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Facultative monogamy in obligate coral-dwelling hawkfishes (Cirrhitidae)

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Synopsis

Obligate coral-dwelling hawkfishes have been hypothesized to be monogamous. This hypothesized mating system is at odds with what is known of those of other cirrhitids. *Neocirrhites armatus,* which inhabits *Pocillopora* spp. corals, and *Oxycirrhites typus,* which inhabits gorgonians and antipatharian corals, were examined for evidence of a monogamous mating system. Life history criteria that favor monogamy in reef fishes (Barlow 1986) were examined for these two species. Facultative monogamy was found in both. In this mating system, males are limited in their ability to acquire and maintain females, and thus have only a single mate, but may acquire additional females if conditions for doing so are favorable.

Introduction

Some workers (e.g. Thresher 1984, Barlow 1986, 1988) have predicted that certain hawkfish species, specifically those found exclusively in corals, usually as paired adults, are monogamous. Two obligate coral-dwelling species, *Neocirrhites armatus* and *Oxycirrhites typus,* are likely candidates. Both are frequently observed in pairs when encountered. However, the possibility that either or both species are monogamous is at odds with what is known of the social organization and mating system of other members of the Cirrhitidae (Thresher 1984, Donaldson 1987). The purpose of this paper is to examine the social organization and mating system of these two cirrhitids to determine if these species are unique from the rest of the family.

Hawkfishes (Cirrhitidae) are a monophyletic fish group consisting of 34–35 species in 9–10 genera (Springer 1982). They are distributed largely in the tropical and subtropical Indo-West Pacific, although three species occur in the tropical Atlantic and a single species is endemic to the eastern Pacific (Randall 1963, Lubbock 1978, Springer 1982, Donaldson 1986a). Hawkfishes occur on coral and rocky reefs, and various species have been classified as having one or more of three major types of microhabitat preference (Donaldson, unpublished): obligate coral-dwelling species, non-obligate coral-dwelling species, and non coral-dwelling species. Recent studies have indicated that hawkfishes are protogynous hermaphrodites (Thresher 1984, Kobayashi et al. 1985, Y. Yogo personal communication, Sadovy & Donaldson unpublished). Those non coral-dwelling and non-obligate coral-dwelling species studied so far are haremic, with social groups consisting of a single male and one or more females (Thresher 1984, Donaldson 1986b, 1987).

Monogamy and reef fishes

Monogamy in reef fishes has been reviewed recently by a number of authors (Gronell 1984, Thresher 1984, Driscoll & Driscoll 1988), but evidence of 'exclusive matings between one male and one female' (Thresher 1984) exists for only a few taxa. Monogamy has been described for a few pomacentrids, including *Amphiprion* (Fricke 1974, Moyer & Bell 1976, Fricke & Fricke 1977) and *Acanthochromis* (Thresher 1984), in syngnathids of the genus *Corythoichthys* (Gronell 1984), in the chaetodontid *Chaetodon multicinctus* (Hourigan in Barlow 1986, 1988), and in the monacanthid *Oxymonacanthus longirostris* (Barlow 1988). Much of the literature on monogamy in reef fishes emphasizes short (at time of courtship; see Gronell 1984) and long-term pairing. This is true of the Acanthuridae (Robertson et al. 1979), Apogonidae (Thresher 1984, Kuwamura 1985), Chaetodontidae (Fricke 1973, Reese 1975, Burgess 1978, Tricas 1985, Driscoll & Driscoll 1988), Gobiidae (Lassing 1976, Schmale in Thresher 1984), Pomacanthidae (Strand 1978 in Thresher 1984), and Serranidae (Donaldson 1989) to name a few.

Thresher (1984) and Gronell (1984) reviewed or described five hypotheses that might explain the formation of monogamous systems in reef fishes. These hypotheses center around the following: biparental care of offspring, resource defense (see also Robertson et al. 1979, and Hourigan in Barlow 1986, 1988, for discussions of male territoriality and female benefits in monogamous pairs), low density and low mobility of individuals, hybridization avoidance and increased reproductive efficiency. Poor diet, affecting the number of suitable females, has also been hypothesised as a condition that promotes monogamy in *Oxymonacanthus longirostris* (Barlow 1988).

