriality and furthermore, how they can be applied to a variety of vertebrates including birds and mammals. Two common themes of aggression for all territorial animals are the defense of a

food supply and the protection of reproductive resources.

Future directions

For future research, I would return to Mo'orea, French Polynesia during a non-breeding period for *S. nigricans* and see if the frequency of aggressive behavior had changed towards labrid fish and carnivorous fish species in general. This would allow me to better understand the reasons for aggression towards these fish species and which resources they threaten. I would also look at male versus female *S. nigricans* and see if there was a difference in the presence and degree of aggressive behavior between the sexes during the breeding season. The male *S. nigricans* are responsible for protection of the eggs so I infer that the males would show greater aggression towards carnivorous fish than the females. It would also be interesting to observe interactions between a non-territorial pomacentrid fish and heterospecifics and compare those observations with my data on *S. nigricans*.

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