Role of female territoriality in social and mating systems of *Canthigaster valentini* (Pisces: Tetraodontidae): evidence from field experiments

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Abstract

Sharpnose puffers, *Canthigaster valentini* (Pisces: Tetraodontidae) at Lizard Island, Australia, live in male-dominated haremic social and mating systems. The hypothesis was that mature females are restricted in their movements and can be monopolized by some males. Field experiments at Lizard Island, Great Barrier Reef, between January and March 1983 showed that mature females were still territorial in the absence of males and movements of females were not controlled by males. Males abandoned their territories when their females were removed. The territorial behavior of those males with access to females (territorial males) restricted the access of other males (bachelor males) to them. Bachelor males took over harems and became territorial males when established territorial males were removed. The results of the experiments thus supported the hypothesis.

Introduction

The male-dominated, haremic social and mating system has been described for many coral reef fishes (e.g. Robertson and Hoffman, 1977; Moyer and Nakazono, 1978; Hoffman, 1985; Hourigan and Kelley, 1985; Koboyashi, 1985; Petersen and Fischer, 1986). In some situations, haremic systems occur where females are permanently site-attached and hence, defendable by males. Females are thought to be site-attached to maintain their access to food (Robertson, 1974; Barlow, 1975; Robertson and Warner, 1978), or shelter and spawning sites (Moyer and Nakazono, 1978; Thresher, 1979), or because they are gregarious (Moyer, 1979). The hypothesis that harems develop when females are defendable has not been tested in field experiments. However, supportive evidence comes from observa-

tions of a species in different parts of its geographic range, e.g. *Halichoeres maculipinna* in Florida (Thresher, 1979) and Panamá (Robertson, 1981). In other situations, haremic systems occur when males defend territories that enclose resources attractive to females, such as food or spawning sites (Fricke, 1980; Neudecker and Lobel, 1982; Tribble, 1982).

In this paper, I report the results of field experiments which test the hypothesis that the social and mating systems of the sharpnose puffer *Canthigaster valentini* are male-dominated, haremic systems because females are territorial, and hence, defendable by males. In testing this hypothesis I asked three questions: (1) Do females maintain territories irrespective of males? (2) Does the area defended by a male depend upon the number of females? (3) Do males remain territorial in the absence of females? If the hypothesis is true, female territories should still occur in the absence of males, but males should defend their territories only in the presence of female territories. My reasons for proposing the above hypothesis are outlined below.

Canthigaster valentini inhabit coral reefs throughout the Indo-West Pacific region. Males at Lizard Island (the study site) grew to a maximum size of 84 mm SL and females to a maximum size of 71 mm SL (Gladstone, 1985). *C. valentini* were not common: at Lizard Island, the mean abundance ($\pm$ SE) was 2.0 ± 0.3 fish/100 m² (Gladstone and Westoby, in preparation). The *C. valentini* at Lizard Island could be divided into five social classes, on the basis of sex, state of sexual maturity, and behavior. Three social classes are mentioned in this paper: territorial female (TF), territorial male (TM), and bachelor male (BM). TFs defended individual territories in which they fed, slept, and spawned. All sexually mature females were TFs. The territories of one or more TFs were always enclosed within the territory of a single, large male, the TM. TMs fed, slept, and spawned within their territory and excluded all other sexually mature males from it. Two other social classes consisted of sexually immature indi-

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viduals: immature males and non-territorial females. So-
cial groups of *C. valentini* consisted of a single TM and one
or more TFs, often with some immature individuals
(Fig. 1). BMs were sexually mature males which did not
have access to TFs; they lived alone either in home ranges
adjacent to social groups, or as wanderers (Galdstone,
1985).

Canthigaster valentini at Lizard Island spawned year-
round. TMs only spawned with the TFs in their social
group. Spawning occurred inside each TF's territory and
the structure of the social system was maintained during
spawning (Gladstone, in press). Social and mating sys-
tems were thus both male-dominated, haremic systems.
Two observations from a three-year study of several social
groups of *C. valentini* (Gladstone, 1985) suggested a role
for female territoriality. Firstly, after the death of a TF in a
social group the TM's territory contracted to include only
the remaining TFs. Secondly, the only sexually mature
males who defended territories were those associated with
TFs.

