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Jenna Sparks

Foraging and Feeding Guild Characteristics in Relation to Fishes Chased from *Microspathodon dorsalis* Nesting Territories

Jenna Sparks
Department of Environmental Studies and Ecology and Evolutionary Biology
University of California, Santa Cruz
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ABSTRACT

Recognizing nest predators is an important adaptation for successful reproduction. Nest guarding ability is likely, in part, a sexually selected trait. Male giant damselfish (*Microspathodon dorsalis*) defend by chasing and biting at fishes that encroach upon their nests. In my study, I observed the relationship between intruder fish phenotype and behavior and response of 16 guarding males. In a series of 10-minute observation periods, I determined that acapulco damselfish (*Stegastes acapulcoensis*) were chased away the most times. To account for variability of fish presence, I additionally noted the number of chases by resident *M. dorsalis*, standardized for the number of appearances of other species. The most frequently chased species was panamic sergent majors (*Abudefduf troschelli*). Based on these results, I considered the common foraging and feeding guild characteristics in *S. acapulcoensis*, *A. troschelli* and other species I observed. *S. acapulcoensis* and *A. troschelli*, known grazers of the Pomacentridae family, prefer the algae *M. dorsalis* cultivates in its garden. However, I also observed *S. acapulcoensis* and other *M. dorsalis* feeding on the eggs of a *M. dorsalis* nest.

Características de forrajeo y gremio alimenticio en relación a los peces perseguidos por *Microspathodon dorsalis* en sus territorios de anidación

RESUMEN

Reconocer depredadores de nidos es una adaptación importante para lograr una reproducción exitosa. Probablemente, la capacidad de cuidar su nido es en parte un rasgo sexualmente seleccionado. Las jaquetas gigantes (*Microspathodon dorsalis*) defienden sus nidos persiguiendo y mordiendo a los peces intrusos que se acercan a sus nidos. En mi estudio, analicé el comportamiento respuesta de 16 machos protegiendo nidos hacia los peces intrusos según su fenotipo y su comportamiento. Durante períodos de observación de 10 minutos, determiné que las jaquetas acapulqueñas (*Stegastes acapulcoensis*) fueron las más perseguidos por *M. dorsalis.* Para determinar si esto se debía a la cantidad proporcional de visitas de S. *acapulcoensis* , estandaricé los datos según el número de visitas de todas las especies. Según este nuevo análisis, la especie que fue perseguida más frecuentemente fue pintaño amarillo (*Abudefduf troschelli*). Basado en estos resultados, consideré características comunes de forrajeo y alimentación de *S. acapulcoensis*, *A. troschelli* y otras especies observadas. *S. acapulcoensis* y *A. troschelli* ambos de la familia Pomacentridae, son conocidas por su pastoreo en el fondo marino y prefieren las algas que *M. dorsalis* cultivan en sus jardines. Sin embargo, observé que *S. acapulcoensis* y *M. dorsalis* se alimentan también de los huevos en los nidos de *M. dorsalis*.

Nest defense and parental investment into that nest defense are exhibited in a variety of taxonomic groups. These behavioral concepts explain that parents choose to defend offspring in an effort to increase their own fitness by ensuring that their genes are carried into the next generation. However, active nest defense is a trade-off between energy spent keeping predators away and other activities that are necessary for survival (Redmond, et al., 2007). For this reason,

it is practical for guarding parents to distinguish between a fish that poses a small threat and species that pose a large threat.

Nest defense and parental investment are observed in giant damselfish (*Microspathodon dorsalis*). Adult male *M. dorsalis* are known to guard eggs before they hatch (DeLoach, 1999). Breeding adult males are distinguishable by their lighter bluish grey color of their anterior (DeLoach, 1999). These male parents chase away egg predators. The act of chasing the intruding species away poses a trade-off. The chasing *M. dorsalis* are inevitably leaving their nest unguarded for the duration of the chase and exposing their undefended nests to predators. Therefore, there is likely a large selective advantage to those individuals who correctly identify the actual threat posed by a particular fish. A guarding male who chases a potential egg predator will have higher fitness. Similarly, a guarding male who does not chase a fish who is not an egg predator will also have reproductive success. Thus, I expect that natural selection has favored individuals who discriminate among fish who are real threats and fish who are not.

