

Benefits of heterospecific foraging by the Caribbean wrasse, *Halichoeres garnoti* (Pisces: Labridae)

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Synopsis

Terminal-phase yellowhead wrasses, *Halichoeres garnoti*, foraged alone or in association with foraging goatfish, *Pseudupeneus maculatus* and *Mulloidides martinicus*. Whereas *H. garnoti* did not dig for benthic infauna, the goatfish foraged almost exclusively on and in sand substrata. Wrasse in the company of goatfish made significantly more strikes on sand substrata than did solitary wrasses, although there were no significant differences in the frequency of strikes on sand and hard substrata combined. The frequencies of other behaviors (searches, scratches, flights, chases, rests, yawns, and cleanings) were not significantly different between solitary and associated wrasses. *H. garnoti* are attracted to foraging goatfish, which provide access to an otherwise unavailable food resource.

Introduction

Mixed-species groups have been described in birds, mammals, and fishes (e.g. Karplus 1978, Montgomery 1981, Dubin 1982, McNaughton 1984, Barnard & Thompson 1985, Berner & Grubb 1985). Morse (1977) reviewed the potential foraging and predator-avoidance advantages of membership in such groups. Mixed-species foraging in herbivorous coral reef fishes has been related to avoidance of attacks from territorial damselfish that defend an algal mat (e.g. Barlow 1974, Robertson et al. 1976, Foster 1985, Reinthal & Lewis 1986). Wolf (1983, 1985) presented information regarding the effects of social organization on diet in such schooling herbivores.

In Jamaica, Itzkowitz (1977) examined the dynamics of mixed-species foraging groups composed of parrotfish, surgeonfish, butterflyfish, the goatfish *Pseudupeneus maculatus*, and the wrasse

Halichoeres bivittatus. While he quantified herbivore foraging behavior and related it to group size and composition, he did not investigate the behavior of the carnivorous wrasse and goatfish. Although there are numerous accounts of heterospecific foraging by carnivorous fishes, few quantitative data are available on the costs and benefits to individuals.

Wrasse (family Labridae) are among the most abundant and diverse fishes on coral reefs worldwide. Randall et al. (1978) commented that they are also among the most opportunistic carnivores in their exploitation of the activities of fishes that forage by digging in the substratum. Goatfishes (family Mullidae) possess a pair of highly developed chemosensory hyoid barbels that are used in foraging to excavate or dislodge prey (Gosline 1984). We present a quantitative analysis of the feeding behavior of the yellowhead wrasse, *Halichoeres garnoti*, in association with the spotted

goatfish, *Pseudupeneus maculatus*, and the yellow goatfish, *Mulloidides martinicus*.

Methods

Field work was conducted between 0830 and 1700 hours during July, 1985 in Salt River Canyon, St. Croix and during August, 1985 in Great Lameshur Bay, St. John, United States Virgin Islands. The heterogeneous substratum at both sites was dominated by small patch reefs and patches of sand and rubble. The Salt River Canyon observations were made at 15.2–19.8 m depth during mission 85-7 of the National Undersea Laboratory System-1 (NULS-1) habitat 'Hydrolab', along the East Slope of the canyon [see Kaufman & Ebersole (1984) for a map of the site, referred to as the 'East Wall']. The East Slope extends north of Hydrolab, and is characterized by limestone pavement, rubble, and sand areas that slope at an angle of approximately 45 degrees. At a distance of about 325 m north of Hydrolab, coral pinnacles, patch reefs and clumps of rubble are separated by sandy areas.

One of the authors (R.B.A.) recorded observations along the margin of Great Lameshur Bay at 3.7–10.7 m depth. This habitat is composed of coral-encrusted volcanic pavement, small patch reefs and sand. The fish ecology of Lameshur Bay is treated in Collette & Earle (1972).

Fish censuses were conducted at both field sites to determine the abundances of carnivorous species that forage with goatfish and the frequencies of such interactions. Divers swam slowly along the East Slope 15.2 m contour and along the western margin of Great Lameshur Bay, recording solitary and interacting fish.

To quantify foraging behavior, individual *Halichoeres garnoti* were followed using snorkel and SCUBA diving techniques. The *H. garnoti* and the goatfish did not appear to avoid or be attracted to the divers during the observation periods. Observations were restricted to terminal-phase wrasses (sensu Thresher 1979), as preliminary data collected in the summer of 1984 indicated that other adults very rarely forage with goatfish. In Salt River Canyon, we recorded the number of feeding

strikes that the wrasses made at different substrata (sand, rock, erect sponge, and branching gorgonian) while foraging alone and with goatfish. Due to the heterogeneity of the substratum, the wrasses had access to all substratum types. Each wrasse was observed for a maximum of 20 min, or until lost from view.

