

Inter-group Movement and Mate Acquisition Tactics of the Protandrous Anemonefish, *Amphiprion clarkii*, on a Coral Reef, Okinawa

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(Received February 14, 1994; in revised form May 27, 1994; accepted May 28, 1994)

Abstract Sexual pattern, group structure and inter-group movement of the anemonefish, *Amphiprion clarkii*, were investigated on a coral reef at Sesoko Island, Okinawa, where host sea anemones were sparsely distributed. An adult group usually consisted of an adult pair, and a varying number of subadults and juveniles. Adults rarely moved between groups because they already occupied large host sea anemones, which were requisite to reproduction. If a female disappeared from a group, the male usually changed sex and a subadult became male. Subadults often moved between groups if it resulted in higher size order. There existed subadult groups, each of which consisted of one or two subadults and a varying number of juveniles. The largest and the second largest subadults in a group became female and male respectively if they occupied large hosts without adults. Subadults never became adults in the presence of adult pairs. It was concluded that labile sexuality of subadult *A. clarkii* is maintained as a mate acquisition tactic irrespective of host density even under the conditions where the habitat is saturated with breeders.

Anemonefishes (Pomacentridae: *Amphiprion*) are protandrous and have a symbiotic relationship with sea anemones (Allen, 1972; Fricke and Fricke, 1977; Moyer and Nakazono, 1978; Ross, 1978a; Fricke, 1979). Most inhabit coral reefs, where host anemones are usually scanty and scattered (Allen, 1972). Their protandry has been regarded as an adaptation to extreme difficulty in movement between hosts because of the unpredictable distribution and low population density of sea anemones (Fricke and Fricke, 1977; Fricke, 1979; Charnov, 1982; Warner, 1984). *Amphiprion* live in a social group, usually composed of a breeding pair and a varying number of nonbreeders. If a female disappears from a group, the remaining male changes sex and a nonbreeder becomes a male (Fricke and Fricke, 1977; Moyer and Nakazono, 1978; Ross, 1978a; Fricke, 1979; Hattori, 1991).

On temperate rocky reefs where host anemones abound, *A. clarkii* have a more complex social structure and sexual pattern (Moyer, 1980; Ochi, 1986, 1989a, b; Hattori and Yanagisawa, 1991a, b). For example, territories of breeding pairs are almost contiguous with each other and nonbreeders have home ranges only on the outskirts of territories. After a

female disappears from a pair, the remaining male usually re-pairs with a neighboring female. Alternatively, some nonbreeders become female without passing through a functional male state. These features have been attributed to the high host density which enables anemonefish to move between hosts (Moyer, 1980; Ochi, 1986, 1989a, b; Hattori and Yanagisawa, 1991a, b), although little is known about patterns of host distributions and the influence of inter-group movement on sexual patterns in coral reefs (see Moyer, 1976; Moyer and Nakazono, 1978).

This paper indicates that, even in a habitat of low host density, nonbreeders move between hosts to acquire mates, and some of them become females without passing through a functional male state. Social structure and sexual pattern of *A. clarkii* at a coral reef are compared with those from a temperate rocky reef.

Materials and Methods

I conducted field research on a fringing reef off of the Sesoko Marine Science Center, University of the Ryukyus at Sesoko Island (26°39'N; 127°57'E),

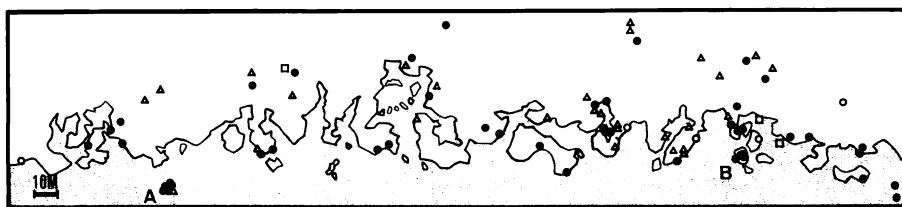


Fig. 1. Distribution of host sea anemones inhabited by *Amphiprion clarkii*. Lines indicate the reef edge or patch reefs, the offshore sandy bottom is shaded. A and B indicate patch reefs. Open circles, triangles and squares indicate large ($>400\text{ cm}^2$) and small *Radianthus kuekenthali*, and *R. simplex*, respectively. Solid marks indicate hosts occupied by adult groups.

