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Female defense polygyny in territorial triggerfish *Sufflamen chrysopterum*

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Abstract The occurrence of polygyny requires specific environmental conditions such as female aggregation or patchy resource distribution. However, it is difficult to determine the factors responsible for polygyny in species wherein the territories of both sexes overlap. To overcome this, we performed female removal experiments in the polygynous triggerfish *Sufflamen chrysopterum* (Balistidae) in the Okinawa coral reef. Both sexes defended their territories exclusively against consexuals of the same species and female aggregation was absent. Each male territory included 1–3 female territories, and nonterritorial males were significantly smaller than territorial males. Further, the body size of territorial males positively correlated with that of the largest female in their territories, and larger males tended to mate with more females. The results of the female removal experiments (n = 10 females) indicated that females competed for better territories rather than larger mates. In contrast, males abandoned the territories once the females emigrated. These results strongly suggest that males defend females rather than sites and compete for larger and a greater number of females. Thus, in *S. chrysopterum*, female defense polygyny occurs in the absence of female aggregation.

Introduction

Polygyny is a common attribute throughout the animal kingdom, where a few dominant males monopolize mating and shunt subordinates from the breeding population (Emlen and Oring 1977; Davies 1991). Males may potentially achieve polygyny through various tactics. However, differentiating between the various tactics has remained difficult, particularly in species where both females and males show high levels of territoriality and resource defense. Understanding the factors driving polygyny is an important component of evolutionary theory.

It is considered that different kinds of polygyny require specific environmental conditions such as female aggregation or patchy distribution of resources (Emlen and Oring 1977). Female aggregation within a compact space enables a male to effectively monopolize the group and mate with all its females. Such female defense polygyny has been observed in various mammals (reviewed by Clutton-Brock 1989), some birds (Webster 1994), several insects (Heinze and Hölldobler 1993), and amphipods (Just 1988). Furthermore an uneven or patchy distribution of food, shelter or breeding sites enables a male to mate with multiple females by monopolizing a region abundant in those resources (Emlen and Oring 1977). Such resource defense polygyny has been observed in many birds (reviewed by Orians 1969; Davies 1991) and a few mammals (Downhower and Armitage 1971).

Many types of polygynous mating systems adopted by a variety of fish species have recently been documented (reviewed by Warner 1975, 1984; Kuwamura 1984; Turner 1993). For example, typical resource defense polygyny has been reported in wrasses (Warner 1987, 1990) and cichlids (Sato and Gashagaza 1997; Schradin and Lamprecht 2000, 2002). In these species, each male defends a territory such as a spawning site that has a patchy resource distribution and is visited by multiple females. However, in certain other fish species, the male and female territories overlap such that a male territory includes both females and the resources that attract them. In such cases, it is difficult to determine the factor—female defense or resource defense—responsible for polygyny (Kuwamura 1984, 1997). It has been reported that the males of the

angelfish *Centropyge* (Thresher 1982; Moyer 1987) and sand tilefish *Malacanthus plumieri* (Baird and Liley 1989) defend both resources and females. On the other hand, female defense polygyny has been reported in the rock beauty *Holacanthus tricolor* (Hourigan and Kelley 1985) and the sharpnose puffer *Canthigaster valentini* (Gladstone 1987). However, the female defense polygyny occurring in both these species is atypical in that it does not involve female aggregation. Gladstone (1987) conducted male and female removal experiments on *C. valentini* in its natural habitat and concluded that the factor responsible for polygyny in this species was the capability of males defends territorial females.

To determine the factor responsible for polygyny in fish species where the male and female territories overlap, we studied the halfmoon triggerfish *Sufflamen chrysopterum* (Balistidae), a commonly occurring species in coral reefs that exhibits female territoriality and polygyny (Ishihara and Kuwamura 1996). We conducted female removal experiments in the field to determine whether the polygyny occurring among this species is based on resource defense or female defense. In the case of female defense polygyny, we expected the males to abandon their territories in the absence of the females, whereas in the case of resource defense polygyny, we expected them to maintain their territories regardless of the presence or absence of females.

