

Social and mating systems of the protandrous anemonefish *Amphiprion perideraion* under the influence of a larger congener

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Abstract The effect of a larger anemonefish *Amphiprion clarkii* (Bennett) on the social and mating system of a smaller congener *Amphiprion perideraion* (Bleeker) was investigated on a coral reef at Okinawa, Japan, where both species use the same host sea anemone *Heteractis crispa* (Ehrenberg). The population of *A. perideraion* consisted of adult, subadult and juvenile groups. Adult groups, which consisted of one or two adults and a varying number of subadults and juveniles, usually did not share the host with *A. clarkii*. In contrast, subadult and juvenile groups, which included no adults, always cohabited with *A. clarkii*. In the heterospecific groups, subadult *A. perideraion* were able to mature histologically, and changed to female when they were the largest among conspecific members, although their reproduction was suppressed by *A. clarkii*. After all members of *A. clarkii* emigrated or disappeared from a heterospecific group, adult *A. perideraion* could begin breeding. I suggest that *A. perideraion* in both heterospecific and conspecific groups adopt a mating strategy that involves waiting for vacated breeding posts because of their low mobility and a low host density.

Key words: coral reef fish, interspecific competition, sex change, size-structured population.

INTRODUCTION

Body size is often an important determinant for behavioural dominance in local fish assemblages that consist of ecologically similar species (Robertson 1996, 1998). In some territorial herbivorous damselfishes (genus *Stegastes*), for example, the largest species is competitively dominant over other smaller congeners (Robertson 1996). Furthermore, in congeneric fishes living in social groups, the largest species may control the growth and reproduction of smaller congeners and its presence may influence the distribution pattern and behaviour of the smaller ones. For example, in two damselfishes (genus *Dascyllus*), which inhabit the same isolated corals forming social groups and which have similar body size and behaviour, only the largest individual of either species in a group reproduces, suppressing the reproduction of the other species (Shpigel 1982; Shpigel & Fishelson 1985). Juveniles of the two damselfishes settle on corals where conspecific fish predominate (Sweatman 1983, 1985). Little is known about social and mating systems of coexisting fishes under the influence of competing congeners.

Anemonefishes (genus *Amphiprion*) exhibit socially controlled protandry with monogamous mating systems (Fricke & Fricke 1977; Moyer & Nakazono 1978; Ross 1978a; Fricke 1979). They always live on or

around the host sea anemones, an essential resource for their shelter and spawning sites (Allen 1972). Distribution patterns of host sea anemones are the crucial determinant of their social and mating systems (Fricke & Fricke 1977; Ross 1978a; Fricke 1979; Moyer 1980; Yanagisawa & Ochi 1986; Ochi 1989a) and influence their sex change patterns (Ochi 1989a, b; Hattori & Yanagisawa 1991a, b; Hattori 1991, 1994; Hattori & Yamamura 1995).

Both *Amphiprion perideraion* (Bleeker) and *Amphiprion clarkii* (Bennett) are common on coral reefs of Okinawa Island, Japan, where they inhabit the same host species *Heteractis crispa* (Ehrenberg) (Moyer 1976; Moyer & Nakazono 1978; Hattori 1994, 1995; Hirose 1995). At Sesoko Island, Okinawa, *A. clarkii* are almost always larger and suppress the growth and reproduction of coexisting *A. perideraion* (Hattori 1995). In contrast, *A. perideraion* prevent juvenile *A. clarkii* from settling on their hosts (Hattori 1995). *Amphiprion perideraion* often form groups in the presence of *A. clarkii*, because *A. clarkii* do not prevent juvenile *A. perideraion* from settling. My previous study showed that the social and mating system of *A. clarkii* are less affected by the presence of *A. perideraion* (Hattori 1993, 1994).

The purpose of the present study is to understand the mating system of *A. perideraion* and their group structure and individual sexual state in the presence of the large congener. The pattern of juvenile

settlement and life-history pathways of this species are also described.