Materials and methods

Study site

Observations and experiments reported here were done,
using SCUBA, between January and March 1983 at Lizard
Island (14°38'S; 145°28'E), Great Barrier Reef, Australia.
Social groups from several widely separated sites around
Lizard Island were used, and social groups were not used
for more than one experiment.

Identity, sex, and size of fish

Individuals of *Canthigaster valentini* (Pisces: Tetraodonti-
dae) were recognized by variations in the patterns of dots
on the head and sides, and the shape of the four bars on
the body. The pattern of dots and bars was drawn for each
individual. Sexes could be distinguished externally by
differences in color patterns. Males had blue-green irides-
cent lines which radiated posteriorly from both eyes, blue-
grey lines on a light orange background under their lower
jaw, and a blue-grey patch anterior to their anus. Females
lacked all of these characters. Size was measured by
capturing fish with a weighted, circular net and measuring
standard length (SL) to the nearest 1 mm.

Territory area and territorial behavior

Territory areas were measured by the maximum-area
method of Odum and Kuenzler (1955). Individuals were
observed for several non-consecutive 30 min periods each
and their position plotted every 30 s on a map of the area.
At the end of the last observation period, the outermost
points on the map were connected to form a maximum-

area polygon. Polygon areas were calculated using a
digitizing program for an Apple II computer and a Texas
Instruments plotter.

In those sites where the bottom topography was not
mapped, territory area was measured by following an
individual and placing weighted markers where the fish
stopped and changed direction, and where it turned away
from neighboring territory holders. Observations contin-
ued until the fish's movements no longer exceeded the
marked area. The outermost markers were then connected
by a tape measure and the distance and angles between
them recorded. A scale diagram of the territory was drawn
from this data and the area of the polygon was calculated.

Territorial behavior between individuals was tested by
introducing one fish into another's territory; the "model-
bottle" test (Myrberg and Thresher, 1974) was used. A fish
of known social class was captured and transferred to a
large glass jar which was then placed in the territory of the
fish to be tested. The jar was watched from a distance of
4 to 5 m and time taken for the territory owner to discover
the "intruder" noted. The behavior of the territory owner
was recorded for 5 min, after which time the "intruder"
was released and the owner's response noted. The location
where the owner stopped chasing, or responding to, the
"intruder" was plotted. As a control, a different species of
fish (*Dascyllus reticulatus*) was used prior to each test and
any responses were noted.

Female territoriality in absence of males

Four social groups with a total of 13 TFs were used in
Experiment 1. Individual TFs were identified and their
territories were mapped over four non-consecutive 30 min
periods. The locations of aggressive displays or fights
between neighboring TFs were plotted as well as the
direction in which TFs were chased or charged by their
TM (a "charge" is a rapid movement by one fish towards
another which results in the latter shifting position). The
territorial behavior of every TF was tested by introducing
an unknown TF into each territory. A single *Dascyllus
reticulatus* acted as a control. After these preparations, the
four TMs and all BMs were removed at sunset from each
social group. I returned to each site over the following
days and removed all wandering BMs that had since
entered. I continued to visit each site until five "male-free"
days had passed. The above observations and tests were
then repeated on the remaining TFs. Each TF was then
captured and measured.

Male territoriality in absence of females

Two series of experiments were done. Five social groups
were used for Experiment 2. Each TM was followed for six
non-consecutive 30 min periods, their territories were
mapped and the areas calculated. Territories of TFs were
plotted as in Experiment 1. One TF was to be removed

from each social group. To verify that each TM was defending the area covered by that TF, a BM in a bottle was placed well inside the TF's territory and the behavior of the TM was recorded. After these tests the TF was captured and removed from each social group; this was done at sunset over five successive days. Seven days after TF removal the territory area of each TM was re-measured and a different BM re-introduced.

Seven different social groups were chosen from three areas for Experiment 3. The territory of each TM was mapped and their territorial behavior was tested by moving a BM into the centre of each territory. All TFs from each social group were then captured and removed at sunset over seven successive days. Each area was visited each day after TF removal, and the movements of the TMs were recorded.