Male *M. dorsalis* will graze upon and maintain algal gardens on even substrates in hopes of attracting a female to mate with (Montgomery, 1980). After successful mating, the female will lay her eggs near or on the gardens, where the adhesion on the outside of the eggs causes them to stick. On account of the nest location and careful maintenance of these nesting sites, I wondered if these nests lured both predators interested in grazing upon the algae as well as predators interested in consuming the eggs. This preference of the predator species for the *M. dorsalis* nests would imply that they are frequent visitors to these nests, and consequently, it would benefit guarding *M. dorsalis* to recognize them.

With the above information I addressed the question: what characteristics of the chased species are important in eliciting an aggressive response from male *M. dorsalis* defending their nests? Foraging behavior and feeding guild characteristics of intruder fish were my primary focus.

MATERIALS/ METHODS

Ten-Minute Analysis: Amount of Chases

From 11 May 2018 to 19 May 2018, I found and observed *M. dorsalis*' nests at Bajo Rojo, a site inside the Cuajiniquil Bay on the Santa Elena peninsula of Costa Rica. Bajo Rojo is a rocky reef that is approximately two kilometers from Cuajiniquil's *muelle*. During high tide, the water around Bajo Rojo is no deeper than 8 meters. Each day we traveled to the test site by boat. I snorkeled around Bajo Rojo and found *M. dorsalis* nests that could be identified by gray patches on a flat surface with a *M. dorsalis* guarding the area. Another key way to recognize nests is their placement on algal gardens. Male *M. dorsalis* maintain these gardens as a courtship display during mating time as well as a reliable source of food (DeLoach, 1999).

Once I located a nest, I recorded ten-minute videos with my GoPro (underwater camera) zip-tied to a rock on a stable boulder in the water. While the camera was recording the first nest I had found, I went to find another nest and watched it from at least 1-meter away for ten minutes. Throughout these ten-minute periods I recorded the species of fish that were chased and the proximity to the outside of the circular, gray nests. In the course of taking these data, I noted

some species of fish were able to get close to the nest without being chased. Through this method I was able to observe which fish were chased the most. I examined 16 nests using this method.

Two-Minute Analysis: Frequency Chased

I further analyzed videos to determine which fishes were chased in relation to their presence. I did this by counting the amount of times the fishes swam within a one-by-one meter radius with one nest inside. I watched a two-minute clip of each ten-minute video and noted all of the fishes that entered the predetermined zone and whether the fish was chased or not. This method helped me establish the fish that were chased the most frequently.

I defined a chase as the event in which a guarding *M. dorsalis* swam rapidly, moved its dorsal, anal, and caudal fins, and approached a particular fish. In some cases these chases included contact.

Table 1. This table serves as a key for abbreviations I used to record the fish species in my data and further in my graphs. (Gotshall 1998, Deloach et al. 2004, Allen 1994).

Abbreviation Used	**English Name**	**Spanish Name**	**Scientific Name**
GD	giant damselfish	jaqueta gigante	*Microspathodon dorsalis*
AD	acapulco damselfish	jaqueta acapulqueña	*Stegastes acapulcoensis*
BF	barberfish	mariposa amarilla	*Johnrandallia nigrirostris*
KA	king angelfish	angel real	*Holacanthus passer*
MH	mexican hogfish	vieja de piedra	*Bodianus diplotaenia*
SM	panamic sergent major	pintaño amarillo	*Abudefduf troschelli*
CS	chancho surgeonfish	barbero	*Prionurus laticlavius*
PF	parrotfish	loro	*Scarus*
RS	round stingray	raya sureña	*Urolophus halleri*
RC	rainbow chub	chopa salema	*Sectator ocyurus*
TB	three-banded butterfly fish	mariposa de tres bandas	*Chaetodon humeralis*
juv.	juvenile giant damselfish	jaqueta gigante juvenil	*Microspathodon dorsalis*
FRW	female Cortez rainbow wrasse	arco iris	*Thalassoma lucasanum*
GG	graybar grunt	burro almejera	*Haemulon sexfasciatum*
STG	spottail grunt	roncador rayado	*Haemulon muculicauda*
PB	panamic fanged blenny	borracho mono	*Ophioblennius steindacneri*
YS	yellow snapper	pargo amarillo	*Lutjanus argentiventris*
MG	mojarra grunt	burro pecoso	*Haemulon scudderii*
FC	flag cabrilla	mero pintado	*Epinephelus labriformis*

