

Foraging by Mixed-Species Groups Involving a Small Angelfish, *Centropyge ferrugatus* (Pomacanthidae)

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(Received August 29, 1994; in revised form December 2, 1994; accepted December 17, 1994)

Abstract Feeding ecology of the small angelfish *Centropyge ferrugatus* was studied at the coral reefs of Okinawa, Japan. This angelfish fed mainly on detritus and algae by nipping substrate within a small home range. In the breeding season, both sexes allocated usually about 60% of their time to foraging in the daylight hours, but females foraged more frequently than males. *Centropyge ferrugatus* frequently approached and followed similar-sized fishes of various species. Both sexes nipped more quickly and frequently in the association than in solitary foragings. Smaller individuals (females) more frequently associated with other fishes. Circumstantial evidence suggested a high predation pressure on the angelfish. We suggest that the association provides an antipredatory benefit to the angelfish, and enables the angelfish to devote more time to feeding because of less time required for the vigilance against predators.

Heterospecific foraging associations have been reported in various vertebrates (reviewed by Morse, 1977). Within coral-reef communities, many fishes join heterospecific associations, e.g., wrasses, parrotfishes, surgeonfishes, goatfishes and butterflyfishes (Ogden and Buckman, 1973; Itzkowitz, 1977; Gushima and Murakami, 1979). The major functions of such groups in fishes have been suggested to be enhanced feeding (Barlow, 1974; Vine, 1974; Robertson et al., 1976; Foster, 1985; Reinthal and Lewis, 1986; Sikkil and Hardison, 1992; Baird, 1993) and decreased predation (Eibl-Eibesfeldt, 1962; Ehrlich and Ehrlich, 1973; Barlow, 1974; Alevizon, 1976). Most studies, however, have dealt with schools consisting of large-sized fishes, and the two major functions have been analyzed separately.

The angelfishes of the genus *Centropyge* often forage with other fishes (Moyer and Nakazono, 1978). The angelfish *C. ferrugatus* is a small-sized fish, common on the coral reefs of Okinawa, Japan (Yoshino and Nishijima, 1981). The species is a protogynous hermaphrodite, living in harems composed of one dominant male and several females (Moyer, 1987); each forages within a small home range (averaging about 30 m² for females, 80 m² for males). During a study of the feeding ecology of *C. ferrugatus*, we observed that the angelfish frequently swam and foraged with other fishes of other species entering the home range. The angelfish foraged

more frequently when swimming in such groups than when solitary. Here we report the feeding behavior and ecology of the angelfish, *C. ferrugatus*, focusing on the function of this associative foraging.

Materials and Methods

Field work was conducted with the aid of SCUBA on the coral reefs in front of the Sesoko Marine Science Center of the University of the Ryukyus, Sesoko Island (26°38'N, 127°54'E), Okinawa, Japan. An observation area (25 m × 10 m) was set up along the reef edge at depths of 1–4 m. Water temperature range from 21.8°C in winter to 29.5°C in summer. On the reefs around the study area, about 330 species of fish have been recorded, including many piscivores, e.g., lizard fishes, snappers and serranid rockcods (Yoshino and Nishijima, 1981).

Individuals of *Centropyge ferrugatus* were distinguished by unique spot-pattern on its body. Body size was estimated visually to the nearest 3 mm in total length (TL). Gender was determined by courtship and spawning behaviors (see Moyer and Nakazono, 1978).

Underwater observations were conducted from 8 to 24 November 1989 (in the nonbreeding season) and from 16 to 28 May 1990 (in the breeding season). Two harems of *C. ferrugatus* were present

in the study area in each season. Each harem consisted of one male (1989: 11.0–11.3 cm TL, $n=2$; 1990: 10.4–11.6 cm, $n=2$) and several females. Home ranges of males completely encompassed those of females (Sakai, unpubl. data). We designated the largest female in each harem as female-1 (1989: 7.4–8.3 cm, $n=3$; 1990: 7.7–8.3 cm, $n=2$), and the other smaller females as female-2 (1989: 6.5–7.1 cm, $n=3$; 1990: 7.1–7.4 cm, $n=3$). One harem in 1989 included two female-1 individuals of nearly equal size which were territorial toward each other.