Barlow (1984, 1986, 1988) discussed monogamy in both freshwater fishes and marine reef fishes. His points, with respect to obligate coral-dwelling hawkfishes, are considered here.

In Barlow's definition, monogamy in fishes occurs when a pair of fishes remains together through a reproductive cycle that includes biparental care of offspring, or when a pair of fishes spawned together with the same partners, during short intervals of time, over a long period without practicing parental care of offspring. Barlow found that freshwater fishes conformed to the former condition, whereas marine reef fishes to the latter. With reef fishes, monogamy may result from two causes: the pattern of dispersion of females in a given area, and the subsequent inability of the male to secure access to more than one female because of that pattern.

Barlow (1986) listed certain life history criteria that can be applied to describe potentially monogamous species. Fishes should be relatively small in body size, and be strongly site-attached or territorial. They should spawn without seasonality or with weak seasonality over a long period of time and produce planktonic eggs or larvae that disperse without parental care. These criteria were considered in relation to known life history patterns of *N. armatus* and *O. typus*.

Methods

Obligate coral-dwelling hawkfishes were surveyed at six localities in the central and western Pacific to determine the proportion of adults occurring in pairs within the same coral. In addition, fishes were observed repeatedly over time at a number of study sites to determine their social organization, site fidelity, social behavior, and reproductive behavior. Observations were made using scuba, and data were recorded on plastic slates and by underwater photography.

Species accounts

Neocirrhites armatus

This brightly colored species is distributed from French Polynesia (Society Islands and Tuamotu Archipelago) west to the Phoenix Islands, northeast Australia, Fiji, the Mariana Islands, Wake Island, and southern Japan (Randall 1963, Carlson 1975, Myers & Shepard 1981, Masuda et al. 1985). *N. armatus* is an obligate coral-dweller, preferring corals of the genus *Pocillopora*, especially *P. eydouxi* and *P. elegans* (Donaldson, unpublished), although also found in *P. verracosa* in Fiji (Carlson 1975).

N. armatus was surveyed and observed at the following localities and sites: Guam, Mariana Islands (Tanguisson Reef, Gun Beach, Agana Bay, Cabras Island, Luminao Reef, Anae Island and Pago Bay); Saipan, Mariana Islands (the Grotto); Tinian, Mariana Islands (Herman's Beach, Tachogna Beach); Moorea, Society Islands (outer reef on E. and W. sides of Tareu Pass, Opunohu Bay). This species was relatively common at Guam, particularly at Tanguisson Reef and Pago Bay, and at Moorea, but was less common elsewhere. Relative abundance in general seemed limited by the availability of live *Pocillopora* corals; these corals were often dead, damaged, or absent from many sites because of the activities of man or the crown-of-thorns starfish, *Acanthaster planci.*

Corals were surveyed to determine the number of individuals occurring in each coral. Of 166 sampled corals containing *N. armatus* , 45.2% had fish that occurred in pairs, 42.2% singly, 10.8% as a single male and two females (triplets), 1.2% as a single male and three females, and 0.6% as a single male and four females. The differences are significant (Chi-square goodness-of-fit; $\chi^2 = 160.9$, $p<0.001$, df = 4). The number of individuals occurring in the same coral head seemed limited by both the size of the coral and the availability of suitable corals (Donaldson, unpublished).

Social groups at Guam, Tinian, and Moorea were single male-dominated and ranged in size from 2–5 individuals ($\bar{x} = 2.4 \pm 0.57$ SD, $n = 44$). Social groups occupied 1–4 corals, depending upon coral size and relative proximity to one another (Donaldson, unpublished). Social groups consisting of a single male and two or more females were more common if corals were large (>50 cm in diameter) or scarce (Table 1).

Individuals living alone in coral heads may have been associated with other individuals in the following ways: (1) paired with others living singly in adjacent corals, (2) grouped with pairs living in adjacent corals, or (3) grouped with social groups consisting of two or more females, either living together in the same coral or in two or more adjacent corals. In the first example, paired fishes were believed to be monogamous; in the second, a male living with a female often made visits to a second adjacent female during courtship periods but returned to the coral where the first female resided. Similar behavior of the cirrhitid *Cirrhitichthys oxycephalus* has been observed at Lizard Island, Great Barrier Reef (personal observation). In the third example, the male visited each of the females in adjacent coral heads during courtship periods but returned to its own coral head when courtship had been completed. This behavior has also been observed in three non-obligate coral-dwelling species, *Paracirrhites arcatus, P. forsteri* and *P. hemistictus* (Donaldson, unpublished).