RESULTS

Through my observations I can conclude that acapulco damselfish (*Stegastes acapulcoensis*) was the species chased the most. This result is shown in Figure 1. The remaining fishes mentioned in this histogram were chased at least 30 less times than the *S. acapulcoensis*. The chases that are labeled as "unknown" indicate that the guarding *M. dorsalis* exited the video footage to chase an unseen (or unknown) attacker. In addition, I noted when the guarding *M. dorsalis* attempted to chase me away. I found that the amount of chases in relation to species is significant.

In the histogram in Figure 2, the two-minute analysis shows the fish with the highest likelihood to get chased was the panamic sergent major (*Abudefduf troschelli*). *A. troschelli* was chased 29% of the time it appeared in the one-by-one meter radius on the screen. The fishes that were not chased when they entered the zone were flag cabrillas (*Epinephelus labriformis*), other *M. doralis,* and yellow snappers (*Lutjanus argentiventris*). These results can also be interpreted through Table 2 where foraging patterns are displayed. The most chased fish is a grazer and two of the three of the fishes that were never chased are carnivorous. Foraging and feeding guild characteristics are thoroughly explained in Figure 3. It is pertinent that *E. labriformis* was also absent in Figure 1 in which I recorded all of the instances where a fish was chased in a 10-minute observation period. I did not observe any of the guarding *M. dorsalis* attacking the stationary GoPro.

Through both of my methods of observations, I concluded that *S. acapulcoensis* was chased the most and *A. troschelli* was chased the most frequently.

Incidental Observations

On 9 May 2018, I observed a feeding frenzy of fishes grazing on a *M. dorsalis* nest at Bajo Rojo. *M. dorsalis* and *S. acapulcoensis* were the species that appeared in the greatest abundance during this frenzy. The guarding *M. dorsalis* was dashing around rapidly chasing away these fishes. However, this guarding *M. dorsalis* could not keep up with the influx and there were visible bite marks taken out of the clutch. When I returned to the same site the next day all of the eggs were gone, leaving just the algae garden.

Table 2. In this table, the foraging characteristics are seen in relation to the family to which each fish belongs. (Gotshall 1998, Humann et al. 2004, Allen 1994). I defined grazers as species that eat by plucking their food from substrates. Carnivores are fishes that eat other animals such as invertebrates and other fishes. Finally, these omnivores eat both algae and animal matter. For this reason, the omnivores can also be classified as grazers.

Family	Fish Observed	Most Common Food	Grazing	Foraging Characteristics
Chaetodontidae	BF, TB	coral polyps, small benthic invertebrates, algae	X	omnivorous
Pomacanthidae	KA	sponges, benthic invertebrates		carnivorous
Pomacentridae	SM, GD, AD, juv.	algae	X	grazing
Labridae	FRW, MH	hard-shelled invertebrates, zooplankton		carnivorous
Haemulidae	GG, MG, STG	benthic invertebrates		carnivorous
Lutjanidae	YS	other fishes		carnivorous
Urolophidae	RS	benthic invertebrates		carnivorous
Acanthuridae	CS	wide variety of plants (algae)	X	grazing
Scaridae	PF	algae, calcium carbonate	X	grazing
Blennidae	PB	crustaceans		carnivorous
Kyphosidae	RC	benthic algae	X	grazing
Serranidae	FC	other fishes		carnivorous

