

## **A new heterospecific foraging association between the puddingwife wrasse, *Halichoeres radiatus*, and the bar jack, *Caranx ruber*: evaluation of the foraging consequences**

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### **Synopsis**

The bar jack, *Caranx ruber*, was commonly observed to follow individual puddingwife wrasses, *Halichoeres radiatus*, that were foraging on the substrate. Individuals of both species actively pursued the other to maintain these heterospecific foraging 'teams', were sometimes attracted to feeding acts initiated by team partners, and the foraging rates of teamed jacks and wrasses were positively correlated. Pilfering of food items was rare, suggesting little, if any, competition cost of this foraging association. The ratio of bites to search in teamed jacks was over three times that when solitary, and jacks were sometimes aggressive to conspecifics attempting to join their team, suggesting that the association is beneficial to the jacks. Both bite and search rates were higher in puddingwives when teamed with a jack, indicating that the association also benefits the wrasses. Benefits to puddingwives may be derived directly from attendants because wrasses were sometimes attracted to jack foraging acts. However, increased foraging in wrasses may also be a consequence of heightened motivation to feed owing to heterospecific social facilitation.

### **Introduction**

Foraging in social groups is well known among vertebrates (Pulliam & Millikan 1982, Pulliam & Caraco 1984, Clark & Mangel 1986), and feeding together with conspecifics has been shown to enhance the foraging effectiveness of individual birds (Krebs et al. 1972, Götmark et al. 1986, Benkman 1988) and fishes (Pitcher et al. 1982, Baird et al. 1991). Although social foraging generally involves individuals of the same species, heterospecific foraging associations have also been reported in mammals (Devore & Hall 1965), birds (Moynihan 1962, Cody 1971) and fishes (reviewed by Strand 1988). In fishes, these associations are usually characterized by one or more individuals of an 'attendant' species

swimming closely to and above or beside a single individual of the 'nuclear' species (Moynihan 1962, Strand 1988, Sikkel & Hardison 1992).

Although it is widely held that heterospecific associations in fishes increase feeding opportunities for attendants (Strand 1988), apparently only three studies have involved collection of the quantitative data necessary to evaluate this hypothesis. Both yellow-headed wrasses, *Halichoeres garnoti*, and yellowtail snapper, *Ocyurus chrysurus*, exhibit higher feeding rates when attending groups of goatfishes (Aronson & Sanderson 1987, Sikkel & Hardison 1992), while grouper, *Cephalopholis* spp., increased feeding rates by following octopus (Diamant & Shpigel 1985). The influence of being attended by a heterospecific on the foraging

performance of nuclear individuals has not been quantified. In many cases, foraging associations involve species with little dietary overlap, hence, competition from attendants is unlikely (Strand 1988). Other associations involve two species that sometimes eat the same prey. Attendant pilfering of food items uncovered by nuclear individuals sometimes occurs (Dubin 1982, Strand 1988), suggesting a potential foraging cost to nuclear individuals.

Here I report on a previously undescribed foraging association involving the puddingwife wrasse, *Halichoeres radiatus*, and the bar jack, *Caranx ruber*. Puddingwife wrasses feed exclusively on benthic invertebrates (Randall 1967). Although bar jacks feed largely on fish, remains of benthic-dwelling mollusks and crustaceans, and sand in the guts of jacks indicates that this species sometimes eats the same invertebrate prey as the wrasses (Randall 1967). Bar jacks are the faster, more mobile of these two species, and following wrasses that are searching the substrate is a striking departure from the usual tendency of jacks to swim higher in the water column. Therefore, I expected that jacks might attend wrasses in order to exploit benthic prey items uncovered by puddingwives, perhaps reducing the foraging effectiveness of wrasses through increased interspecific competition. To assess the influence of this association on the foraging performance of both species, I recorded rates of feeding activities when individual fish were foraging solitarily, and when teamed together with one heterospecific.

## Methods

Observations were conducted from 13 July to 8 August 1991 at Glover's Reef, Belize, Central America, in the channel between Long and Northeast Cays (described in Baird & Baird 1992). Fish were observed between 1300 and 1700 h while snorkeling, and data were recorded on slates. When not attended by a jack, puddingwife wrasses swam independently from conspecifics or other species. Jacks often swam with conspecifics, but solitary foraging was not unusual. I conducted separate 10 min focal observations on puddingwife wrasses foraging solitarily ( $n = 24$  sessions) and when they were attended

by a jack (teamed,  $n = 24$ ). During this set of observations, I recorded only the foraging acts of the wrasses. Five minute focal observations were recorded on jacks when attending a puddingwife (teamed,  $n = 18$ ) and when foraging independently from a wrasse or conspecifics (solitary,  $n = 18$ ). During 5 min focal observations on teams, I recorded the foraging acts of both species. For both data sets, the order of observations on solitary and teamed subjects was randomized. The number of foraging acts (defined below) per observation session was divided by the total minutes of observation to yield per minute rates of foraging acts which were used in all analyses.