Body sizes of this species were small and sexual dimorphism was present within pairs or social groups. Males were larger ($\bar{x} = 53.8 \pm 15.9$ (SD) mm TL, $n = 51$) than females ($\bar{x} = 49.6 \pm 6.4$ (SD) mm TL, $n \pm 77$), and the differences were significant (T-test, $t \pm 2.08$, $p<0.05$).

Neocirrhites armatus had strong site fidelity to specific coral heads. Carlson (1975) has also indicated strong site fidelity among members of a Fiji population. Duration of residence for some pairs, triplets, and individuals in the same coral heads at Tanguisson Reef, Guam, exceeded 2.5 years. This species was both intra- and interspecifically territorial, defending all or part of the coral head from intruders. Interactions between individuals in pairs or social groups within the same coral were less intense than those from outside the coral. Preliminary experimental introductions at Tanguisson Reef indicated that males and females vigorously defended against introduced males and larger females; males tended to ignore smaller females and juveniles, although resident females defended against both. Resident females that lived alone in corals excluded larger or equally sized females. These females tended to ignore smaller females and juveniles and often allowed them to stay (Donaldson, unpublished).

Courtship was paired, and began just prior to or after sunset. Courtship concluded after dusk throughout the year at Tanguisson Reef, Guam. There was no apparent seasonality. Males in social groups of two or more females courted females in sequence and often made multiple visits to each if they shared the same coral or occupied a second coral less than 1.5 m away. Pelagic spawning has not yet been confirmed, although quick rushes by pairs to the edge of corals have been observed. This species most likely spawns pelagically, as do other cirrhitids (Thresher 1984, Donaldson 1986b, 1987, Donaldson & Colin 1989), only after dark, when the deep red coloration of this species may afford cryptic coloration against visually-oriented predators. It could be a demersal spawner, laying eggs within the coral where it resides, but I have seen no evidence of such deposition. Life history characteristics are summarized in Table 2.

Oxycirrhites typus

This uncommonly seen species has one of the widest distributions of any cirrhitid and occurs from the tropical eastern Pacific westward to the Red Sea (Randall 1963). *O. typus* is an obligate coral-dwelling hawkfish that lives on gorgonians and antipatharian corals in deep slope (20–150 m) habitats (Randall 1963, Thomson et al. 1987, Masuda et al. 1985).

O. typus was surveyed at the Papuan Barrier Reef, east of Port Moresby, Papua New Guinea (see Donaldson & Colin 1989, for details of the study sites), and at Mwahn Channel, Ponape, Caroline Islands. This species was observed at depths of 20–28 m at three sites in Papua New Guinea and 48 m at a single site at Ponape. The distribution of these hawkfishes at each locality seemed limited by the availability of suitably-sized corals. This hawkfish was absent from gorgonians with diameters less than 1.8 m and antipatharians less than 1.6 m in height. Fewer *O. typus* individuals could be surveyed and observed compared to *N. armatus* because: (a) there were no suitable corals in large numbers at the localities examined and, (b) individuals occurred at depths which limited observation time because of diver-safety considerations.

In corals that supported one or more *O. typus* (n = 10), 40% had fish that were paired (one male and one female), and 60% had single fish. Of the paired fishes, three pairs consisted of two adults and one consisted of a female and a juvenile. Of the single fishes in corals, two were paired together socially and lived in adjacent corals, three were part of a male-dominated harem, and one was alone. The paired individuals not occurring on the same coral each used separate corals, but migrated to a common coral for courtship and spawning. Afterwards, they remained in that coral for an undetermined length of time but returned to their separate corals by morning (Donaldson & Colin 1989). Those individuals from the harem lived in corals adjacent to one another; during the courtship period, the male visited each female in sequence before returning to his own coral for the night. Social group sizes ($\bar{x} = 2.2 \pm 0.45$ (SD), n = 5) are given in Table 1.