This angelfish spawns near sunset (Sakai and Kohda, in press). About one hour before sunset, males begin to spend much time in reproductive activity, and they hardly forage. The data of this paper were collected daily from three to one hour before sunset, to exclude the influence of spawning activity. Twenty-min observations were conducted eight times for each individual in 1989 ($n=8$ individuals), and seven times in 1990 ($n=7$ individuals). The number of foraging nips and foraging bouts (duration of each foraging bout), sites, and intra- and interspecific interactions were recorded.

A single foraging bout was defined as a continuous series of nips (max=4 sec including 15 nips). During a foraging bout, a fish maintains a head-down posture against the substrate. Once a fish lifted its head, and an interval of over one sec occurred between consecutive nips, the foraging bout was considered to have ended. Angelfish frequently accompanied fishes of different species which entered the home range. Foragings were categorized into three types: solitary ("solo"), foraging with a single fish within 30 cm ("duet") and with two or more fish within 30 cm ("group").

The home range of each fish was divided into a grid of 30 cm \times 30 cm quadrats, and the substrate of each quadrat was categorized into 6 types: sand, rock, dead coral, soft coral, branching hard coral, and massive hard coral. The feeding area of an individual was calculated as the total number of grids in which foraging behavior was observed.

Seven and four specimens of the angelfish were collected outside the study area during the breeding season and the nonbreeding season, respectively. The body cavity was immediately injected with undiluted formalin for fixation. Stomachs of all specimens were placed into 10% formalin 30–90 min after capturing. Percent volume of food items in stomachs was estimated under a binocular microscope fitted with an ocular grid.

Data were statistically analyzed; the Mann-Whitney U -test was used for comparison between the two treatment, the Kruskal-Wallis test was used for multiple comparison, and the chi-square test was used for contingency tables.

Results

Foraging behavior and ecology

The main foraging behavior of *Centropyge ferrugatus* was to nip at the surface of the substrate. The home ranges of males were 2–3 times larger than those of females (Table 1). The feeding areas of most females covered about 80% of the home range. Those of males covered about 50% of their home ranges, but their foraging areas were about 1.5 times larger than those of females (Table 1). The fish

Table 1. Size of home ranges and feeding areas of *Centropyge ferrugatus*

	n	Mean \pm SD or range		
		Home range (Ho) (m ²)	Feeding area (Fe) (m ²)	Coverage of feeding area (%; Fe/Ho \times 100)
Male	2	75.2–80.8	36.2–36.4	45.0–48.1
Female-1	3	31.0 \pm 5.9	26.3 \pm 4.7	84.8 \pm 1.8
Female-2	3	29.2 \pm 13.7	20.5 \pm 6.6	75.6 \pm 18.9

Each individual was observed for 160 min.

Table 2. Numbers of nips and foraging bouts per 20 min in *Centropyge ferrugatus*

	<i>n</i>	Mean \pm SD or range	
		Nips	Bouts
a) Nonbreeding season			
Male	2	103.1–140.6	36.3–47.0
Female-1	3	112.5 \pm 12.9	44.1 \pm 2.8
Female-2	3	124.2 \pm 36.7	49.2 \pm 13.2
		<i>H</i> =0.03, <i>p</i> >0.05	<i>H</i> =0.47, <i>p</i> >0.05
b) Breeding season			
Male	2	74.0–108.0	40.4–51.7
Female-1	2	127.6–148.0	73.6–75.0
Female-2	3	163.6 \pm 27.7	90.8 \pm 13.8
		<i>H</i> =4.5, <i>p</i> >0.05	<i>H</i> =4.5, <i>p</i> >0.05

Statistical differences were examined by Kruskal-Wallis test.

foraged on substrate of any types; the six substrate types of the feeding area did not differ significantly from those of the entire home range in each individual ($\chi^2=0.2-6.8$, $df=5$, all $p>0.05$ for 8 individuals).