METHODS

Study site and general methods

I conducted the field research on a fringing reef in front of Sesoko Station, Tropical Biosphere Research Center, University of the Ryukyus at Sesoko Island (26°39'N; 127°57'E), Okinawa, Japan. A map of the study area (87 m × 373 m) was made based on an aerial photograph and underwater observations. Locations of host sea anemones *H. crista* (Ehrenberg) (previously known as *Radianthus kuekenthali*) larger than 400 cm², which *A. perideraion* inhabited (Hattori 1995), were plotted on the map. The long and short axial lengths of each sea anemone were measured twice in August 1988 and twice in August 1989. The area covered by the tentacles of each sea anemone was regarded as an oval and was estimated as (long axial length) × (short axial length) × $\pi/4$ (see Hattori 1994, 1995). The larger of the two measurements was used as an index of the size of sea anemones. Breeding activities of *A. perideraion* continued throughout the year except mid-summer (August) and winter (January and February) (A. Hattori, unpublished observations). Field observations were conducted in three 6-month periods: from June to November 1988, from December 1988 to May 1989, and from June to November 1989. Data for the three 6-month periods were combined for analysis. I recorded swimming tracks of each fish for 15 min in the first period and regarded the outline of the tracks as the border of its home range (see Ochi 1986; Hattori 1991, 1994, 1995). Conspecific individuals with overlapping home ranges were viewed as constituting a social group, and were called alpha-, beta- and gamma-individuals, and so on, according to the body size order.

Sexual states

Amphiprion perideraion, at the present study site, is sexually dichromatic in the caudal fin colouration (Moyer 1976; Hirose 1995). In my preliminary observations, the caudal fin of males was edged with an orange band (0.5–1.0 mm), and that of females and subadults with or without a faint orange band (<0.5 mm). To clarify the relationship between sexual state and social ranking of individual fish and their caudal fin colouration, 49 *A. perideraion* were randomly collected at the end of the study period. They were all of different social ranking (23 alpha-individuals, 31–82 mm standard length (SL); 14 beta-individuals, 30–67 mm SL; 12 others, 32–56 mm SL) cohabiting

with ($n = 41$) or without *A. clarkii* ($n = 8$). Cohabiting groups were more abundant than conspecific groups in the present study site (Hattori 1995). The specimens were fixed and preserved in Bouin's solution, and each gonad was embedded in a paraffin block. Serial cross sections (6 or 8 μm thick) of two parts of a gonad were stained with haematoxylin and eosin, and examined under a microscope. Since the gonad structure of *A. perideraion* was basically identical to that of *A. clarkii*, terminology and categorization of gonads for *A. clarkii* (see Hattori & Yanagisawa 1991a; Hattori 1994) were used for *A. perideraion*.

Group structure and life-history pathways

In the beginning of the study period (June 1988), I captured all individuals larger than 20 mm SL and some smaller individuals, and marked them by injecting acrylic paint under the skin (Thresher & Gronell 1978). Their standard lengths were measured underwater to the nearest mm with an acrylic ruler (see Ochi 1986; Hattori 1991, 1994, 1995). To check their breeding condition and changes in their caudal fin colouration, I patrolled the study area every four days during the period from June to September 1988, in March 1989, and during the period from May to November 1989 (except one week in July, two weeks in August and two weeks in October). When I found an egg mass in the vicinity of sea anemones, I judged the largest two of the group to be breeders because smaller group members are always non-breeders in anemonefishes (Allen 1972; Fricke & Fricke 1977; Moyer & Nakazono 1978; Ross 1978a; Hattori 1994, 1995). Inter-host movement of *A. perideraion* was also recorded. At the end of each period, the number of recruits to each host was checked. I counted individuals smaller than 20 mm SL and regarded those as juveniles that had settled within the period; nearly all of them became larger than 20 mm SL within 6 months (12 of 14 fish).

RESULTS

Sexual state, social ranking and caudal fin colouration

Four gonad phases were discriminated among sampled fish ($n = 49$): 'immature' ($n = 6$), 'preripe male' ($n = 28$), 'ripe male' ($n = 7$), and 'ripe female' ($n = 8$). Of eight individuals whose transparent caudal fin had orange bands, seven had ripe male phase gonads, and the remaining one, which had gained the coloration only a few days before collection, had preripe male phase gonads. Of the other 41 individuals that had transparent caudal fins with ($n = 30$) or without

Table 1. Standard lengths (mm) of female, male and subadult *Amphiprion perideraion* in groups with or without *Amphiprion clarkii*