This species appeared to be sexually dimorphic for body size within pairs or groups of adults. Males were slightly larger ($\bar{x} = 78.3 \pm 18.2$ (SD) mm TL, n = 3) than females ($\bar{x} = 61.5 \pm 7.9$ (SD) mm TL, n = 4). Sample sizes were too small to attempt statistical analyses.

Oxycirrhites typus appeared to have strong site fidelity where suitable corals were few in number. However, at one site the male and female of a single pair lived separately in more than one coral and moved between those corals on different days. These two hawkfishes were the only *O. typus* present, although corals at this site were common. Both male and female favored a single coral over others and met at a common coral only during courtship. Territoriality was not observed in pairs or in the harem. It was not possible to make experi-

Table 1. Social group sizes of the obligate coral-dwelling hawkfishes *Neocirrhites armatus* and *Oxycirrhites typus*.

Species	Group size	No. of groups	Percent
*Neocirrhites armatus**	2	30	66.6
	3	12	26.6
	4	2	4.4
	5	1	2.4
Oxycirrhites typus	2	4	80.0
	3	1	20.0

* $X^2 = 48.3$, $p<0.001$, df = 3.

mental introductions of individuals into corals where pairs resided because of the relative scarcity of individuals in the area.

Courtship began just prior to or after sunset at Papua New Guinea and concluded at dusk. Courtship and spawning may occur year round in the tropics and seasonally higher latitudes, where water temperatures during cooler parts of the year may be an influence. Spawning was paired and pelagic (Donaldson & Colin 1989) and not demersal, as has been previously indicated (Lobel 1974, Randall 1985). Eggs and larvae were pelagic. Life history characteristics are summarized in Table 2.

Discussion

Obligate coral-dwelling cirrhitids such as *Neocirrhites armatus* and *Oxycirrhites typus* have characteristics that satisfy those life history criteria proposed by Barlow (1986), yet are monogamous only under certain circumstances, which are discussed here. Both species are strongly site-specific, often used the same coral for shelter, feeding and reproduction, but they tend to occur in monogamous pairs if suitable corals are too few or too small. If corals are more plentiful, are of a larger size, or are in close proximity to one another, then multi-female harems may occur. Territoriality has not been observed in *O. typus*, thus far. *N. armatus* is territorial, and defends space against intruders if alone, or, if not, against one or more mates or harem members in addition to intruders. Males may strongly defend against intruding males or large females, but not necessarily against smaller females, which are potential mates if they can be accomodated within the coral or in a nearby coral. Females will defend against both males and females, regardless of size. This behavior is indicative of male choice as a function of monogamy in reef fishes (Barlow 1986) or size-selective territoriality (R.E. Thresher, personal communication). Males ultimately will spawn with as many females as possible but may be limited in their ability to do so. Such a condition allows for the appearence and maintenance of a monogamous mating system (Barlow 1986). Two potential limitations, with respect to the cirrhitids described here, are: (1) the availability of females, in relation to the availability of suitable corals, and, (2) the possibility that large females may undergo early sex change and succeed in sneaking or stealing females from the dominant male (Moyer & Zaiser 1984, Donaldson 1987). Females are expected to exclude other females since they may be potential competitors for access to both the same male, and the limited space that can be shared with that male, and failure to exclude rival females may result in a lowering of fitness.

Table 2. Summary of life history characteristics of two obligate coral-dwelling hawkfishes. M = male; F = female.

Variable	*Neocirrhites armatus*	*Oxycirrhites typus*
Site attachment	very strong	very strong
Territoriality	strong	not seen
Adult body size (range; mm TL)	M- 44.5–70.0 F- 37.0–62.0	M- 65.0–99.5 F- 52.0–92.0
Sexual dimorphism (body size)	M greater than F within groups	M greater than F within groups
Courtship periodicity	daily	daily
Seasonality in courtship	lacking	at higher latitudes (?)
Courtship type	paired, sequential	paired, sequential
Spawning type	pelagic (?)	pelagic
Eggs, embryos and larvae	planktonic (?)	planktonic
Social organization (range in group size)	2–5	2–3
Mating system	facultative monogamy/ male-dominated harem	facultative monogamy/ male-dominated harem

The success that a female has in excluding rival females may reinforce a monogamous mating system. The failure to do so may result in the formation and maintenance of a haremic system, although the probability of this occurring may also be limited by size, availability and proximity of suitable corals to support that system.