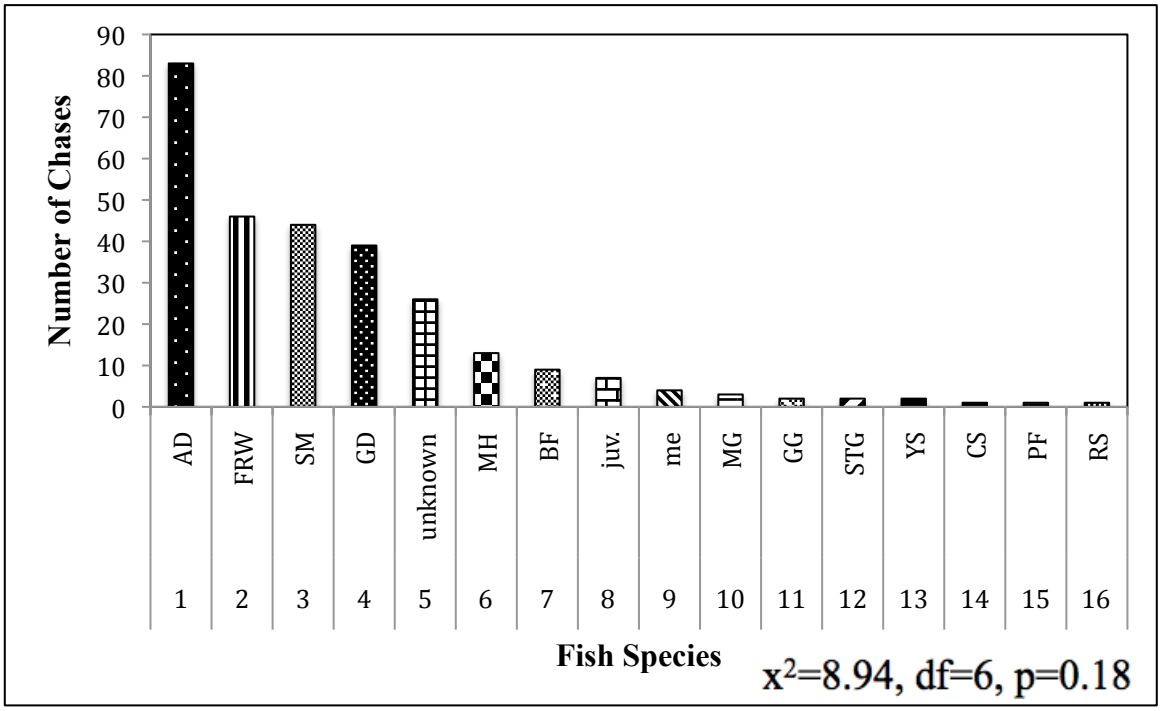

Fig. 1 The fishes shown in this graph are acapulco damselfish (*Stegastes acapulcoensis*), female Cortez rainbow wrasse (*Thalassoma lucasanum*), panamic sergent major (*Abudefduf troschelli*), *M. doralis* adults, unknown, mexican hogfish (*Bodianus diplotaenia*), barberfish (*Johnrandallia nigrirostris*), juvenile giant damselfish (*M. dorsalis*), me, mojarra grunt (*Haemulon scudderii*), graybar grunt (*Haemulon sexfasciatum*), spottail grunt (*Haemulon muculicauda*), yellow snapper (*Lutjanus argentiventris*), chancho surgeonfish (*Prionurus laticlavius*), parrotfish (*Scarus*), and round stingray (*Urolophus halleri*). This list mentions the fish with the most chases to the least respectively.