More than 10 territories of the herbivorous damselfishes *Pteroglyphidodon lacrymatus* and *Stegastes nigricans* were adjacent to the home ranges of the angelfish. These territories contain a rich algal community (Yamamoto, 1979; Polunin and Klumpp, 1989). These damselfishes attacked *C. ferrugatus* at border of the territories, as well as other herbivores. This angelfish never intruded deep into these territories.

Stomachs and guts of collected individuals were fully packed. Detritus and algae comprised more

than 75% of the stomach contents of each individual in volume. Benthic animals, mainly coral polyps, sponges and small snails, occupied less than 20% volume of the contents.

Numbers of both nips and foraging bouts did not differ between males and females in the nonbreeding season (Table 2). The numbers of nips and foraging bouts in females significantly increased in the breeding season (Mann-Whitney *U*-test; for nips, $U_{cal}=3$, $p<0.05$; for bouts, $U_{cal}=0$, $p<0.01$; Table 2), while those of males seem not to increase (Table 2). In the breeding season, females foraged more frequently on average (>73 bouts/20 min) than males (<52 bouts/20 min). However, none of these differences between the sexes were significant due to low sample sizes (Table 2). Moreover, the feeding-time budget did

Table 3. Number and type of fishes accompanied with foraging *Centropyge ferrugatus* during 60 min observations

	<i>n</i>	Number of fishes accompanied with a foraging angelfish					Type of accompanied fishes	
		1	2	3	4	>5	Conspecifics	Other species
Male	2	30-35	7-11	0-3	0	0	0-2	47-61
Female-1	3	31.0±11.1	8.3±9.5	3.3±3.5	0.3±0.6	0.3±0.6	4.0±5.3	56.7±39.4
Female-2	3	47.7±24.2	13.0±4.4	0.3±0.6	0	0	0.3±0.6	74.6±21.2

Number of foraging bouts (mean with SD or range values) is shown.

Table 4. Fishes accompanied by *Centropyge ferrugatus*

Family	Genus and species	TL	Tp
Labridae	<i>Halichoeres</i> sp. (young)	4-9	B (1)
	<i>Thalassoma lutescens</i>	13-15	B (1)
	<i>Thalassoma hardwickii</i>	15-20	B (1)
	<i>Gomphosus varius</i>	10-13	B (1)
Scaridae	<i>Scarus</i> spp. (young)	5-9	H (1)
Acanthuridae	<i>Ctenochaetus binotatus</i>	8-15	U
	<i>Zebrasoma flavescens</i> (young)	5-10	H (1)
Mullidae	<i>Parupeneus trifasciatus</i>	15-20	B (1)
Chaetodontidae	<i>Chaetodon plebeius</i>	10-15	B (2)
	<i>Chaetodon xanthurus</i>	10-12	U
	<i>Chaetodon argentatus</i>	10-12	O (2)
	<i>Pomacentrus alexanderae</i>	7-10	U
Pomacentridae	<i>Pomacentrus moluccensis</i>	4-6	O (1)
	<i>Paraglyphidodon nigroris</i>	10-12	U
	<i>Chrysiptera unimaculata</i>	6-9	H (1)
	<i>Chrysiptera rex</i>	5-7	O (1)
Blenniidae	<i>Salarias fasciatus</i>	9-10	H (1)
	<i>Meiacanthus kamoharai</i>	6-8	O (1)
	<i>Meiacanthus atrodorsalis</i>	6-7	O (3)
Apogonidae	<i>Cheilodipterus quinquelineatus</i>	9-10	B (1)
Pseudochromidae	<i>Dampiera cyclophthalma</i>	13-16	B (1)

Total length (cm) and trophic categories (Tp) are listed. B, benthic animal feeder; H, herbivore; O, omnivore; U, unknown. Sources for trophic categories are shown in parentheses: 1, Sano et al. (1984); 2, Sano (1989); 3, Losey (1972).

not differ between sexes: both males and females spent about 60% of their time foraging during the daylight hours in the breeding season ($\chi^2=0.04$, $df=1$, $p>0.05$).