Okinawa, Japan. A map of an $87\text{ m} \times 373\text{ m}$ study area was drawn based on an aerial photograph and underwater observations (Fig. 1). Locations of host sea anemones, *Radianthus kuekenthali* and *R. simplex* which *Amphiprion clarkii* inhabited, were plotted on the map. The long and short axial lengths of the hosts were measured twice in August, 1988 and twice in August, 1989. The area that a sea anemone covered (including spread tentacles) was calculated as $(\text{long axial length}) \times (\text{short axial length}) \times \pi/4$, and the larger value of the 2 measurements in each period was used as an index of its size.

Field observations on *A. clarkii* were conducted in three six-month periods. Periods were from June to November, 1988 (Period I), from December, 1988 to May, 1989 (Period II) and from June to November, 1989 (Period III). All individuals of *A. clarkii* larger than about 20 mm in standard length (SL) were captured with hand nets and marked by injecting acrylic paint under the skin (see Thresher and Gronell, 1978). Standard lengths were measured nearest mm and caudal fin coloration was recorded at the end of each period.

Swimming tracks of each individual larger than 50 mm SL were recorded for 15 min at least once in Period I. The outline of the tracks was regarded as the border of the home range (see Ochi, 1986). Individuals with overlapping home ranges were regarded as constituting a social group, and were called α -individuals, β -individuals, γ -individuals, and so on, according to body size order. When an egg mass was found near the host sea anemone, α - and β -individuals of the group were called breeders. A breeder was defined as fish which had an experience of reproduction.

To investigate the presence of an egg mass in the vicinity of sea anemones, I patrolled the study area every four days during June and September, 1988, in

March and during May and November (except one week in July, two weeks in August and two weeks in October), 1989. At the same time, changes of the coloration in the caudal fin and inter-group movements were also recorded. The date when such a change or movement was confirmed was regarded, for convenience, as the day of its occurrence.

To investigate the relationship between color phases in the caudal fin (Moyer, 1976; Moyer and Nakazono, 1978) and gonad structure, 36 *A. clarkii* were collected in November, 1989. Specimens were fixed and preserved in Bouin's solution. The gonads of fish larger than 30 mm SL and the whole body of fish smaller than 30 mm SL were embedded in paraffin blocks. Serial cross sections (6 or $8\ \mu\text{m}$ thick) of two parts of a gonad or those of the whole body were stained with haematoxylin and eosin and examined by light microscopy.

Results

Color and gonad phases of the anemonefish

Five color phases were discriminated in the caudal fin: (1) phase I, transparent fin with or without a white spot; (2) phase II, transparent fin with narrow ($<1\text{ mm}$) orange border; (3) phase III, transparent fin with wide (2–3 mm) orange border; (4) phase IV, transparent fin with basally orange border; and, (5) phase V, white fin (see Moyer, 1976; Hattori and Yanagisawa, 1991a).

Six sexual phases were distinguished in the gonad structure, which were also seen in a temperate population of the anemonefish (see Hattori and Yanagisawa, 1991a): immature, pre-ripe male, ripe male, transitional, pre-ripe female and ripe female phases. Relationships between color and sexual phases are

given in Table 1.

Of 11 color phase I fish, 7 (63.6%, 28–44 mm SL) had immature phase gonads and the others had all pre-ripe male phase gonads (31–44 mm SL). Of 12 color phase II fish, 10 (83.3%, 55–87 mm SL) had pre-ripe male and the others had all immature phase gonads (64 and 76 mm SL). Color phase III fish (85 and 98 mm SL) had all ripe male phase gonads. A color phase IV fish (91 mm SL), which had been collected 44 d after the disappearance of its mate, had a transitional phase gonad. Color phase V was included in 4 gonad phases. However, most of the color phase fish (8/10=80%, 76–105 mm SL) had ripe or pre-ripe female phase gonads, and only 2 individuals had transitional phase (71 mm SL) or immature phase gonads (74 mm SL). Thus, color phases of individuals approximately reflected developmental stages of their gonads (Table 1). Accordingly, individuals of color phases I–V observed in the field were regarded as juveniles, subadults, males, females and sex-changing fish, respectively. Some discordances between the color phases and the gonad phases may be explained by a small time-lag between the change of coloration and that of gonadal conditions (see Hattori and Yanagisawa, 1991a).