Effects of territorial males upon the movements and behavior of bachelor males

Five social groups were chosen for Experiment 4 from two sites around Lizard Island. Each group had one BM living in a home range on the periphery of the TMs' territory. The groups chosen were isolated from other groups. The territory of each TM and TF, and the home range of each BM, was mapped and measured. TMs and BMs were each followed for a total of 3 h, TFs for 1 h. The amount of time BMs spent in the following activities was recorded to the nearest 1 s: feeding alone, feeding with TFs, patrolling, and aggressive and submissive behaviors. Aggressive behaviors were defined as chases, charges, and threat displays. Submissive behaviors were appeasement displays and yields (where one fish swims away from another). The response of TMs towards their BMs was tested by moving each BM into the centre of the TM's territory. Time taken for TMs to discover these "intruding" BMs, and their behavior towards them, were recorded. TMs were captured around sunset on successive days and removed from their territories. Observations that had been made on BMs were repeated 5 d after TM removal.

Results

Female territoriality in absence of males

TFs of *Canthigaster valentini* in both areas chosen for Experiment 1 restricted their movements to well-defined territories (Fig. 1 A, C). Territories varied in size from 25 to 284 m² (Table 1), and there was a positive correlation between size of TF and area of territory ($r = 0.82$, $P < 0.01$, $N = 13$). TFs were only occasionally chased or charged by their TM and there was no obvious pattern to the direction of charges or chases (Fig. 1 A, C). These two observations suggest that TFs were not restricted in their movements by their TMs.

Table 1. *Canthigaster valentini*. Territory sizes of territorial females (TFs) before and after removal of territorial males (Expt 1); –: absent. Territory sizes before and after compared by paired *t*-test (excluding TF No. D2T2): $t = -1.51$, $P > 0.10$

TF No.	Territory size (m²)	
	before	after
D5T1	86	82
D2T2	78	–
D6T2	40	41
D2T4	27	33
D3T4	25	26
D2T5	38	38
D4T5	32	34
A5T1	243	235
A23T2	271	263
A14T8	121	119
A2T3	197	192
A5T3	229	227
A17T3	284	276

Threat displays and fights between neighbouring TFs occurred infrequently (Fig. 1). In both sites, however, the bottles containing "intruders" were vigorously pecked by the territory owner when placed inside each territory. Sites where TFs stopped chasing liberated "intruders" generally coincided with the location of borders drawn from their movements (Fig. 1 A, C). Control fish were always ignored by TFs.

New BMs continued to arrive in both areas for several days after the four TMs were removed. Three new BMs had moved into the Granite Bluff site the morning after TM removal. Another new BM had arrived by the next morning and was already patrolling the area, visiting several TFs, and spawned with one of the TFs (No. D2T5). These males were removed.

All TFs except one (D2T2) were still present in both study sites after five male-free days. D2T2 was not found within a radius of 100 m from her former territory. All TFs continued to defend their territories in the absence of sexually mature males (Fig. 1 B, D). Each TF used the same area as she did before male removal. There was no significant difference in territory size before and after male removal (Table 1).

There were no changes in the responses of TFs to "intruders" after male removal: bottles containing " intruders" were pecked, and TFs immediately chased liberated "intruders". Sites where TFs stopped chasing "intruders" coincided with the location of borders drawn from their movements (Fig. 1 B, D). Control fish were ignored. There was no obvious change in the number of threat displays or fights between neighbouring TFs at Mermaid Cove (Fig. 1 C, D). At Granite Bluff, however, there was a significant increase in the number of fights between neighboring TFs after male removal (Fig. 1 A, B; paired *t*-test $= 2.98$, $P < 0.05$), but the test was weak at Mermaid Cove because few fights were recorded initially.