Materials and methods

Study species

Sufflamen chrysopterum inhabits the coral reefs in the Indo-West Pacific, including Southern Japan (Hayashi 1993). The males grow larger than the females, and the species exhibits sexual dichromatism—the lower head region and abdomen are deep purplish blue in males but brownish in females (Kawase and Nakazono 1994; Ishihara and Kuwamura 1996). Further, it has been confirmed that female-to-male sex change occurs in this species (Takamoto et al. 2003). *S. chrysopterum* mainly feeds on small benthic animals such as crustaceans (Kuwamura 1991) during the daytime. The mating system

is polygynous, wherein each male territory encompasses 1–3 female territories (Ishihara and Kuwamura 1996; Takamoto et al. 2003). Pair spawning occurs early in the morning within hollow spaces on the substrate, and females exclusively care for the eggs until they are hatched at dusk on the same day (Ishihara and Kuwamura 1996). In the study area, the reproductive season was from May to September.

Field observations

Observations were conducted while snorkeling and scuba diving along the fringing reef of Sesoko Island (26˚38´ N, 127˚52´ E), Okinawa, Southern Japan, from July to November 2000 and April to October 2001. The study area comprised a north zone (30 × 300 m in 2001) and south zone (80 × 80 m in 2000 and 140 × 80 m in 2001) and included reef flats, reef edges, and sandy floors at depths of 2–5 m below the mean sea level. We drew a map of the study area by tracing out an aerial photograph.

Prior to the observations conducted each year, most of the *S. chrysopterum* individuals within the study area were captured using screen and dip nets, and their standard length (SL) was measured to the nearest 1 mm. After measuring the SL, the fish were tagged with small pieces of colored plastic using a tag-gun (Japan Bano'k Co.) to facilitate temporary differentiation; further, one or two dorsal or anal fin rays were dissected to facilitate permanent differentiation among individuals (Goto 1985). If untagged or immigrant fish were noticed, they were captured and tagged, and their SL was measured. We distinguished between male and female fish by observing their reproductive behavior and body coloration. Individuals that exhibited deep purplish blue coloration in the lower head region and abdomen were regarded as males. The minimum SL of spawning females was 108 mm; therefore, individuals with the female coloration pattern and an SL of less than 108 mm were regarded as subadults, while those with an SL of more than 108 mm were regarded as females.

Based on observations conducted for approximately one week, the territory of each fish was determined as the area comprising its swimming routes and feeding sites. Since the male and female territories were continuously distributed (Ishihara and

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Kuwamura 1996), adjacent same-sex territories with an interstice of less than 5 m are referred to as neighboring territories in this study. Observations were conducted in the south study zone almost daily throughout the breeding season in order to record the location, swimming track, foraging sites of each individual, interactions between individuals, and the presence of egg clutches. We used the data obtained from observations of the whole study zone in 2001 to determine the population structure.

Removal experiments

We removed three and seven females from the south study zone in September 2000 and July 2001, respectively; they were removed early in the morning. Immediately after the removals, we began to observe the individuals in and around the vacant territories to record the migration into these vacant territories and the type of interaction between individuals, such as chasing. The observations were conducted once all the individuals stopped attempting to migrate or after four hours. In two cases in 2001, interactions between individuals continued for over four hours, and additional observations were conducted for two hours in the afternoon of the removal day and two hours on the following day. In one of these two cases, such interactions continued even after the following day and were recorded during the daily observations until the end of the breeding season.

Results

Population structure

In the study area in 2001, we recorded a total of 39 territorial males that included 1–3 female territories. The males were mainly distributed along the reef edges, and a few were observed around rocks or corals in the sandy area away from the reef edges (Fig. 1). Further, in 2001, ten males were found to be non-territorial, i.e., single. The single

males were significantly smaller than the territorial males (SL of single males, 130.3 mm ± 12.5 SD, $n = 10$; SL of territorial males, 144.6 mm ± 8.7 SD, $n = 39$; Mann-Whitney U test, $Z = 3.39$, $P < 0.001$). The males were larger than the females (SL of males, 141.7 mm ± 11.1 SD, $n = 49$; SL of females, 121.8 mm ± 6.3 SD, $n = 68$; Mann-Whitney U test, $Z = -7.52$, $P < 0.0001$). Both males and females exclusively defended their territories against consexuals of the same species. The body size of the territorial males positively correlated with that of the largest female in their territories (Spearman's rank correlation coefficient $r_s = 0.72$, $n = 39$, $P < 0.0001$ in 2001; Fig. 2a). Further, larger males tended to acquire a greater number of females in their territories ($r_s = 0.29$, $n = 39$, $P = 0.07$ in 2001; Fig. 2b), although the correlation was not significant at the 5% level. Including single males, larger males tended to acquire a greater number of females ($r_s = 0.53$, $n = 49$, $P < 0.001$ in 2001).