Feeding rates may vary as a function of body size or time of day. To control for such variation, subjects were categorized according to estimated fork length (small < 20 cm, medium 20–30 cm, large > 30 cm), and solitary and teamed observations were conducted on different individuals of the same size class, within 15 min of one another. Because teamed and solitary observations were conducted close together in time and on individuals of the same size class, I used a paired design for statistical analyses (Snedecor & Cochran 1980, p. 89). The size class distribution of 24 wrasse subject pairs was; small = 5, medium = 9, large = 10, and for 18 jack subject pairs was; small = 4, medium = 9, large = 5.

Although it is possible that subjects could have been observed more than once, the potential for repeated observations was low because study sessions were spread over a 500 m<sup>2</sup> area where both species were abundant. An inability to capture fish prohibited correlation of food intake with the rate of foraging acts. Rather, I assumed that rates of bite and search are correlates of food intake. Samples of benthic invertebrates taken previously on this study area show that prey are distributed randomly (Baird & Liley 1989). Also, because many benthic invertebrates are mobile and secretive, it is probable that detection of prey is correlated positively with rate of foraging.

A foraging search was defined as the fish stopping its forward swimming motion and angling its snout and visual field downward to scan the bottom. Each of these species swam continuously except when foraging. Therefore, search acts were obvi-

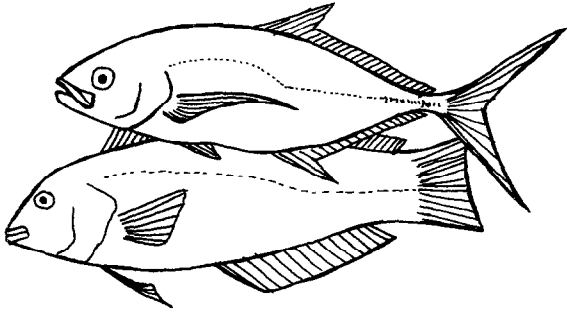


Fig. 1. Bar jack (top) shown in typical position when attending a puddingwife wrasse (bottom) in a heterospecific team.

ous. A foraging bite was recorded each time the fish in search posture contacted the substrate with its mouth.

I also recorded the frequency with which either of the two teamed fish temporarily swam more than three body lengths away from the other fish (separations), and whether either fish swam back to re-join the other within 15 sec. When teams separated for longer than 15 sec prior to completion of a focal session, observations were terminated and these data were not used in analyses. Food pilfering events and interactions between the two teamed fish or with other conspecifics were also recorded.

## Results

Bar jacks attended puddingwife wrasses by swimming parallel with, and above or to the side of the wrasse, usually with less than one body length separating the two fish (Fig. 1). Whether foraging solitarily or in a team, the wrasses swam continuously along the bottom pausing only to search and take bites. Formation of jack-wrasse foraging teams was common, with many lasting longer than the duration of focal observations. Jacks initiated 91.4% (96 of 105) of the temporary separations between teamed fish, compared with only 8.6% that resulted from wrasses leaving teams. Of the 96 temporary separations initiated by jacks, teams were reformed within 15 sec in 50 cases (52.1%) because the wrasse pursued the jack, whereas the jack swam to rejoin the wrasse in 46 (47.9%) of the separations. In two of the most striking examples of team separation and re-formation, the puddingwife

swam beneath a coral formation whereupon the jack rapidly circled the coral, appearing to 'wait' for the wrasse to emerge. Of the nine separations initiated by wrasses, the team was maintained because jacks followed in eight instances (88.9%) and in the other case the wrasse returned to the jack.

Examination of the stomach contents of two specimens of each species, together with direct observations on feeding, confirmed that both bar jacks and puddingwife wrasses eat benthic invertebrates. The wrasses were not observed to pilfer food items from jacks. Jacks attempted to pilfer food items uncovered by wrasses during only 3 of 70 bites taken