A

B

C

D

TF territory   TM territory

Boulders and patch reefs

Acropora pulchra thickets   reef edge

location and direction of charges and chases
performed by TMs to their TFs

O   site of threat display between TFs
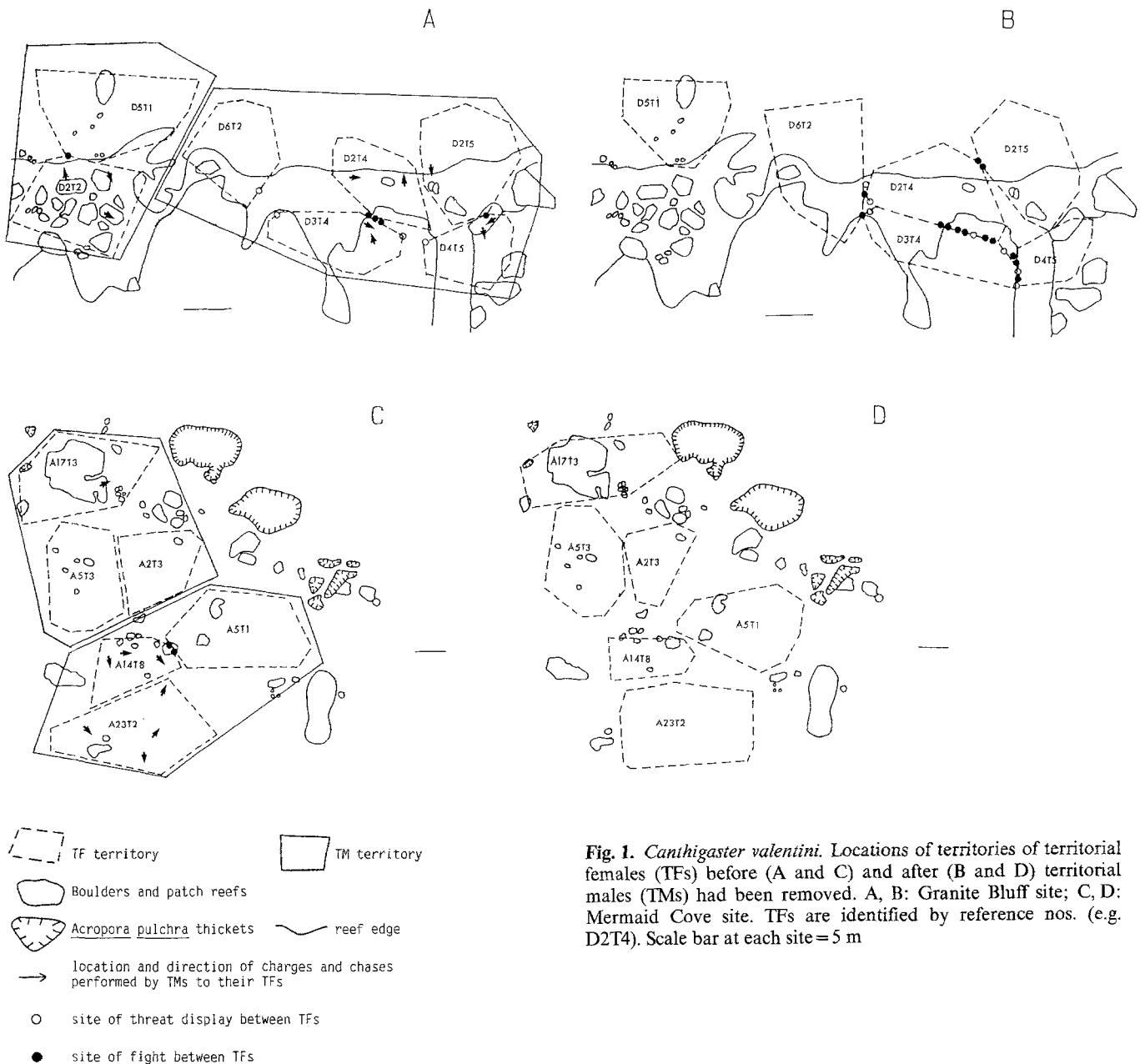
●   site of fight between TFs

Fig. 1. *Canthigaster valentini*. Locations of territories of territorial females (TFs) before (A and C) and after (B and D) territorial males (TMs) had been removed. A, B: Granite Bluff site; C, D: Mermaid Cove site. TFs are identified by reference nos. (e.g. D2T4). Scale bar at each site = 5 m

Male territoriality in absence of females

The territories of all TMs chosen for Experiment 2 enclosed the territories of their TFs. Numbers of TFs varied from two to four. Each TM vigorously pecked the bottle containing the BM that was placed inside the territory of the TF that was later removed. When released, each BM was immediately chased out of the area by the TM. Sites where TMs stopped chasing BMs generally coincided with the location of borders plotted from the movements of TMs. Control fish were ignored.