Body sizes (mm SL) of juveniles, subadults, males, females averaged $37.6 \text{ mm} \pm 10.5 \text{ SD}$ (range=20–67 mm, $n=212$, the total number counted at the end of each study period), $68.6 \text{ mm} \pm 9.2 \text{ SD}$ (range=50–86 mm, $n=59$), $89.9 \text{ mm} \pm 8.0 \text{ SD}$ (range=71–111 mm, $n=65$) and $98.3 \text{ mm} \pm 10.7 \text{ SD}$ (range=71–118 mm, $n=84$), respectively. These differed significantly from one another (Mann-Whitney U-test of all pairwise combinations, $z > 5.5$, $p < 0.0001$). Sex changing fish were observed on only 4 occasions ($\bar{x} =$

$95.5 \text{ mm SL} \pm 5.4 \text{ SD}$, range=91–103 mm).

Of 154 individuals observed for more than 2 months, 38 changed their coloration once, 3 twice and the others did not (Table 2). Juveniles changed into subadults, or females when they were α -individuals in each group. Subadults changed to female and male when they were α - and β -individuals, respectively. Four widowed males (α -individuals) changed sex to female. No females changed color.

Group composition and reproduction

Host sea anemones of *Amphiprion clarkii* were sparsely distributed (Fig. 1). The number of host anemones averaged 73.5 (63 in 1988 and 84 in 1989); during the study period 2 disappeared and 23 were recruited. The average host density during the 2 years was 0.23 per 100 m², and the average distance between the nearest neighbors in 1989 was $5.1 \text{ m} \pm 4.8 \text{ SD}$ (range=0.4–29.3 m, $n=84$). Except for 4 *Radianthus simplex*, which were all smaller than 290 cm², all host anemones were *R. kuekenthali*. The size of host sea anemones averaged $583 \text{ cm}^2 \pm 402 \text{ SD}$ (range=22–1728 cm², $n=147$).

The average number of social groups of *A. clarkii* was 59 (50 in 1988 and 68 in 1989). Home ranges of these groups were isolated from each other except for 2 groups on patch reef B, which was densely inhabited by sea anemones (Fig. 1). The average distance between the nearest neighbors (represented as the nearest host distance between two groups) in 1989 was $7.0 \text{ m} \pm 5.6 \text{ SD}$ (range=1.3–29.3 m, $n=65$). A group used 1 to 4 host anemones ($\bar{x} = 1.2 \pm 0.54 \text{ SD}$, $n=181$), and group size varied from 1 to 10 individuals ($\bar{x} = 3.0 \pm 2.0 \text{ SD}$). Home range size of an α -individual, which covered home ranges of low-

Table 1. Correspondence between color phases and gonad phases. The number of reproductive fish is in parentheses

Gonad phase	Color phase*				
	I	II	III	IV	V
Immature	7	2			1
Pre-ripe male	4	10			
Ripe male			2 (2)		
Transitional				1	1
Pre-ripe female					1
Ripe female I					6 (2)
Ripe female II					1
Total	11	12	2	1	10

* See text for explanation of I to V.

Table 2. Change in life state of an individual in the 1.5-year study period and its size order in a group when the change was confirmed

Change in life state	Number of fish	Size order in a group*			
		α	β	γ	δ
J→S	23	6	7	9	1
J→F	3	3	0	0	0
S→M	8	0	8	0	0
S→F	6	6	0	0	0
M→F	4	4	0	0	0

J = juvenile, S = subadult, M = male, F = female; * See text for explanation of α , β , γ and δ .

er-ranking individuals, averaged $5.5 \text{ m}^2 \pm 6.0 \text{ SD}$ ($n=86$).

Four group types were distinguished: (1) adult pair group ($n=65$, the total number counted at the end of each study period), which consisted of one adult pair and a varying number of subadults and juveniles; (2) one-adult group ($n=19$), which consisted of one adult, usually a female ($n=18$) or sex changing fish ($n=1$), and a varying number of subadults and juveniles; (3) subadult group ($n=15$), which consisted of 1 ($n=12$) or 2 subadults ($n=3$), and a varying number of juveniles; and, (4) juvenile group ($n=82$), which consisted of only juveniles.