Removal experiments

A total of 15 vacant female territories were observed during the study period—ten vacant territories were formed due to the female removal experiments and five due to the subsequent migration of neighboring females to the ten vacant territories. The number of female territories adjacent to the vacant territories was 3.8 ± 1.3 SD on average (comprising 47 females and 10 subadults). No females immigrated into five territories that became vacant, but the new occupants came into the other ten. There were no significant differences between the SLs of the original female occupants of the five vacant territories (SL, 117.8 mm ± 4.4 SD, n = 5) and those of the other ten territories (121.4 mm ± 7.2 SD, n = 10; Mann-Whitney U test, $U = 17$, $P > 0.05$). All the five vacant territories had been abandoned by their male occupants once the females were no longer present, and by April 2002, subadults had occupied these vacant territories. In two of the five vacant territories, the males that had left followed the female emigrants from their own territories and fought against the neighboring male to take over the harem. One of these males often invaded the neighboring territory to fight against the neighboring male until the end of the breeding season.

The remaining ten of the 15 vacant territories were occupied by females from the neighboring territories within one day. In six of these ten territories, the immigrants were the largest individuals among the nonspawning individuals of the neighboring territories (females or subadults), and in three of these six territories, the immigrants spawned for the first time in the breeding season after settling into the new territories. The other four of the ten territories were occupied as follows: two territories were occupied by females that had spawned previously; one, by an untagged female whose breeding history was unknown; and one, by a neighboring female who had extended her territory.

In all the ten territories, the immigrant females were smaller than the original female occupants (Wilcoxon signed-ranks test, $n = 10$, $T = 0$, $P < 0.01$; Fig.3). All the new mates of the immigrant females were larger than the original mates of these females, but the sample size ($n = 4$) was too small to analyze statistically. In a female removal experiment, we removed two females (SLs of 120 and 127 mm) from two territories where the mate of the smaller female was larger than that of the larger female (male SLs of 150 and 143 mm). After the removal, a single female (SL, 110 mm), who had occupied the region between the territories of the two females, migrated to the territory of the larger female who had mated with the smaller male. This migrated female did not choose the larger male.

Discussion

The present study revealed that the polygynous mating system of *S. chrysopterum* is characterized by female territoriality and female defense by the males. The females never aggregated and defended their territories exclusively against each other. The results of the female removal experiments indicate that the females compete for better territories and that larger females occupy better territories; some females spawned for the first time after they had settled into the new territories. The tendency of the females to migrate toward larger males was probably related to the correlation between the body

size of the territorial males and that of the largest female in their territories. In previous male removal experiments, three out of six females maintained their territories by themselves for 1–3 months until the arrival of new males (Takamoto et al. 2003). A plausible explanation is that the quality of female territories (e.g., abundance of food and shelter quality) directly affects the fecundity of the females; therefore, females primarily select territories and not males. The males usually defended the territories including multiple female territories. However, in the female removal experiments, the males abandoned these territories once the females emigrated, and some of the males followed the emigrant females into the neighboring territories. These results strongly suggest that the males primarily defend the females rather than the territories with ecological resources.

Baird and Liley (1989) discussed that it is difficult to distinguish between resource and female defense polygyny in pelagic-spawning fish that breed throughout the year. This is because in most of these species, the males appear to defend permanent territories that include both females and the resources that attract the females. This distinction is also difficult in demersal-spawning fish species wherein a male territory includes both females and the resources that attract them, such as *S. chrysopterum.* In these species, female defense polygyny can only be demonstrated by evidence that males abandon the territories once the females emigrate.

The contiguous distribution of female territories probably leads to female defense polygyny. Gladstone (1987) conducted female and male removal experiments on *C. valentini,* a polygynous species with female territoriality. Female territories were distributed contiguously, and most males abandoned the territories once the females emigrated. Based on the results, Gladstone (1987) suggested that female defense polygyny occurred in *C. valentini* and a polygynous system could result from males' defensibility of multiple territorial females. In *S. chrysopterum*, the female territories are also distributed contiguously and males can defend several female territories according to their ability to defend a large area.