Maximum observation time for the Great Lameshur Bay field work was reduced to 5 min after it was determined that no wrasse-goatfish interactions exceeded 5 min in length. Feeding strikes at rock, sponge, and gorgonian substrata were combined into a 'non-sand substrata' strike category. The behaviors recorded were expanded to include the following:

1. strike at sand substratum,
2. strike at non-sand substrata,
3. search – wrasse hovered and appeared to examine substratum directly in front of and below its head,
4. scratch – wrasse vigorously rubbed one side of body across substratum,
5. flee – wrasse was chased by, and swam away from, a damselfish or a conspecific,
6. chase – wrasse lunged at a conspecific,
7. yawn – wrasse opened and closed mouth while swimming,
8. rest – wrasse was immobile in contact with the substratum, and
9. cleaned – wrasse was serviced by cleaner gobies (*Gobiosoma* spp.).

Results

Goatfish followers

In approximately 35 hours of underwater observation, 12 carnivorous species belonging to 7 families were seen in association with goatfish. Census totals for six of these species are presented in Table 1. The following additional species were occasional associates during the study period but were not observed in the censuses: *Caranx latus* (horse-eye jack; juveniles), *Eucinostomus* sp. (mojarra), *Gerres cinereus* (yellowfin mojarra), *Calamus calamus* (saucereye porgy), *Haemulon flavolineatum*

Table 1. Censuses of carnivorous species known to associate with goatfish at Salt River Canyon (80 min census) and Great Lameshur Bay (60 min census).

	Salt River Canyon	Great Lameshur Bay
A. Census totals		
Mullidae		
<i>Mulloides martinicus</i> (yellow goatfish)	7	60
<i>Pseudupeneus maculatus</i> (spotted goatfish)	9	60
Labridae		
<i>Halichoeres garnoti</i> (terminal-phase)	12	33
<i>Halichoeres garnoti</i> (initial-phase)	72	5
<i>Halichoeres bivittatus</i> (slippery dick)	9	5
<i>Halichoeres radiatus</i> (puddingwife)	0	19
Serranidae		
<i>Cephalopholis fulva</i> (coney)	9*	0
Carangidae		
<i>Carangoides ruber</i> (bar jack)	11	0
Lutjanidae		
<i>Ocyurus chrysurus</i> (yellowtail snapper)	13	0
B. Number following goatfish during censuses		
Labridae		
<i>Halichoeres garnoti</i> (terminal-phase)	1	10
<i>Halichoeres bivittatus</i>	0	1
<i>Halichoeres radiatus</i>	0	1
Serranidae		
<i>Cephalopholis fulva</i>	1	0
Carangidae		
<i>Carangoides ruber</i>	1	0

* Not counted during first 40 min.

(french grunt), and *Haemulon plumieri* (white grunt). Species are as illustrated by Randall (1983).

Halichoeres garnoti, *H. bivittatus*, *Carangoides ruber*, *Cephalopholis fulva*, and *Eucinostomus* sp. fed on the substratum near the goatfish with which they were associated. The other species were never seen striking at the substratum while associated with goatfish.

Herbivorous parrotfish (Scaridae) sometimes swam with goatfish. They struck at the substratum rarely during association, and never near where the goatfish were foraging. One parrotfish (*Scarus* sp.) ingested a fecal pellet that a goatfish was in the process of defecating. Herbivorous surgeonfish (Acanthuridae) also swam with goatfish occasionally.

Yellowhead wrasse behavior

Halichoeres garnoti was the most common hetero-specific associate of goatfish (Table 1). It generally followed solitary individuals (Table 2), but was occasionally seen with groups of 3–4 goatfish. Although initial-phase adult *H. garnoti* foraged with goatfish in rare instances, the majority of interacting individuals was in terminal phase.

In Great Lameshur Bay, 12 *H. garnoti* foraged with goatfish and 18 were solitary (Table 3). Wrasse following goatfish struck more on sand substrata than did solitary wrasses ($X^2 = 48.89$, $df = 1$, $p < 0.005$). Similar results were obtained at Salt River Canyon (Table 4) ($X^2 = 12.07$, $df = 1$, $p < 0.005$, using Yates' continuity correction; Sokal & Rohlf 1969). Wrasse-goatfish interactions were short-lived. The mean interaction time was 111 ± 34 (SD) sec ($N = 12$) at Great Lameshur Bay.

Table 2. Frequency distribution of goatfish group sizes recorded in the fish censuses, and frequency distribution of terminal phase *Halichoeres garnoti* following groups of those sizes (one wrasse per group in all cases).

Goatfish group size	Number of groups observed	Number of groups with a wrasse
1	45	7
2	15	3
3	3	0
4	3	1
5	1	0
6	1	0
14	1	0
16	1	0

The data for each of the other behaviors examined at Great Lameshur Bay (searches, scratches, flights, chases, rests, yawns, and cleanings) are presented in Table 3. The number of a given behavior per minute was calculated for each fish, and these rates were averaged over all solitary or associated fish to give behaviors per min per fish. The rates obtained for each behavior from the 12 associated wrasses and the 18 solitary wrasses were subjected to a one-way ANOVA. There were no significant differences between solitary and associated wrasses in the rates of any of the behaviors ($p > 0.05$). Similarly, the rate of strikes on sand and

non-sand substrata combined was not significantly different ($p > 0.05$).