Most (89.2%) adult pair groups reproduced during the study period. Body sizes of males (range = 68–111 mm SL) and females (range = 82–118 mm SL) in a breeding pair were positively correlated ($r=0.75$, $p<0.01$, $n=58$). A-individuals of one-adult groups were significantly smaller than those of adult pair groups ($\bar{x}=87.7 \text{ mm SL} \pm 13.2 \text{ SD}$, $n=19$, and $101.3 \text{ mm} \pm 7.8$, $n=64$, respectively; Mann-Whitney U-test, $z=3.3$, $p=0.0007$). The number of subadults per group did not differ significantly between one-adult group ($0.8 \pm 0.7 \text{ SD}$) and adult pair group ($0.4 \pm 0.6 \text{ SD}$; Mann-Whitney U-test, $z=1.95$, $p=0.051$).

One-adult and adult pair groups occupied 1 to 4 host anemones ($\bar{x}=1.45 \pm 0.70 \text{ SD}$, $n=84$), while juvenile and subadult groups usually used only one host ($\bar{x}=1.04 \pm 0.19 \text{ SD}$, range = 1–2, $n=97$; Mann-Whitney U-test, $z=3.56$, $p=0.0004$). The former groups occupied large hosts ($\bar{x}=826 \text{ cm}^2 \pm 353 \text{ SD}$, $n=81$), while the latter groups occupied small ones ($\bar{x}=286 \text{ cm}^2 \pm 220 \text{ SD}$, $n=66$; Mann-Whitney U-test, $z=8.48$, $p<0.0001$). Breeding of *A. clarkii* occurred only on hosts larger than 415 cm^2 . Most of large hosts (97.6% of hosts larger than 800 cm^2 and 80.0% of hosts larger than 400 cm^2) were occupied by adults, and all subadults and juveniles which later became adults (Table 2) occupied hosts larger than 415 cm^2 .

Formation of new pairs after disappearance of mates

When one or both adults disappeared in an adult pair group, a new pair was formed as follows:

Disappearance of a female was observed on 5 occasions. In one case, the widowed male later paired with a female which immigrated from an one-adult group (50 m apart) 12 d after the disappearance. In the remaining four cases, the widowed males changed sex; it took $55.8 \text{ d} \pm 19.3 \text{ SD}$ to

change the color phase. Two of the sex changers later bred with a subadult which had stayed in the same group or which had immigrated from a subadult group (19 m apart) 4 d after the disappearance. Another widowed male had already cohabited with a subadult before the female disappeared, but disappeared after the completion of the sex change. The other sex changer lived solitarily until the end of the study period (218 d) and had ripe female phase gonads. The group where the sex changer lived was exceptionally isolated from other groups (the distance between the nearest neighbors was 29.3 m).

Disappearance of a male was observed on 3 occasions. After a male disappeared from a group in the patch reef B, the remaining female paired tentatively with a male which immigrated within 4 d from a neighboring adult group. He often moved between the two groups for at least 90 d but finally settled in the new group: the new mate was larger than the old mate (110 mm SL vs. 93 mm SL). After the male settled in the new group, one subadult in the previous group became male. In another case, after disappearance of a male, a subadult visited the widowed female within 20 d from a subadult group (19 m apart). This fish often moved between the two groups for 44 d and finally became male in the new group. In the third case, after disappearance of a male, the widowed female cohabited with a small subadult but without a male until the end of the study period (52 d).

Both male and female disappeared simultaneously on 2 occasions. In both cases, a neighboring pair (5 m and 15 m apart) immigrated into the vacant site within 8 and 38 d, respectively: the new hosts were larger than the old hosts (491 cm^2 vs. 1084 cm^2 ; 683 cm^2 vs. 1296 cm^2). In the group from which the pair had left, the large vacant host disappeared 20 d after the emigration. In the other group from which a pair had emigrated, the remaining subadults did not change color until the end of the study period (206 d).