Associative foraging

Centropyge ferrugatus frequently swam with other fishes while foraging (Table 3). However, the angelfish rarely did so with conspecifics (Table 3), due to infrequent encounters among conspecifics in the daylight hours (male: 3.3 encounters with other individuals/20 min \pm 1.7 SD, $n=16$; female: 2.2 ± 3.0 , $n=48$). This angelfish usually accompanied one or two fish at a time (Table 3). The associated fishes included 21 species of various taxa (Table 4). The food habits of the accompanied fishes varied. The body sizes of many fishes overlapped with that of the angelfish (7–12 cm TL) (Table 4). *Centropyge ferrugatus* foraged beside those fishes irrespective of whether or not they were feeding.

Associative foraging of *C. ferrugatus* was mostly demonstrated at the same feeding areas as solitary foraging was done; 73.1% of feeding areas in duet or group overlapped with those of solo (SD = 14.8, $n=8$). The six substrate types of the feeding area by associative foraging also did not differ with those of solitary foraging ($\chi^2=0.1$ –7.1, $df=5$, all $p>0.05$ for 8 individuals).

Time allocated to the three association types, solo, duet and group, differed significantly between the males and females (male vs. female-1, $\chi^2=11.6$, $df=2$, $p<0.01$; male vs. female-2, $\chi^2=55.5$, $df=2$, $p<0.001$; Table 5). The males and female-1 spent more time in solo than in the other two types, but female-2 spent less time solo than accompanied by other fish (Table 5).

In males, time allocation to foraging did not differ among association types ($\chi^2=1.1$, $df=2$, $p>0.05$, Table 5), but females devoted more time to associa-

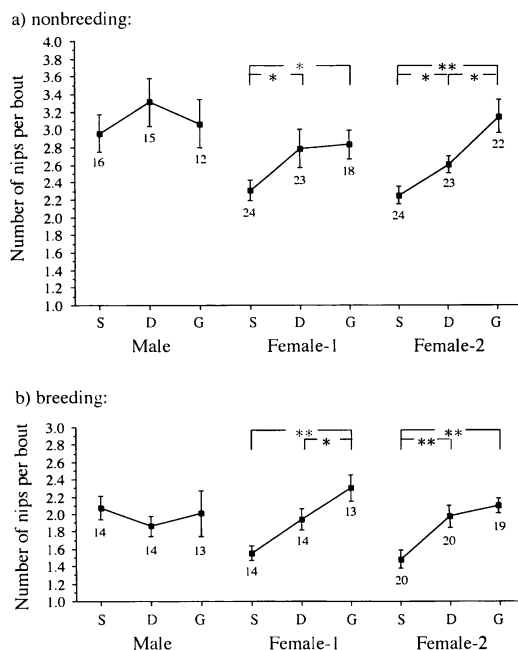


Fig. 1. Number of nips per foraging bout in each association type (S, solo; D, duet; G, group) in the nonbreeding season (a), and in the breeding season (b). Bars indicate SE. Numerals below the bars indicate sample sizes. * $p<0.05$; ** $p<0.01$ in Mann-Whitney *U*-test.

tive foraging (female-1, solo vs. duet, $\chi^2=2.7$, $df=1$, $p>0.05$, solo vs. group, $\chi^2=4.8$, $df=1$, $p<0.05$; female-2, $\chi^2=5.1$, $df=1$, $p<0.05$, $\chi^2=8.8$, $df=1$, $p<0.01$; Table 5).

In females, the average number of nips per foraging bout increased with the number of associated fish in both seasons (Fig. 1). Females nipped more continuously in associative foraging than in solitary. However, no such tendency was seen in the males (Fig. 1). Males showed a significantly higher number of nips per bout than females in solitary foraging in both seasons (*U*-test; nonbreeding

Table 5. Allocation of the time for foraging (F.T.; sec) while swimming (S.T.; sec) per 20 min in association of different sizes

	n	Solo			Duet			Group		
		S.T.	F.T.	%	S.T.	F.T.	%	F.T.	S.T.	%
Male	2	858.4	700.5	81.6	149.2	128.4	86.1	167.2	146.1	87.4
Female-1	2	588.8	538.2	91.4	171.2	168.6	98.5	230.0	229.2	99.7
Female-2	3	481.6	426.8	88.6	225.6	222.2	98.5	409.6	404.0	98.6

Mean values are shown with percentage of foraging time (F.T./S.T. $\times 100$).