Discussion

Heterospecific carnivores often associate with goatfish (Smith & Tyler 1972, Hobson 1974, Ormond 1980). *H. garnoti* was selected for the present study because preliminary observations indicated that it was one of the more frequent heterospecific foraging associates of goatfish.

The only significant difference in the behavioral repertoires of solitary and associated *H. garnoti* was related to substratum preference during foraging. Wrasse feeding in the vicinity of goatfish made significantly more strikes at sand substrata than did solitary wrasses, despite the heterogeneity of the substratum. This change in foraging behavior occurred in the absence of significant differences in the rate of strikes on all substrata combined or in the rates of any of the other behaviors examined (searches, scratches, flights, chases, rests, yawns, and cleanings).

Goatfish are the only species commonly followed by wrasses. The two goatfish species under study foraged almost exclusively in sand, swimming rapidly from one sand patch to the next. Itzkowitz (1977) remarked that *Pseudupeneus mac-*

Table 3. Summary of observations on terminal-phase *Halichoeres garnoti* in Great Lameshur Bay.

	Foraging mode	
	Solitary	With goatfish
Number of wrasses observed	18	12
Total observation time (min)	63.35	22.27
Strikes at sand substratum	22	38
Strikes at non-sand substrata	100	14
Behavior	Frequency (behaviors per min per fish \pm S.D.)	
search	2.02 \pm 1.17	2.46 \pm 1.59
scratch	0.15 \pm 0.27	0.07 \pm 0.27
flight	0.46 \pm 0.65	0.18 \pm 0.36
chase	0.07 \pm 0.12	0.17 \pm 0.32
rest	0.09 \pm 0.16	0
yawn	0.07 \pm 0.15	0
cleaned	0.06 \pm 0.13	0

Table 4. Summary of feeding observations on terminal-phase *Halichoeres garnoti* in Salt River Canyon.

Foraging mode	Number of wrasses observed	Total observation time (min)	Number of strikes at substratum				
			Sand	Rock	Gorgonian	Sponge	Total non-sand
Solitary	13	177.05	41	176	6	5	187
With goatfish	2	4.25	4	0	0	0	0

ulatus in Jamaica were never observed to forage outside of a sand substratum. Fricke's (1975) experiments suggested that the 'sand cloud' produced by foraging goatfish is a strong attractive stimulus. We noted that *H. garnoti* individuals often hovered around sand substrata that were disturbed by surge or by divers' fins. Occasionally, these individuals nipped at the substratum in the immediate area of the fins. Ormond (1980) reported similar behavior by *H. centriquadrus* in the Red Sea.

Randall (1967) listed polychaetes, bivalves, and crustaceans and their larvae as the major components of the diets of *P. maculatus* and *M. martinicus*. Since goatfish actively probe the sand for these prey, it is likely that wrasses fed on prey 'flushed' by foraging goatfish or exposed by the excavations.

According to Randall (1967), the diet of *H. garnoti* is that of a generalist, including crustaceans, gastropods, echinoderms, polychaetes, and sipunculids. Kaufman & Liem (1982) hypothesized that the 'trophic mobility' of wrasses is made possible by the functional versatility of the feeding apparatus, particularly the pharyngeal jaw mechanism. This ability of wrasses to capture and masticate a diversity of prey means that modifications in foraging behavior can lead to alterations in diet. Since solitary *H. garnoti* do not dig for benthic infauna (Thresher 1979), wrasses that forage in association with goatfish gain access to an otherwise restricted source of food. During the course of this study, an *H. garnoti* was observed to consume an infaunal gastropod and two infaunal starfish (*Astropecten* sp.) that were uncovered when a diver stirred the sand with his fingers.

Heterospecific foraging did not appear to involve costs or benefits to the goatfish. However, on

three separate occasions, a goatfish followed the wrasse that had previously been foraging with it. Fricke (1975) suggested that some goatfish species might follow wrasses to obtain food from wrasse feeding activity on hard substrata, but we found no evidence for such a relationship in the present study.

The brevity of wrasse-goatfish interactions may be attributable to goatfish foraging behavior. Compared to *H. garnoti*, the goatfish covered much larger areas while foraging and spent much more time swimming. Whereas solitary foraging wrasses tended to swim erratically in a limited area, returning periodically to repeat inspections of particular rocks, goatfish swam rapidly between sand patches and rarely returned to the same patch during the observation period. Solitary wrasses were observed to join foraging goatfish that arrived in the vicinity and began to excavate a sand patch. Rarely, however, did wrasses pursue goatfish to new patches. Since Thresher (1979) reported that terminal-phase *H. garnoti* have immense home ranges of 2500 to 5000 m², it is unlikely that the goatfish were swimming out of the wrasses' home ranges. Wrasses were opportunistic in their use of foraging goatfish and it is possible that the energetic cost of pursuing swimming goatfish outweighs the potential foraging benefits.

Our data represent one of the few quantitative analyses of heterospecific foraging behavior in carnivorous reef fishes. Other such associations are common on coral reefs. Continued study of these relationships will increase our understanding of the factors influencing social organization and foraging behavior in fishes.

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