Sexual state	Group without <i>Amphiprion clarkii</i>				Group with <i>Amphiprion clarkii</i>				Mann-Whitney <i>U</i> -test
	<i>n</i>	Mean	SD	Range	<i>n</i>	Mean	SD	Range	
Female	44 (37)	66.7 (67.4)	7.4 (7.0)	51–82 (57–82)	7	48.6	3.0	44–53	<i>P</i> < 0.001
Male	45 (37)	51.1 (51.7)	8.2 (7.7)	33–67 (39–67)	7	39.6	5.6	30–49	<i>P</i> < 0.01
Subadult	55	37.7	8.4	21–56	101	31.4	7.0	21–47	<i>P</i> < 0.001

Data for breeders are given in parentheses.

(*n* = 11) faint orange bands, none had ripe male phase gonads. These results confirmed that fish with transparent caudal fins bordered by orange bands were all males. All alpha-individuals that cohabited with males (*n* = 8) had ripe female phase gonads, and the other 33 individuals had preripe male phase gonads (*n* = 27) or immature phase gonads (*n* = 6). These results indicate that alpha-individuals cohabiting with males were all females and the other fish were subadults or juveniles.

Group structure in relation to individual sexual state

Four group types were distinguished.

1. Adult pair groups (*n* = 47) consisting of one adult pair and a varying number of subadults (range = 0–5, mode = 0 and 1, \bar{x} = 0.96 ± 1.1 SD) and juveniles.
2. One-adult groups (*n* = 5) consisting of one adult male (*n* = 3) or female (*n* = 2), and a varying number of subadults (range = 0–2, mode = 0) and juveniles.
3. Subadult groups (*n* = 73) consisting of one (*n* = 54) or two (*n* = 19) subadults and juveniles.
4. Juvenile groups (*n* = 15).

The group size of adult groups (adult pair groups and one-adult groups were combined, \bar{x} = 3.06 ± 1.34 SD, *n* = 52) was significantly larger than that of other groups (subadult and juvenile groups combined, \bar{x} = 1.43 ± 0.77 SD, *n* = 88, Mann-Whitney *U*-test, *z* = 7.68, *P* < 0.0001). There were relatively few one-adult groups. The ratio of one-adult groups to all adult groups was only 0.096. All of the one-adult groups resulted from disappearance of one adult from adult pair groups. Most of the adult groups (94.4%) did not cohabit with *A. clarkii*, whereas all subadult and juvenile groups did so. Reproductive activities were observed in most (88.1%) of the adult pair groups without *A. clarkii*, but adult pair groups without *A. clarkii* (*n* = 42) were rarer than other groups (*n* = 98). Adult pairs with *A. clarkii* never reproduced (*n* = 3), but two females cohabiting with *A. clarkii* had ripe female phase gonads and two males had ripe male phase gonads. In two heterospecific groups, all members (adult pairs in

Table 2. Inter-group movement and change in size order in a new group in the 1.5-year study period

Sexual state	Total		Final size order		
	number of marked fish	Number of fish moved	higher	same	lower
Female	48	1	0	1	0
Male	55	2	0	1	1
Subadult	145	13	8	0	5
Total	248	16	8	2	6

these cases) of *A. clarkii* disappeared or emigrated and, consequently, adult pairs of *A. perideraion* obtained hosts without *A. clarkii*, although these pairs had not spawned by the end of the study period. Males and females cohabiting with *A. clarkii* were significantly smaller than those without *A. clarkii* (Table 1).

There were no significant differences in the numbers of juveniles per group between adult groups (\bar{x} = 0.26 ± 0.52 SD, *n* = 52) and subadult groups (\bar{x} = 0.36 ± 0.67 SD, *n* = 73, Mann-Whitney *U*-test, *z* = 0.70, *P* > 0.05). The number of juveniles per group in a host larger than the smallest host size (400 cm²), and unoccupied by conspecific adults and subadults (\bar{x} = 0.35 ± 0.57 SD, *n* = 48), did not differ significantly from that in a host occupied by adult groups or subadult groups (see above, Kruskal-Wallis test, d.f. = 2, *H* = 1.01, *P* = 0.604).

The sizes of host sea anemones occupied by adult groups (\bar{x} = 1173 cm² ± 474 SD, *n* = 36), by subadult groups (\bar{x} = 938 cm² ± 349 SD, *n* = 48), and by juvenile groups (\bar{x} = 779 cm² ± 300 SD, *n* = 13) differed significantly (Kruskal-Wallis test, d.f. = 2; *H* = 9.57, *P* = 0.0083).