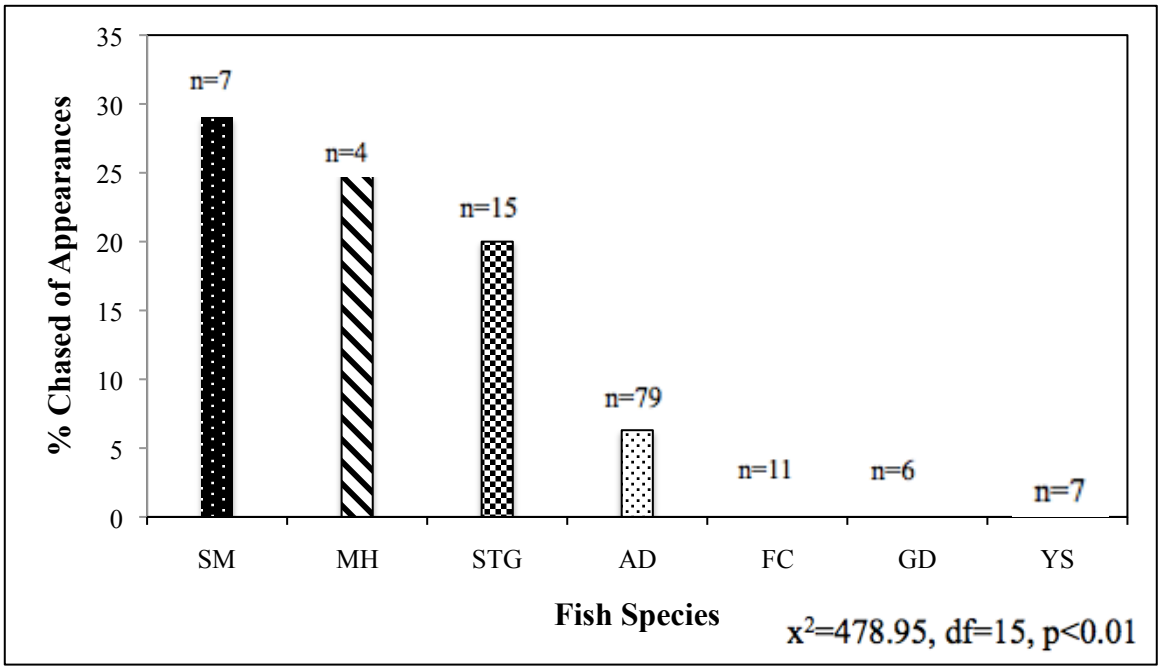

Fig 2. The two-minute analysis from the videos is shown here. The highest percentage of chases occurred with the panamic sergent major (*Abudefduf troschelli*). No chases occurred with the flag cabrilla (*Epinephelus labriformis*), giant damselfish (*Microspathodon dorsalis*), or the yellow snapper (*Lutjanus argentiventris*).

Table. 3 This table displays the relationship between foraging characteristics and species chased from the two-minute analysis. Panamic sergent major (*Abudefduf troschelli*) was chased in two out of seven appearances. Acapulco damselfish (*Stegastes acapulcoensis*) was chased in five out of 79 appearances. Giant damselfish (*Microspathodon dorsalis*) was not chased in its six appearances. Mexican hogfish (*Bodianus diplotaenia*) was chased in one out of four appearances. Spottail grunt (*Haemulon muculicauda*) was chased in three out of 15 appearances. Yellow snapper (*Lutjanus argentiventris*) was not chased in its seven appearances. Flag cabrilla (*Epinephelus labriformis*) was not chased in its 11 appearances.

Foraging Characteristic

Tendency to be Chased	Grazing	Omnivores	Carnivorous
Yes	-	-	-
Sometimes	SM, AD		MH, STG
No	GD		YS, FC

DISCUSSION

Grazing

While observing the nests, I noted repetition of multiple guarding *M. dorsalis* grazing on and maintaining their algae gardens. The even substrate and algae of the gardens are ideal for

other grazing species as well (DeLoach 1999). The author of Reef Fish Behavior: Florida Caribbean Bahamas, Ned DeLoach wrote, "Not all fishes are equal in the eyes of territorial damselfishes; during non-breeding periods the most forceful attacks are directed at their own species and algae-eating surgeonfishes and parrotfishes" (DeLoach 1999). This statement can be understood as grazing species are seen as the largest threat to *M. dorsalis*. DeLoach makes a specification that the surgeonfishes and parrotfishes are threats during non-mating periods. However, during non-mating periods *M. dorsalis* cultivate algal gardens as well. This supports the idea that grazing fishes are more frequent visitors and predators to the nest territory.