Both *N. armatus* and *O. typus* have relatively small body sizes compared to many other cirrhitids (see Randall 1963). *Neocirrhites armatus* is sexually dimorphic for size, and *O. typus* appears to be so, with males larger than females within pairs or groups, though not always between pairs or groups. This dimorphism could be indicative of protogynous hermaphroditism and is currently under investigation. Similar patterns of size dimorphism between sexes occur in *Cirrhitichthys falco* (Donaldson 1987), *C. aprinus, C. oxycephalus, Paracirrhites arcatus, P. forsteri, P. hemistictus, Amblycirrhitus bimacula* and *Cirrhitus pinnulatus* (personal observation).

Oxycirrhites typus spawns pelagically, and its eggs, embryos and larvae are pelagic; *N. armatus* is assumed to have the same pattern of reproduction. Pelagic eggs, embryos and larvae may be produced (see Shapiro et al. 1988 for critical review) providing dispersal of adults (Barlow 1981), predation avoidance of eggs, embryos and larvae (Johannes 1978) and reducing the probability of failure in larval survival (Doherty et al. 1985). Regardless, the need for parental care of early ontogenetic stages is eliminated, as is the need for progeny to be immediately adapted to the reef environment (Barlow 1986). The pattern of producing pelagic eggs, embryos and larvae may, in the absence of parental care, contribute towards monogamy but not exclusively so. This same pattern also occurs in haremic cirrhitids (Thresher 1984, Donaldson 1986b, 1987, unpublished).

Courtship by both species is frequent and, at least for *N. armatus,* lacks seasonality at low latitudes. Similar patterns have been observed (Donaldson 1986b, 1987) for haremic *C. falco* at Guam (lower latitude: 13° 23′ N) and Miyake-jima, Japan (higher latitude: 34° 05′). Hawkfishes that release small 'packets' of gametes on a daily basis may realize greater fitness by compensating for relatively small body sizes even though the daily fecundity of females is lowered. At higher latitudes, females with relatively larger body sizes, and thus relatively greater fecundities, may be able to compensate for the inability to spawn throughout the year because of a shorter breeding season. Larger body sizes may contribute to greater daily fecundity if there is not also latitudinal variation in egg sizes (see Thresher 1988). Although frequent spawning may contribute towards monogamy, it too is not exclusive to this mating system.

Possession of life history characteristics that satisfy those criteria proposed for a monogamous mating system does not mean necessarily that monogamy will occur. Monogamy in reef fishes may occur if (a) defense of a resource is enhanced by pairing (e.g., Robertson et al. 1979), (b) pairing reduces the opportunity for hybridization between closely related species (Fricke 1973), (c) reproductive efficiency is enhanced, as has been demonstrated for syngnathids of the genus *Corythoichthys* (Gronell 1984), and (d) pairing allows for more successful parental care (see Gronell 1984, for review). Two of these conditions are irrelevant with respect to obligate coral-dwelling hawkfishes: hybridization is unlikely in both species because they are monotypic genera; and parental care is probably absent in both because *O. typus* spawns pelagically and *N. armatus* presumably does as well. The likelihood of increased success at defending a resource and increased reproductive efficiency are both under investigation.

Monogamy may also occur if it is a function of male choice in relation to the density and distribution of females (Barlow 1986). In obligate coral-dwelling hawkfishes male choice will also depend upon the density and dispersion of suitably sized corals that can support potential mates. This dependence is in agreement with the 'low density' and 'low mobility' hypothesis, which states that monogamy may be selected for when individuals are widely dispersed, have restricted mobility, and have social units whose size may be influenced by available habitat (Ghiselin 1969, Wilson 1975; see summaries in Gronell 1984, and Thresher 1984). Such monogamy can be facultative (see Thresher 1984 for examples in other taxa, i.e., labrids); males will be monogamous only if they cannot acquire and support additional females. Males can acquire additional females if the corals in which they reside are large enough to accommodate additional females, or if suitable corals supporting single females are within close proximity to resident corals. If paired females are unsuccessful in defending resident corals from new females, a haremic mating system will also result. Female success in 'sequestering males' by territorial defense against intruding females then, may serve to maintain monogamy once it is established.

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