Both adults and subadults rarely moved between groups (Table 2), and the ratio of migrants to all individuals did not differ significantly between subadults and adults (Fisher's exact test, *P* > 0.05). Most (81.3%) of the migrations were restricted within small patch reefs where host sea anemones abounded (see Hattori 1995). Among subadult migrants (*n* = 13), six emigrated from groups without *A. clarkii* and seven from groups with *A. clarkii*. The former individuals all advanced in size ranking after movement, whereas some of the latter lowered their ranking (Table 2).

Life-history pathways

Fourteen individuals changed their sexual state (Table 3). Four subadults, that were larger than the average body size of subadults (see Table 1), became female when they were alpha-individuals cohabiting with a smaller conspecific in subadult groups (i.e. groups containing *A. clarkii*). Seven subadults, which were larger than the average size of subadults except one fish (see Table 1), changed to male when they were beta-individuals: four in subadult groups and three in one-adult groups (i.e. groups without *A. clarkii*). The ratio of subadults that became adults to all subadults did not differ significantly between groups with and without *A. clarkii* (8/90 vs 3/55, Fisher's exact test, $P > 0.679$). Solitary subadults ($N = 43$) never became male or female.

Two widowed males (alpha-individuals) in adult groups changed sex to female (Table 3): one was solitary and the other cohabited with a subadult. The latter subsequently spawned with the male who had been subadult. One breeding male, whose host disappeared, changed into a subadult after moving to a new group where it became a gamma-individual. Histological examination showed that this individual had a preripectoral phase gonad. Females never changed sex. Thus, four life-history pathways were detected in *A. perideraion*: (i) from subadult to female ($n = 4$), (ii) from subadult to male ($n = 7$), (iii) from male to female ($n = 2$), and (iv) from male to subadult ($n = 1$).

DISCUSSION

Four group types were found in *A. perideraion*, as in *A. clarkii* (Hattori 1994). Unlike *A. clarkii*, however, all groups of *A. perideraion* used only host sea anemones larger than 400 cm² (Hattori 1995). In anemonefishes, only alpha- and beta-individuals that occupy a large host can reproduce and suppress the growth and reproduction of other members in a group (Fricke & Fricke 1977; Moyer & Nakazono 1978; Ross 1978b; Fricke 1983; Hattori 1991, 1994). In the present study site,

subadult and juvenile *A. clarkii* often move between hosts and utilize small hosts as temporary places to escape from social or growth suppression by dominant adults (Hattori 1994; see also Ochi 1989b; Hattori & Yanagisawa 1991a, b). After subadult *A. clarkii* immigrate into large hosts without adults, they become female forming one-adult groups (Hattori 1994). In contrast, *A. perideraion* rarely moved between hosts except in small patch reefs where host anemones abounded, and the frequency of movement of subadults was as low as that of adults. Furthermore, all one-adult groups resulted from disappearance of one adult from adult pair groups and, consequently, the ratio of one-adult groups to all adult groups (0.096) was much lower than that in *A. clarkii* (0.226) at the present study site (see Hattori 1994). Probably because of low mobility (Hirose 1995) and low host density, subadult and juvenile *A. perideraion* cannot utilize small hosts as temporary places to escape from growth suppression by larger fish.

Adult pairs of *A. perideraion* never reproduced in the presence of *A. clarkii*, and subadult and juvenile groups of *A. perideraion* always cohabited with *A. clarkii*. However, *A. perideraion* in heterospecific groups seem to have an opportunity for the future reproduction because of high mobility of the larger congener: *A. clarkii* have wide home ranges, often using two or more hosts, and sometimes move between groups (Hattori 1994, 1995; Hirose 1995). Since subadult and juvenile *A. clarkii* tend to use small hosts, large hosts are often occupied by only adult *A. clarkii* (Hattori 1994). Actually, some adult pairs of *A. perideraion* obtained hosts without *A. clarkii* just after adult pairs of *A. clarkii* disappeared or emigrated. Although *A. clarkii* suppressed the growth and reproduction of *A. perideraion* (Hattori 1995), *A. perideraion* matured histologically in heterospecific groups: adult *A. perideraion* cohabiting with *A. clarkii* had ripe male or female phase gonads. This suggests that adult pairs in cohabiting groups prepared for reproduction before the disappearance or emigration of *A. clarkii*.