Seven days after the removal of the TF, each TM had stopped entering and feeding in the area previously occupied by her. Each TM's territory enclosed only the territories of the remaining TFs. There was a significant drop in the territory size of TMs (Table 2). Different BMs

placed in the area previously occupied by the TF which had been removed were ignored by the TMs.

TMs used in Experiment 3 ranged in size from 60 to 83 mm SL, the area of their territories ranged from 186 to 1287 m² , and there were from one to three TFs in each social group. TMs performed threat displays and pecked the bottle when BMs were transferred to the centre of their territory. Released BMs were vigorously chased by the TMs until they crossed the TM's territory boundary as determined by his movements. Control fish introduced into territories in the bottles were ignored by the TMs.

Five of the seven TMs left the area after their TFs had been removed. Time taken for them to leave varied from 5 to 21 d (Mean ± SE = 11.8 ± 3.0 d). Up until the time they left, these TMs were seen feeding at various sites through-

out the area formerly occupied by their TFs. The area surrounding the former territory was searched after a TM's absence was noted. None were found within a radius of 250 m.

Two TMs (C1T3, B1T6) did not leave their areas. C1T3's TFs were removed on 10 February, 1983. By 15 February, he had taken control of a TF from a neighboring social group and was defending a territory around her. The neighbouring TM, C1T15 (71 mm SL), was smaller than C1T3 (75 mm SL). B1T6's TFs were removed on February 15. B1T6 was still in the area on 3 March and spending most of his time feeding with an immature female. The area of his movements (55 m²) was much smaller than his previous territory (186 m²).

Effect of territorial male removal upon bachelor males

The harem sizes of the five TMs used in Experiment 4 varied from one to five TFs. The territory of each TM completely enclosed the territories of all TFs. Each BM lived in a home range that slightly overlapped the TM's territory.

All TMs performed threat displays towards the BMs when they were moved into the centre of their territories. TMs took 1 to 22 min to locate BMs (Mean ± SE = 11.2 ± 4.2 min). TMs immediately chased liberated BMs. Sites where TMs stopped chasing BMs were close to the borders that were drawn from their movements. Control fish

placed in bottles in the centre of each territory before each test were always ignored by the TM.

Each of the BMs occasionally swam into the TM's territory. All were quickly seen by the TM and chased out. They spent no time with TFs, most time was spent feeding alone (Table 3). The small amounts of time spent by some of the BMs in aggressive behaviors involved behaviors directed at wandering BMs that passed through the area during the observations.

By the morning after TMs had been removed, all former BMs (I will refer to these males as "former bachelor males") had moved into the area previously defended by the TMs. All had begun visiting and feeding with the TFs. Two former BMs (F2T1 and F2T2) spawned with the TFs on the first morning. Five days later each former BM had taken control of the TFs from which he was previously excluded. There were no changes in the number, identity, or location of TFs. The area used by the former BMs now enclosed the territories of all TFs. There was a significant increase in the area used by BMs after TM removal (Table 4). There was no significant difference between the size of areas being used by them and the territory sizes of the former TMs (Table 5).

There were significant changes in the time budgets of all former BMs (Table 3): much less time was spent feeding alone; more time was spent feeding with TFs; time was spent patrolling; there was more time spent on aggressive behaviors (directed at TFs and wandering BMs); and no time was spent on submissive behavior. When the time budgets of former BMs were compared

Table 2. *Canthigaster valentini.* Territory sizes of territorial males (TMs) before and after removal of one TF from their social group (Expt 2). Territory sizes before and after compared by paired *t*-test: $t = 1.81$, $P < 0.02$

TM No.	Territory size (m²)	
	before	after
C1T11	646	493
C1T12	483	406
G1T4	373	333
G1T5	143	105
G1T6	444	322

Table 4. *Canthigaster valentini.* Area occupied by BMs before and after removal of TMs. Area occupied before and after compared by paired *t*-test; $t = 3.96$, $P < 0.02$