Another factor conducive to polygyny is probably that polygyny incurs low cost to the females. It has been reported earlier that when polygyny comes with many

disadvantages, females may prevent its occurrence. When polygyny is less advantageous to the female than monogamy, the female behaves aggressively toward consexuals to prevent polygyny (Wittenberger and Tilson 1980). This relationship between the costs of polygyny and female aggression has been reported in many bird species (Orians 1969; Wittenberger and Tilson 1980; Davis 1991), where both the male and female care for their offspring. Due to polygyny, males tend to care less for each clutch and the fitness of each female decreases. It has also been reported that the females of longnose filefish *Oxymonacanthus longirostris* aggressively attempt to prevent polygyny (Kokita and Nakazono 2001; Kokita 2002). *O. longirostris* is a predominantly monogamous species that dose not show parental care, and a pair jointly defends a feeding territory (Kokita and Nakazono 1998). The growth rate of polygynous females is reported to be lower than that of monogamous females, which consume more food (Kokita 2002). Therefore, monogamous females behave aggressively toward floater females to prevent polygyny (Kokita and Nakazono 2001; Kokita 2002). In *S. chrysopterum*, males do not care for the eggs, and the females can maintain their territories even in the absence of the males (Takamoto et al. 2003). In *C. valentini*, neither the males nor females care for the demersal eggs (Gladstone and Westoby 1988), and the females can maintain their territories even in the absence of males (Gladstone 1987). Therefore, in these species, polygyny is not a threat to egg care or territory maintenance.

Emlen and Oring (1977) predicted that female defense polygyny would occur when there is female aggregation because males can defend the females with lesser effort. However, we showed even without female aggregation, dominant males can defend multiple females to mate polygynously when the female territories are continuously distributed. Many fish species are reported to have polygynous mating systems (reviewed by Warner 1975, 1984; Kuwamura 1984; Turner 1993), but the factors responsible for polygyny have not been discussed sufficiently. It is possible that in some fish species similar to *S. chrysopterum*, although female aggregation is absent, the contiguous arrangement of female territories leads to female defense polygyny. The range of the mature body size in fish is much greater than that in birds and mammals

due to the indeterminate growth of fish, and the wide range of body size elicits alternative mating tactics such as sneaking. Therefore, further studies on fish polygyny are required to reveal the existence of certain other factors that require investigation.

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Figure legends

Fig. 1. Distribution of territories in the south study zone in 2001. The territory and body size of each male (thick gray line with large figure outside the territory), female (black line with small figure inside the territory), and subadult (broken line with small figure inside the territory) are indicated. The shaded and white areas represent the reef edges and sandy floors, respectively.

Fig. 2. Relationship between the body size of the territorial males and (a) the body size of the largest female within their territories and (b) the number of females in their territories as recorded in 2001.