In monogamous anemonefishes, sex change from male to female allows the larger member of a mated

Table 3. Social ranking and change of individual sexual state in a group during the 1.5-year study period

Social ranking	Sexual state	Number of marked fish	Change of sexual state	Number of fish changed
Alpha	female	51	no change	
	male	2	to female	2 (39, 49)
	subadult	72	to female	4 (42, 44, 45, 47)
Beta	male	49	no change	
	subadult	20	to male	7 (30, 33, 36, 38, 39, 47, 47)
Lower than beta	male	1	to subadult	1 (49)
	subadult	53	no change	
Total		248		14

Standard lengths (mm) of fish that changed sexual state are given in parentheses.

pair to be a female, consequently assuring the pair's high fecundity (Fricke & Fricke 1977; Moyer & Nakazono 1978; Ross 1978b; Fricke 1979; Ochi 1989a; Hattori 1991, 1994). In some anemonefishes, *A. clarkii* and *Amphiprion frenatus* (Brevoort), some non-breeders become female without passing through a functional male state when the opportunity arises (Ochi 1989a, b; Hattori & Yanagisawa 1991a; Hattori 1991, 1994). The present study confirmed that the largest subadult *A. perideraion* in a subadult group became female directly when cohabiting with a smaller conspecific. The sexual lability of non-breeders is suggested to facilitate adult pair formation under conditions of restricted mobility (Ghiselin 1969; Fricke & Fricke 1977; Lassig 1977; Hattori 1991) or under conditions of breeding space shortage (Ochi 1989b; Hattori & Yanagisawa 1991a; Hattori 1994; Hattori & Yamamura 1995). The present study indicates that mobility of *A. perideraion* is restricted, as mentioned earlier (see also Hirose 1995; Hattori 1995). Since reproduction occurred only in adult pair groups without *A. clarkii*, and such groups ($n = 44$) were much rarer than other groups ($n = 96$), there may be a shortage of breeding space at the present study site. After an adult disappeared from an adult pair group without *A. clarkii*, the largest subadult became male and mated with the widowed female or a new female that had been male. In subadult groups (i.e. cohabiting with *A. clarkii*), the largest subadults became female and paired with males that had been subadult; but solitary subadults never became male or female. This suggests that the sexual lability of *A. perideraion* both in heterospecific groups and conspecific groups has a functional significance in the ready formation of an adult pair. Since the ratio of subadults that became adults to all subadults did not differ significantly between groups with and without *A. clarkii*, alpha- and beta-individuals in cohabiting groups may not be less successful than gamma- and delta-individuals in conspecific groups in becoming members of breeding pairs.

Habitat selection by presettling larvae is often important for determining the group structure and distribution patterns of coral reef fishes (Sweetman 1983, 1985; Jones 1991; Williams 1991; Booth & Wellington 1998). Juvenile *A. perideraion* avoided settling on small hosts, suggesting that they are capable of habitat selection. However, they settled on hosts occupied by *A. clarkii* as well as on hosts occupied by conspecifics (Hattori 1995). In anemonefishes living in isolated groups, a juvenile with higher social ranking among other juveniles can become subadult quickly, and a subadult with higher ranking among other subadults has an earlier opportunity to be a breeder (Allen 1972; Ochi 1985, 1989b; Hattori 1991, 1994). At the present study site, juveniles sometimes formed juvenile groups and subsequently became subadult groups. The group size of juvenile and subadult groups (cohabiting groups) was

significantly smaller than that of adult groups, indicating that juveniles and subadults cohabiting with *A. clarkii* had higher social rankings among conspecific individuals than those in adult groups. Since subadults in subadult groups were smaller than subadults in adult groups, juveniles in cohabiting groups may be able to change their sexual state at smaller size because of their higher rankings. Probably, some juveniles are aiming at higher rankings among the conspecific individuals when settling, even in the presence of the congener. However, there was no significant difference in the number of juveniles among hosts occupied by adult groups and subadult groups, and other hosts larger than 400 cm². More information on the settlement of juveniles is necessary to clarify their individual life-history strategies.

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