In a study conducted by a fellow student during the same time period, Alice Beittel, found that there was a higher aggregation of sea urchins (*Diadema mexicanum*) in an area with low algae abundance. With low algal abundance there were less instances of feeding from grazing fishes (Beittel, 2018). *D. mexicanum* and *M. dorsalis* are both grazing species that feed on algae. They, therefore compete for the same food source (Beittel 2018). A future study using Beittel's exclosures placed on *M. dorsalis* gardens and then allowed to grow could cause an increase in diversity of algae. With the exclusion of *M. dorsalis* and *D. mexicanum*, the algal growth at Bajo Rojo would have the opportunity to grow with minimal disturbance (Montgomery 1980).

In Beittel's paper, she also talks about how the presence of *D. mexicanum* negatively affects coral reefs (2018). This is due to the fact that some coral have a symbiosis with some algae (Sammarco, P. & Williams, A. 1982). It was speculated that at Bajo Rojo, coral diversity was positively affected by damselfish algal gardens. Therefore an abundance of *D. mexicanum* would likely be detrimental to coral community structure (Sammarco, P. & Williams, A. 1982). Further research on the impacts each of these species has on the coral community structure at Bajo Rojo would help conservation efforts in the Bay of Cuajiniquil.

Perching Fishes

In my Table 1, I have included one fish that I never observed being chased although it was sometimes perched on the reef near *M. dorsalis* nests. Panamic fanged blennies (*Ophioblennius steindacneri*) perched close to the nest and did not evoke aggressive responses. I observed the same behavior and subsequent response between *E. labriformis* and guarding *M. dorsalis* as well. *E. labriformis* also perch in and upon the reef. A fish exposed while resting on a substrate and not moving their fins defines the action of perching. *O. steindacneri* and *E. labriformis* are both perching species and not chased by *M. dorsalis* in my data (DeLouch 1999). These are two of the species I observed that regularly perched. In the results, I mentioned that the camera was never chased, but when I was watching the nest, I was. This is another observation that led me to realize that stationary fish were not perceived threats for the guarding *M. dorsalis.*

Chases in Relation to Appearances

Two-minute video analysis shows the largest sample size of *S. acapulcoensis*. This could be attributed to their abundance in Bajo Rojo. During my two-week study period *S. acapulcoensis* were one of the fishes I saw most. Another finding in the two-minute analysis was that other *M. dorsalis* were not chased when they were present in the one-by-one meter zone. However it is important to acknowledge that only six entered the zone at all, but several were chased away before they got close enough to the nest. During my observations at Bajo Rojo I watched male *M. dorsalis* swim aggressively toward many fishes, but consistently watched other

M. dorsalis get chased the furthest by the guarding *M. dorsalis.* In addition, I also observed the most biting at other *M. dorsalis.* During an interview with Minor Lara, he said *M. dorsalis* are not fished for food or sport, and, therefore they have a relatively high abundance at Bajo Rojo. Further, predators of the *M. dorsalis,* as well as other species who prefer to eat algae, have been overfished in most of Cuajiniquil Bay (Minor Lara, pers. comm.). The large population size of *M. dorsalis* causes competition for even substrates to place algae gardens and subsequently nesting territories (Minor Lara, pers.comm.). This competition for an optimal nesting could be one of the reasons why other *M. dorsalis* are nest predators to other *M. dorsalis*. Finding an optimal nesting site is an adaptive trait that increases fitness (Miller, Grand, Fondell, Anthony 2007). An increase in competition for these nesting sites has been observed at Bajo Rojo (Minor Lara, pers.comm.).

Feeding Frenzy Observations

In my incidental observations, I saw a feeding frenzy and noted that grazing species were frequently feeding, and successfully eating the *M. dorsalis* clutch. The fishes that were most abundant in this frenzy were other *M. dorsalis* and *S. acapulcoensis. M. dorsalis* and *S. acapulcoensis* are known grazers and documented as preferring algae (DeLouch 1999; Montgomery 1980; Allen et al. 1994). I speculate that this behavior from these typically algae eating predators could accrue benefits for the intruders because it may cause the owners to move away and abandon their gardens.

Concluding Remarks

In conclusion, my study focused on the characteristics of the intruder species that evoked a chase from male *M. dorsalis* defending their nests. Foraging behavior of grazers positively related to the instances of chases of fishes. Grazers were chased and perchers were not. My results indicate that guarding *M. dorsalis* have the ability to recognize nest predators.

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