Fig. 3. Body size of the individuals that emigrated or were removed and that of the immigrants. The open circles represent the body size of the females whose territories were not occupied by new females. The digit "3" in an open circle indicates three females of the same size.
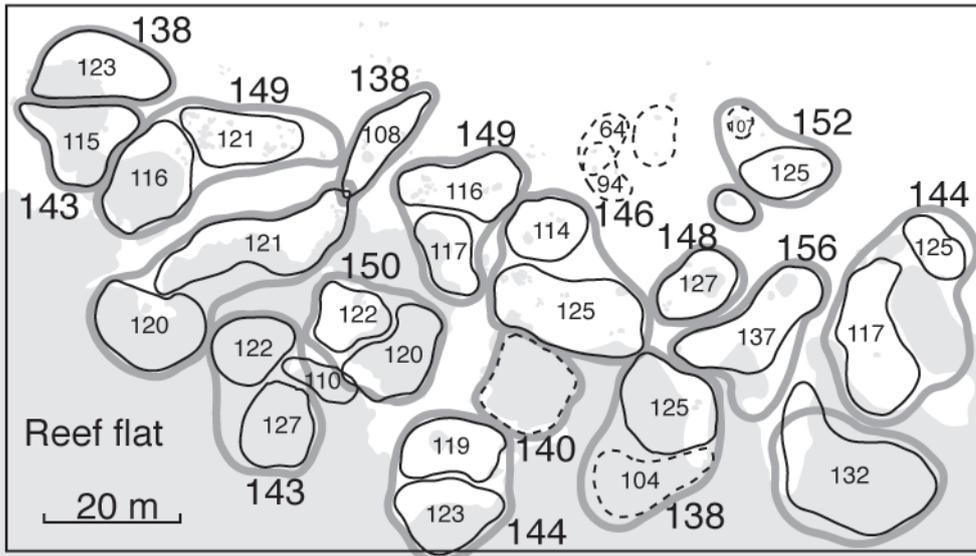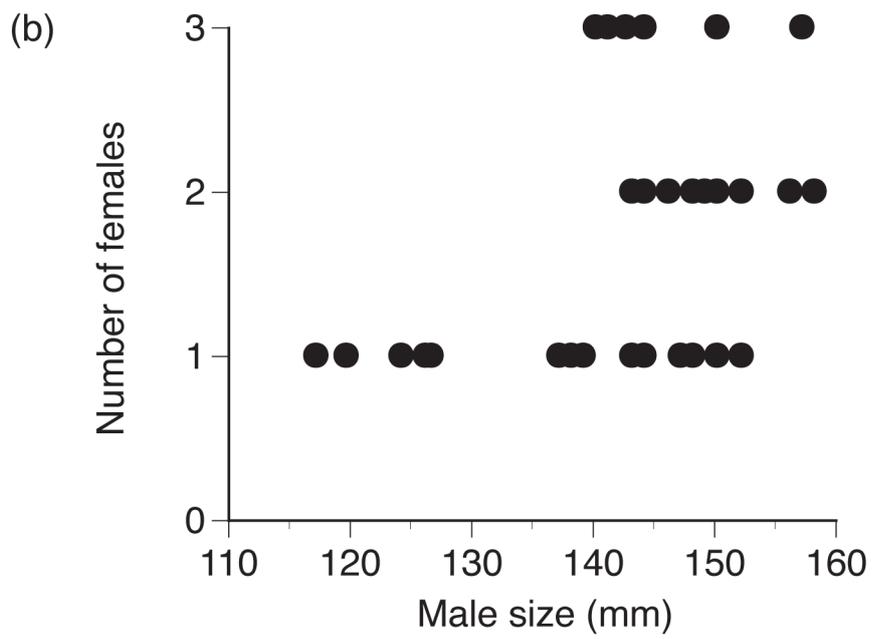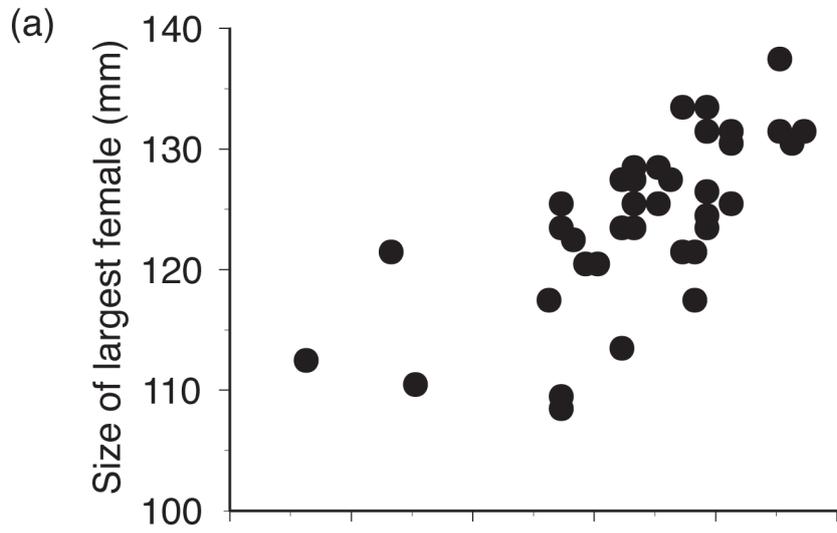
Fig. 1.

Offshore

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104
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20 m
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144

Fig. 2.

(a)

Size of largest female (mm)

(b)

Number of females

Male size (mm)

Fig. 3.