

Determinants of feeding territory size in the corallivorous butterflyfish, *Chaetodon multicinctus*

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Abstract. Both sexes of the monogamous coral-feeding butterflyfish, *Chaetodon multicinctus*, forage as energy maximizers, are constrained by the time available for feeding, and vigorously defend their feeding territories from intrusions by conspecific competitors. Territory area was positively correlated with coral abundance when data were pooled from coral-poor and coral-rich habitats. In contrast, male length and total food were correlated with territory area within the coral-rich habitat. When food supply was increased, fish attempted to defend all food within original borders but were limited by aggressive interactions with conspecifics attracted to supplemental food. When coral abundance was reduced, residents expanded their territories. In comparison, territories were adjusted as an inverse function of competitor abundance and related costs of defence. Although these experiments support competitor-mediated models of territory size, food resources are also important in that they set a lower limit for minimum territory area and, when possible, are defended in surplus by this species.

Although permanent territories often function to defend mates and shelter sites, food supply is of fundamental importance because it supplies energetic and nutritional requirements for maintenance, growth and reproduction (Davies 1978; Wittenberger 1981). The proximate determinants of feeding territory size in natural populations, however, are not clearly understood or rigorously tested (reviewed by Myers et al. 1979). For example, the food maintenance hypothesis states that animals defend areas that contain a food supply adequate to satisfy their short-term energy requirements, predicts that territory size is adjusted by residents as an inverse function of local food abundance, and is largely supported by studies in which feeding territory area was inversely related to food supply (Stimson 1973; Slaney & Northcote 1974; Gill & Wolf 1975; Simon 1975; Gass et al. 1976; Kodric-Brown & Brown 1978). In contrast, the competitor constraint hypothesis states that food competitors act to constrain territory area below some maximum through competitive interference for increased food resources and predicts that territory size is adjusted as an inverse function of competitor abundance (i.e. defence costs) rather than direct assessment of food supply (Krebs 1971;

Myers et al. 1979; Franzblau & Collins 1980; Norton et al. 1982).

It must be recognized that in natural systems changes in food and competitor abundance are not always mutually exclusive events. In populations where food is limited, for example, competitor density often covaries with food abundance (reviewed by Myers et al. 1981). Although animals may defend smaller territories in resource-rich habitats, it is difficult to establish, a priori, whether territories are adjusted to accommodate higher food density, higher concomitant costs of resource defence, or some synergistic effect. Furthermore, in poor or stressed habitats, food abundance alone may set the lower limit to the territory size necessary to supply basic metabolic requirements. Thus, it is crucial to assess the independent effects of increased and decreased food supply and competitor abundance when studying natural systems rather than depend strictly upon correlation analyses.

Several recent theoretical papers have examined how energy maximizers (animals that maximize net food consumption) should adjust feeding territories in response to changes in food abundance and competitor density (reviewed by Schoener 1983). Hixon's (1980) model for an energy maximizer limited by time available for feeding predicts that territory size should be inversely related to both food supply and competitor density, and also how foraging and defence time should covary. Eber-

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sole's (1980) model for the effects of food supply in which increased costs of defence were associated with increased food supply predicts territory size to be inversely related to food abundance when defence costs change proportionally with food supply. If defence costs remain stable during increased food density, however, territory size should increase. Unfortunately, both models have received few empirical tests (Hixon et al. 1983; Norman & Jones 1984).

This paper examines the influence of food and competitors on feeding territory size in the coral-feeding butterflyfish, *Chaetodon multicinctus*, and presents results of experimental manipulations of increased and decreased food resources and conspecifics. Although this study supports competitor-mediated models of territory size, it also illustrates the importance of food resources in determining minimum feeding area and that under conditions of surplus food fish behave in ways that maximize total food resources.

METHODS

Study Species

The banded butterflyfish, *Chaetodon multicinctus*, is endemic to the shallow coral reefs of the Hawaiian Islands and Johnston Atoll. Adults are less than 10 cm standard length (SL), and have a white laterally compressed body with a series of six conspicuous brown vertical bands. It has a small protrusible jaw and feeds upon polyps and surface tissues of hard corals (Hobson 1974; Reese 1975; Motta 1988). Adults occur almost exclusively in male-female pairs (Reese 1975) that spawn in the spring (Tricas, in press a) and vigorously defend permanent contiguous feeding territories against intrusion by conspecifics and other corallivores (Tricas 1985).

Study Area

All field work was conducted on Puako reef in South Kohala District on the island of Hawaii between June and September 1981-1984. A shallow reef flat (2-5 m deep) extends seaward approximately 100 m from the shore and is composed of bare lava, interspersed patches of living coral, rubble and sand. Rose coral, *Pocillopora meandrina*, is a small erect species with robust branches and the most common coral near the seaward edge

of the reef flat. *Porites lobata*, which occurs in both encrusting and massive morphologies, forms large mounds in sheltered areas of the flat. At the seaward edge of the reef is a precipitous drop to a coral rich shelf (7-10 m deep) with extensive mixed fields of *P. lobata* and branched finger coral, *Porites compressa*.

Observations

Divers using scuba recorded more than 3000 h of movement and activity data of fish pairs on the reef. Individual fish were identified by distinctive variations in patterns of body spots and bars. Observers remained at distances greater than 1 m to minimize their influence on the foraging path or behaviour of fish. Each member of a fish pair was observed for alternate 5-min sample periods during which activity budgets were recorded and feeding territories were marked. One morning and one afternoon dive was made each day during an experiment to provide samples of 10 5-min observations per fish per day.