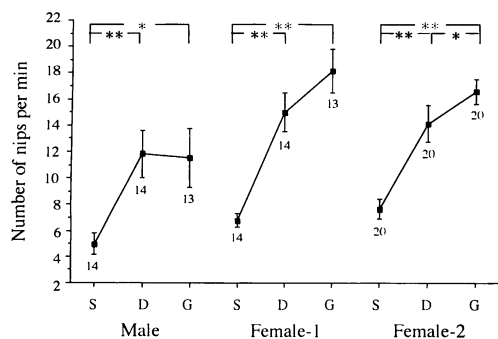


Fig. 2. Feeding rate of each association type (S, solo; D, duet; G, group). Data were calculated as (number of nips in each association type)/(total min of each association type). Bars indicate SE. Numerals below the bars indicate sample sizes. * $p < 0.05$; ** $p < 0.01$ in Mann-Whitney U -test.

season, female-1, $U_{cal} = 102$, $p < 0.05$, female-2, $U_{cal} = 95.5$, $p < 0.01$; breeding season, $U_{cal} = 36$, $p < 0.01$, $U_{cal} = 36$, $p < 0.001$). This number did not differ from those of females in associative foraging in both seasons (Kruskal-Wallis test; nonbreeding season, solo male vs. duet females, $H = 1.0$, solo male vs. group females, $H = 0.8$; breeding season, $H = 0.5$, $H = 3.4$; all $df = 2$ and $p > 0.05$).

The feeding rate was higher in associative foraging than in solitary foraging in both sexes (Fig. 2). Only in female-2 was the frequency higher in group foraging than in duet (Fig. 2). In general, *C. ferrugatus* foraged more frequently in associative foraging than in solitary.

Discussion

Sexual difference in foraging efforts

Centropyge ferrugatus is basically herbivore, mainly feeding on detritus and algae, like other members of the genus (Hobson, 1974; Moyer and Nakazono, 1978). Food composition did not differ among individuals. Therefore foraging-time budget and feeding rate will largely determine energy gains.

In the nonbreeding season, the number of nips and foraging bouts did not differ between sexes nor among females. Females nipped more frequently in the breeding season than in the non-breeding season. This difference of nip number seems to be related to increased energy requirement for egg production.

On the contrary, males showed a similar number of nips in both seasons; therefore they tended to nip lower than females in the breeding season. The lower rate of males' feeding behavior may also be due to lower energy cost of sperm production than that of egg production. Such sexual differences on feeding frequency have been reported in some of harem hermaphroditic fishes, e.g., an angelfish (Moyer, 1987), wrasses (Robertson, 1974; Hoffman, 1983) and a sandperch (Sano, 1993).

Effect of heterospecific associative foraging

Females of *C. ferrugatus* had more feeding nips per foraging bout in associative foraging than in solitary foraging, and both sexes fed at higher rates in group than in solitary foraging. Thus, heterospecific accompanied swimming might provide advantages in feeding for *C. ferrugatus*. What factors could make this angelfish forage more effectively in a group?

One suggested function of group swimming is the enhancement of feeding capability: 1) by trespassing on feeding territories or elsewhere outside the feeding area by solitary foraging which contain much food resources (Hypothesis-1: Barlow, 1974; Vine, 1974; Robertson et al., 1976; Foster, 1985; Reinthal and Lewis, 1986); 2) by gaining access to favorable foods which are exposed during disturbance in group foraging (Hypothesis-2: Ormond, 1980; Aronson and Sanderson, 1987; Sikkil and Hardison, 1992) and 3) by finding food faster than solitary fish (Hypothesis-3: Pitcher et al., 1982; Clifton, 1991). However, none of the above-mentioned advantages can be found in *C. ferrugatus*. This angelfish did not trespass into any feeding territories of the damselfishes. Both location and substrate type of feeding areas by associative foraging were considerably close to those in solitary foraging (Hypothesis-1). *Centropyge ferrugatus* foraged mainly on detritus, algae and slug-like animals which are easily taken even by solitary foraging (Hypothesis-2). The main foods of this angelfish are distributed over the home range, and there would thus seem to be no need to search and find food faster (Hypothesis-3).