BM No.	Area (m²)	
	before	after
F2T1	130	585
F2T2	132	394
C4T5	53	186
C3T8	77	216
C2T6	102	292

Table 3. *Canthigaster valentini.* Time spent by bachelor males (BMs) in various activities before and after removal of TMs from social groups (Expt 4). Each value is % of total time each BM was observed. Aggressive actions: charges, chases, threats; submissive actions: appeasement displays, yields. Total for each BM is not 100% because time spent with social classes other than TFs, i.e., immature males and non-territorial females, was not included. Time spent before and after compared by paired *t*-test at bottom of table

BM No.	Feeding alone		With TFs		Patrolling		Aggressive		Submissive	
	before	after	before	after	before	after	before	after	before	after
F2T1	99.4	2.3	0	44.1	0	49.0	0.3	3.6	0.3	0
F2T2	99.7	37.9	0	45.3	0	16.1	0	0	0.3	0
C4T5	93.9	11.2	0	57.5	0	28.8	0	2.5	1.1	0
C3T8	99.6	9.1	0	52.7	0	34.9	0.1	2.5	0.3	0
C2T6	98.3	29.0	0	44.6	0	26.1	1.1	0.3	0	0
	$t = 10.96$		$t = 28.87$		$t = 9.79$		$t = 1.78$		$t = 3.24$	
	$P < 0.001$		$P < 0.001$		$P < 0.001$		NS		$P < 0.05$	

Table 5. *Canthigaster valentini*. Territory sizes (m²) of TMs before their removal and the territory sizes of BMs after they had taken over same groups of TFs. Territory sizes compared by paired t-test: $t = -0.48$, $P > 0.50$

TM No.	m²	BM No.	m²
F1T1	408	F2T1	585
F1T2	301	F2T2	394
C1T5	222	C4T5	186
C1T8	236	C3T8	216
C1T6	313	C2T6	292

with those of established TMs (Gladstone, 1985), there were no significant differences in mean percentage times spent feeding alone (paired t-test $= 0.44$, 30 DF, $P > 0.50$) or feeding with TFs ($t = 0.72$, 30 DF, $P > 0.40$), but former BMs spent more time patrolling ($t = -2.40$, 30 DF, $P < 0.02$).

Discussion

Emlen and Oring (1977) predicted that polygynous mating systems evolve when males can directly monopolize females or resources essential to females. The type of polygynous mating system depends upon the means used by males to control females. For example, "resource defense polygyny" occurs when males can economically defend some resource that is essential to females, but not females themselves. In this situation females are attracted to areas in response to some attribute of the male defending it or the quality of the area, or both. "Female defense polygyny" occurs when females are economically defendable. Males monopolize females by restricting their movements or by establishing a territory around them and excluding other males.

Sexually mature females of *Canthigaster valentini* can be economically monopolized by males. A long-term study of known TFs (Gladstone, 1985) demonstrated that they defended lifetime territories. Experiment 1 verified that TFs were naturally site-attached and their movements were not restricted by their TMs. TFs continued to actively defend their territories in the absence of sexually mature males. Further, they did not have to migrate between feeding and spawning sites. The movements of TFs were thus limited in space and time. This allowed sexually mature males to establish territories around TFs. Several studies have shown that permanent, well-defined harems occur when feeding and spawning grounds overlap, and females are thus defendable (Robertson, 1974, 1981; Robertson and Hoffman, 1977; Robertson and Warner, 1978; Thresher, 1979).

I regularly visited the TFs used in Experiment 1 for two weeks after the end of the experiment. All were still present and no new males had taken control of them. There is also no other evidence to suggest that, in the absence of new males, TFs might abandon their territories and search for them. Over almost three years of observa-

tions of known TFs at two study sites at Lizard Island, no females entered as TFs; all new female arrivals were sexually immature (Gladstone, 1985). This argues against female migration.