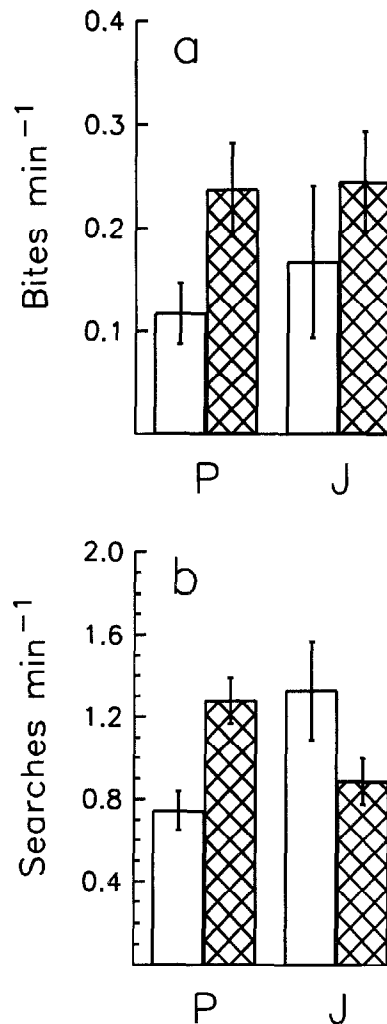


Fig. 2. a – Bites per min ( $\bar{x}$  + SE) in puddingwife wrasses (P,  $n = 24$ ) and jacks (J,  $n = 18$ ) when foraging solitarily (open bars) and in teams (hatched bars). b – Searches per min ( $\bar{x}$  + SE) when solitary and in a team.

by puddingwives, and only one of these attempts was successful. No aggression between wrasses and jacks was observed. However, in 17 of 42 observations on teams, jacks initiated aggression (short chases and displacements) toward conspecifics that were attempting to join the team. In three observation sessions, a second jack successfully supplanted and took the place of the jack participating in the team at the beginning of the observation session.

When a jack was attending, wrasse search and bite rates were 1.71 and 2.03 times higher ( $t = 3.98$ ,  $p < 0.01$ ,  $t = 2.65$ ,  $p < 0.05$  respectively) than when the wrasses foraged solitarily (Fig. 2). Wrasses were attracted to 22.4% (36 of 161) of the total foraging acts (searches + bites) initiated by jacks, whereas jacks were attracted to 31.1% (140 of 450) of the foraging acts initiated by wrasses. Also, the total number of foraging acts per session by jacks was correlated ( $r = 0.48$ ,  $p < 0.05$ ,  $n = 18$ ) with the total foraging acts by wrasses.

For jacks attending a wrasse, the average bite rate was 1.5 times higher than when jacks foraged solitarily (Fig. 2), but this increase was not statistically significant ( $t = 0.78$ ,  $p = 0.44$ ). The search rate of teamed jacks was only 67% of that when solitary ( $t = 1.59$ ,  $p = 0.13$ ). As a consequence, the ratio of bites to searches by teamed jacks ( $\bar{x}$  bite search<sup>-1</sup> = 0.32, SE = 0.08) was more than three times higher ( $t = 2.52$ ,  $p < 0.05$ ) than that of solitary jacks ( $\bar{x} = 0.10$ , SE = 0.03).

## Discussion

Although jacks were attracted to about one-third of the foraging acts initiated by puddingwives and jack foraging rate was correlated positively with that of *H. radiatus*, I observed surprisingly little evidence of jacks pilfering food items that wrasses had located first. The absence of pilfering suggests little if any cost to puddingwives owing to increased competition from attendant jacks.

The foraging activities of individuals of both species appeared to be enhanced by this association, but in different ways for each. In jacks, foraging with puddingwives increased the number of bites taken per search effort. If one assumes that fish bite

when they have detected a food item, then the higher ratio of bite to search suggests that jacks may increase prey detection efficiency by attending wrasses. Stomach content data indicate that bar jacks feed primarily on fish (Randall 1967). Because bar jacks apparently only supplement their diets with benthic invertebrates, it may be particularly beneficial to attend species which are adept at bottom feeding if this increases feeding efficiency during the limited amount of time spent foraging on the benthos. This hypothesis is supported further by the observation that bar jacks also occasionally followed three other species that uncover benthic prey, *Balistes vetula*, *Dasyatis americana*, and *Kyphosus sectatrix*.

Puddingwife wrasses were also attracted to foraging acts initiated by jacks, and displayed higher search and bite rates when attended. Furthermore, wrasses actively followed jacks which temporarily separated from them, and were not aggressive toward jacks. Together these observations suggest that, rather than being exploited by attendant jacks, the wrasses may also benefit from the association. Heightened rates of bite and search suggest that the association may increase foraging opportunities owing to the activities of the attendant jacks. However, one alternative explanation is that social stimuli from attendants may elicit increased feeding motivation in puddingwives. Social facilitation of feeding by conspecifics has been demonstrated previously in fishes (Olla & Samet 1974, Ryer & Olla 1991). If social facilitation explains increased foraging rates in teamed puddingwife wrasses, then stimuli are from heterospecifics that exploit similar food resources.

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