Another suggested function of group swimming is increased vigilance against predators (Eibl-Eibesfeldt, 1962; Ehrlich and Ehrlich, 1973; Barlow, 1974; Alevizon, 1976). Smaller species are more vulnerable to predation than larger ones (Hobson, 1974; Thresher, 1984; review by Hixon, 1991). The

high disappearance rate (maybe mortality rate) of adult *C. ferrugatus* (ca. 50% of individuals per year; Sakai, unpubl. data) suggests that this fish suffers a high predation pressure. This small angelfish frequently hid (ca. 25% of the daylight hours), and rarely went far from the shelter holes except for the swimming in the heterospecific association. This circumstantial evidence suggests that by joining foraging groups, *C. ferrugatus* could take advantage of predator avoidance: by the dilution effect which reduces the probability of being the individual attacked in an encounter with a predator (Foster and Trehene, 1981; Pitcher, 1986), and/or by the advantage of earlier detection of predators (Eibl-Eibesfeldt, 1962; Lazarus, 1979; Magurran et al., 1985). Individuals of this angelfish would thus find it advantageous to forage during accompanied swimming, i.e., under lower risk of predation. If so, more vulnerable individuals should more frequently join accompanied foraging. In fact, the smaller fishes which would suffer heavier predation pressure swam and foraged more frequently in association with other fish. Conversely, the smaller fishes also foraged less frequently in the solitary situation. The small *C. ferrugatus* which infrequently encountered with conspecifics appear to use heterospecific fishes for decreasing the threat of predation, and this enables them to devote more time to foraging.

Most previous studies of heterospecific groups have been conducted on large-sized fishes such as adult surgeonfishes or parrotfishes. These studies have indicated that the two main advantages of enhanced foraging and predator avoidance are rather independent. The present study, however, indicates that associations involving small *C. ferrugatus* provides the advantage of predator avoidance, which is indispensable for effective foraging. Similarly, Wolf (1987) reports such interrelated advantages in schools of juveniles of a surgeonfish, *Acanthurus bahianus* (2.5–7.5 cm TL); individuals of the small surgeonfish in schooling time can devote more time to foraging and less time in vigilance than non-schooling time. Further study of feeding behavior of smaller or juvenile fishes should reveal the multi-functional advantages by schoolings, as *Acanthurus bahianus* and *Centropyge ferrugatus* did.

Acknowledgments

We are grateful to S. Yamagishi and other mem-

bers of the Laboratory of Animal Sociology, Osaka City University, for support, advice and comments on this work. We thank T. Kuwamura, A. Rossiter, M. Sano and two anonymous reviewers for critical readings of the manuscript and helpful suggestions which led to significant improvements. We appreciate the help given by the staff of the Sesoko Marine Science Center (SMSC), University of the Ryukyus. This study was partly supported by a Grant-in-Aid for Scientific Research on Priority Areas (#319) from the Japanese Ministry of Education, Science and Culture: Project "Symbiotic Biosphere: An Ecological Interaction Network Promoting the Coexistence of Many Species." This is contribution #271 from the SMSC.

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アカハラヤッコの摂食生態と随伴行動

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キンチャクダイ科のアカハラヤッコの摂食生態について、沖縄県瀬底島のサンゴ礁で調査した。アカハラヤッコは底質をついて摂餌し、その胃内容の75%以上は有機堆積物と藻類が占めていた。繁殖期には、雌雄ともに日中の約6割の時間を摂餌に費やしていたが、雌は雄よりも頻りに摂餌していた。本種は、体長の近い様々な他魚種に対し随伴を頻りに行った。随伴中は単独時に比べ、高頻度で摂餌し、より小型の個体ほど頻りに随伴を行った。いくつかの点から、小型魚である本種は高い捕食圧を受けていると考えられた。アカハラヤッコは他魚種に随伴することにより捕食圧を下げ、同時にそのことにより効果的に摂餌ができると推察された。

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