An alternative hypothesis, that TMs defended territories which attracted females, was not supported in further experiments. Experiments 2 and 3 verified that TMs defended TFs, not the site. When one TF was removed from each of several social groups, all TMs stopped using and defending the area. Territories contracted to include only the remaining TFs. Most TMs abandoned their territories when all TFs were removed and presumably became wandering BMs and searched for new TFs. An alternative tactic would have been for each male to remain in the area and wait for immature females to arrive, establish home ranges, and eventually become TFs. This tactic is probably uneconomical because of the low and unpredictable juvenile recruitment, the time taken for females to attain sexual maturity, and costs incurred by continuing to exclude other males from the area. By wandering, these males could sneak spawnings, meet new or non-haremic TFs (i.e., TFs who had established territories away from existing social groups), or take over newly vacant harems.

The TM B1T6 remained with an immature female. Female *Canthigaster valentini* become sexually mature at 38 to 44 mm SL (Gladstone and Westoby, in preparation). The female that B1T6 remained with was 39 mm SL which suggests that she was approaching sexual maturity and would soon become a TF. It was probably more advantageous for B1T6 to remain in the area and resume spawning a short time later, rather than leave the area and possibly risk a long delay before beginning to spawn again. The TM C1T3 stopped using his former territory and established a territory around a TF from a neighboring TM. This was an uncommon tactic. C1T3's larger size and recent experience as a TM possibly aided his take-over. Also, C1T5 might have been attempting to maintain too many TFs and have been unable to effectively defend all of them.

Other studies have shown that males defend resources apart from females. Tribble (1982) recorded the behavior of several groups of another species of coral reef fish, *Coris dorsomaculata* (Labridae) over 5 mo. This species has a haremic social system that seems to be based upon the defense of food resources by males. This was supported by observations that males continued to defend an area after all females had left it, unlike TMs of *Canthigaster valentini*. Males of *Coris dorsomaculata* expanded their territories and took over extra females after the disappearance of a neighboring male, like *Canthigaster valentini* (Gladstone, 1985). Tribble (1982) gave no data on the spatial relationships of females; however, movements by females between harems were observed. The considerable turnover of females within Tribble's (1982) study site suggests that females might regularly travel over large areas, possibly in search of males with more favorable territories.

Although the territories of TMs of *Canthigaster valentini* enclosed the territories of several TFs, TMs did not

attempt to herd their TFs or restrict their movements. Experiment 1 showed that TMs did not charge or chase their TFs in only one direction, i.e., towards the centre of their territory. The overall role of charges and chases by TMs towards their TFs is unclear (Gladstone, 1985); however, TMs used charges or chases to disrupt fights between TFs along their shared borders. Removal of TMs in Experiment 1 resulted in an increased frequency of border fights between TFs at Granite Bluff. There was no change in the frequency of border fights at the Mermaid Cove site. TFs at this site defended large, non-overlapping territories. They were less likely to come in contact with one another and so less likely to be involved in border fights. Any effect of TM removal was probably masked by the low frequency of border fights.

The territorial behavior of mature female *Canthigaster valentini* provided the opportunity for some males to monopolize them at the expense of other males. Experiment 4 verified that TMs maintained their territories by excluding other males. BMs placed in the centre of social groups were always chased out by the TMs. Under normal conditions this territorial behavior prevented BMs spawning. When TMs were removed, BMs quickly became TMs, took over TFs, and spawned immediately. TFs always remained when BMs took control. The observation that TFs immediately began spawning with their new TMs suggests that TFs were not selective about the males with which they spawned. TMs did not control the movements of their TFs. They maintained their social group by patrolling territory borders, excluding other sexually mature males, and evicting immature males as they approached sexual maturity. This would seem to be effective: less than 3% of spawnings observed were between TFs and sneaking BMs (Gladstone, 1985).

BMs were either wanderers or home-ranging. I have hypothesized (Gladstone, 1985) that BMs lived in home ranges adjacent to social groups to sneak spawnings and take control of the group when the TM died. Throughout this study, BMs were never seen defending home ranges that were isolated from social groups.

I conclude that the social and mating systems of *Canthigaster valentini* are based upon female territoriality. Further, the mating system is a female-defense polygyny (Emlen and Oring, 1977). The basis of these systems was the defendability of TFs. Males formed social groups when they established a territory around several TFs and excluded other males. Males were able to continually defend territories because they fed in the same areas as females and did not care for their fertilized eggs (Gladstone, in press).

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