Fish movement between groups and mate acquisition by subadults

Thirty-three individuals moved between groups; 13 of them moved twice or more. The average distance of the movements was $19.5 \text{ m} \pm 22.9 \text{ SD}$ ($n=71$, max = 166 m). Adults rarely moved between groups (Table 3). Adult immigrants ($n=6$) did not change their size order (Table 3): after movement,

two adult pairs acquired larger hosts, one male acquired a larger female (but a smaller host) and one female in a one-adult group paired with a male. Subadults moved more frequently than adults (Fisher's exact probability test, subadults vs. females, $p = 0.003$; subadults vs. males, $p = 0.011$). Among α -individuals of subadult groups ($n = 15$), six moved between groups: three became β -individuals in one-adult groups and the other three became α -individuals in other subadult groups. Among γ -subadults in adult pair groups ($n = 24$), three became β -individuals in one-adult groups and two became α -individuals in subadult groups after movement. Subadults of β -individuals in one-adult groups ($n = 18$) never moved. Inter-group movement of juveniles was rarer than that of subadults (Chi-square test, $\chi^2 = 7.37$, $p < 0.01$, Table 3), and most of them (75.0%) gained the same or higher size order in new groups after movement (Table 3).

All of the 8 subadults that later became males (Table 2) acquired mates after movement ($n = 3$) or not ($n = 5$). Among 6 subadults which later became females, one acquired a mate without movement, but 5 did not acquire mates. Among the latter 5 fish, 2 lived solitarily, and the others lived with a subadult in each group. Among 3 juveniles which became females, one acquired a mate without movement, but 2 did not acquire a mate. The latter 2 lived together with a subadult and with a small juvenile, respectively.

Discussion

Anemonefishes in coral reefs where host density is low have been reported to rarely move between groups (Allen, 1972; Fricke and Fricke, 1977; Moyer and Nakazono, 1978; Ross, 1978a, b; Fricke, 1979). For example, *Amphiprion frenatus* formed a small group at an isolated sea anemone, and group members rarely interchanged (Hattori, 1991). However,

A. clarkii in the present study site, particularly subadults, frequently moved between groups, although density of host anemones available for *A. clarkii* (0.23 host per 100 m²) was similar to that for *A. frenatus* (0.17 host per 100 m²). Several authors suggested that *A. clarkii* is less dependent upon host sea anemones and relatively unspecialized with regards to host anemone preferences compared with other anemonefishes (Allen, 1972; Moyer and Nakazono, 1978; Miyagawa, 1989). These features may be related to the mobility of *A. clarkii*.

On a temperate rocky reef where host sea anemones abounded (5.7 per 100 m², Hattori and Yanagisawa, 1991a), *A. clarkii* adults moved between hosts and sometimes showed temporal bigamy and a breeder was sometimes displaced by an intruder of the same sex (Ochi, 1989a; Hattori and Yanagisawa, 1991a, b). Consequently, adults usually got larger mates in new territories after movement. At my study site, adult *A. clarkii* rarely moved between groups and displacement of a breeder was never observed. Temporal bigamy was observed only on a patch reef densely populated by host anemones. Differences in adult behavior between the two sites can be attributed to a large difference in host density between these sites. Because of the cost of movement, migration in a habitat of low host density may not pay adults that occupy large hosts requisite to reproduction.

Protandry in anemonefishes has been regarded as an adaptation to the ecological conditions of extreme difficulty in inter-host movement (Fricke and Fricke, 1977; Moyer and Nakazono, 1978; Ross, 1978a, b; Fricke, 1979). Under such conditions, ability to change sex may increase the possibility of reconstituting a breeding pair within the group after one breeder disappears. In *A. clarkii* at my study site, after a female disappeared from an adult pair group the remaining male usually changed sex and a cohabiting subadult became male. Even widowed males living without subadults changed sex. Since sub-

Table 3. Inter-group movement and change in size order of a new group. Data of three periods are combined

Sex determined by color phase	Total no. of fish	No. of fish moved	Frequency of movements	Final size order		
				Higher	Same	Lower
Female	84	3	3	0	3	0
Male	65	3	7	0	3	0
Subadult	57	11	30	5	3	3
Juvenile	219	16	31	8	4	4

adults often moved between groups while females rarely did, sex change in *A. clarkii* is a good option for widowed males on low-host density reefs. In *A. clarkii* on temperate rocky reefs where adults moved between hosts, widowed males rarely changed sex and usually re-paired with neighboring females (Ochi, 1989a; Hattori and Yanagisawa, 1991a, b). These findings support the hypothesis that sex change in anemonefishes is a mate acquisition tactic of widowed males.

Subadults of *A. clarkii* did not always mature first as males at my study site, as has been reported for this species on a temperate rocky reef (Hattori and Yanagisawa, 1991a, b). Rather, females changed sex from males or were derived from subadults or juveniles (= non-sex changers). Hattori and Yanagisawa (1991a) suggested that different life-history pathways in *A. clarkii* resulted from the difference in the timing of femininity differentiation in the hermaphroditic gonads (FDHG, for definition see Hattori and Yanagisawa, 1991a). In a temperate population, the larger member of a pair which occupied large hosts became female without passing through a functional male state. At the present study, the largest fish (>71 mm SL) in a group which occupied a large host became female. Since anemonefishes are monogamous, the conditional strategy that the larger member of a pair becomes female accords high fecundity to a pair irrespective of host density.

In many sequentially hermaphroditic fishes, subadults may be able to become either males or females. Several authors suggested that this labile sexuality of nonbreeders has a functional significance in the easy formation of a breeding pair under the ecological restriction of mobility (Ghiselin, 1969; Fricke and Fricke, 1977; Lassig, 1977). In *A. clarkii*, however, nonbreeders, though showing labile sexuality, frequently moved between hosts (Ochi, 1989b; Hattori and Yanagisawa, 1991a, b). At my study site, subadults moved between groups to get higher size order. When subadults occupied large hosts without adults, the largest and the second largest in a group became female and male, respectively. Under the conditions of shortage of breeding space, labile sexuality of an unmated individual may be more advantageous for acquisition of breeding sites and mates than genetically fixed sexuality, since it is unpredictable whether a vacant breeding space available for a subadult is for male or for female. At my study site, adult groups usually occupied almost all large hosts while others occupied small ones, suggest-

ing that suitable sites for breeding seemed to be saturated with adult fish. Ochi (1989b) also suggested that labile sexuality is maintained in *A. clarkii* in a temperate population as a way of acquiring a breeding space promptly in a habitat where breeding space is saturated with breeders. The present study indicates that the advantage of labile sexuality in subadult *A. clarkii* may be independent of host density.

Acknowledgments

I am grateful to Y. Yanagisawa, T. Kuwamura and H. Ochi for their critical reading of the manuscript and S. Yamagishi, E. Urano, M. Kohda for their comments on an earlier draft. I also thank K. Koike and E. Yoshioka for their valuable advice on gonad histology. I also wish to thank K. Yamazato and K. Sakai and other members of Sesoko Marine Science Center, University of the Ryukyus and H. Tsukuda and H. Numata, Laboratory of Animal Physiology, Osaka City University for providing facilities during the investigation.

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サンゴ礁におけるクマノミのグループ間移動と配偶者の獲得戦術

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雄性先熟魚であるクマノミのグループ構造と、個体のグループ間移動および雌雄性を、沖縄県瀬底島の裾礁において1988年6月から1989年11月まで観察した。87m×373mの調査域に、約60のグループがまばらに分布し、成魚のグループは大型のイソギンチャクを所有していた。成魚のグループ(約20)は一組の繁殖ペアと2-3個体の未成魚・幼魚から構成されていた。この他、未成魚と幼魚あるいは幼魚だけからなるグループも多数見られた。サンゴ礁のクマノミはグループ間をほとんど移動しないと信じられてきたが、今回71例ものグループ間の移動が観察された。移動個体のほとんどは未成魚であり、未成魚は成魚ペアの存在下では繁殖できないので、単独の成魚や他の未成魚とペアを形成するために移動したと考えられる。大型のイソギンチャクで未成魚同士がペアを形成した場合、大きい方が雌になり、小さい方が雄になった。このような未成魚の雌雄同体性は、繁殖場所が不足している状況では、繁殖をなるべく早く開始できる点と、ペア当りの一回の産卵数を多くできる点で個体にとって有利であると推察された。さらにこの有利性はイソギンチャクの密度とは無関係であることも示唆された。

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