Time budgets were recorded for five pairs as the number of s each sex spent feeding, in agonistic encounters, sheltering in the reef, and at stations of the cleaner wrasse, *Labroides phthiriophagus*. In experimental territories, feeding rates were estimated as the number of bites on each food item per 5-min observation period. Rates of agonistic encounters were recorded as the number of aggressive events (primarily chases) per period. After termination of each experiment, fish were collected underwater with hand nets, measured to the nearest mm (SL), sexed in situ by gonad cannulation (a modified procedure of Ross 1984), and returned to their territories.

Measurement of Territory Size and Food Abundance

Feeding territories were marked by placing coloured strips of weighted 10-cm-long plastic tape at feeding sites as fish foraged. Pair members were usually separated by less than 1 m as they foraged throughout their territory and regularly patrolled territory borders. Approximately 2 h of marking was required to delineate an undisturbed territory perimeter similar to that reported for *Chaetodon trifasciatus* by Sutton (1985). Nearly all borders were entirely contiguous with other conspecific pairs and separated by less than a few cm.

Pre- and post-manipulation territory areas were measured at the end of each experiment. A line was

set to bisect the territory along its major axis. A second line and brass chain (each marked in 0.25-m increments) were then used to measure lateral linear and rugose (relief) distances, respectively, 90° from the bisect line to the location of coloured tags that marked the outer perimeter of pre- and post-manipulation borders. These measurements were taken at 1-m intervals on both sides of the bisect line and perpendicular to it. Two-dimensional planar areas (A_p) were determined on a digitizer from polygon maps of territories. Total surface area, A_t , was calculated as

$$A_t = A_p (R/L)$$

where R is the summed relief distance for all lateral measurements and L is the summed linear distance for all lateral measurements for a territory.

Coral abundance within territories was estimated by subsampling the proportion of bottom cover for each coral species. A 1-m² quadrat (0.1-m grid) was placed at randomly generated 1-m² plot sites from the territory map, and the coral species underlying each grid point tallied. The number of replicate quadrat counts per territory always exceeded asymptotic limits determined by species abundance-area curves.

Field Manipulations

Three classes of experimental manipulations were performed in replicate to test the effects of food and competitor abundance on territory size and the time budgets of residents. Experiments were designed to test the null hypothesis that manipulation treatments had no effect on territory size or activities when compared with pre-manipulation data. At least one control territory was monitored concurrently with each experimental. Unless otherwise indicated, pre- and post-manipulation data were analysed as follows. The paired t -test was used to test for changes in territory size. Feeding rate data were first verified for normality and homoscedasticity, and then tested by analysis of variance (transformation of feeding data did not affect test results). Chases, which were infrequent, followed a Poisson distribution and were analysed with the replicated test of goodness-of-fit G -statistic (Sokal & Rohlf 1981).

Food abundance

Increased food. Previous studies show that the distribution pattern of experimentally added food corals have a major effect on the adjustment of

territory size for *C. multicinctus* (Tricas 1986). To simulate an homogeneous increase in food abundance within the habitat, colonies of *P. meandrina* (approximately 20–30 cm in diameter) were added in a uniform distribution pattern both inside and 1–2 m beyond pre-manipulation borders of experimental territories ($N=4$). At two low density sites supplemental coral colonies were spaced evenly 1.5 m apart, while corals at the two high density sites were spaced at 1.0- and 0.5-m intervals.

Decreased food. Food abundance was reduced by covering the substrate with 1-m² plastic or cloth sheets at randomly determined locations within three territories ($N=3$). In the first experiment, a two-step food reduction was performed by an initial decrease of 7 m² (11% of food and non-food substrates within the original territory) followed by a second 5-m² decrease (8%; total: 19%) 2 weeks later. In the other two experimental territories, *P. lobata* colonies were covered by one 10-m² (19% area = 25% coral) and one 11-m² (24% area = 38% coral) single-step reduction. One additional territory was tested for effects of the coral covers by placement of 10 1-m² plastic sheets over sand patches and within bare crevices (non-food substrates) in the territory.

Competitor abundance

Increased competitors. Increased conspecific intrusions were simulated by introduction of live fish into experimental territories ($N=3$). At three sites, eight adults were placed in clear glass jars and spaced evenly in either pairs ($N=2$) or as individuals ($N=1$) 1 m inside territory borders. The present manipulations differed from realistic encounters primarily by the inability of bottled fish to flee, return an attack, or feed. This experimental technique is useful for 1–2 days while territory residents display strong aggression towards bottled conspecifics which simulates increased costs of defence. After that time fish begin to habituate to bottled intruders and reduce their aggression. In addition to concurrent unmanipulated control sites, a single territory contained eight empty bottles evenly spaced about the territory to test for effects of the glassware.

Decreased competitors. The maintenance of territorial boundaries in the presence of neighbouring pairs primarily involved displays and overt chases against their neighbours. To test the importance of conspecific neighbours, adjacent contiguous pairs were removed around four experimental territories

Table I. Territory size ($\bar{X} \pm \text{SD}$) for experimental fish pairs during periods of pre- and post-manipulations of food and competitors

Experiment	N	Territory Size (m ²)		P
		Pre-manipulation	Post-manipulation	
Increased food				
Low density	2	97.0 \pm 22.6	103.7 \pm 27.6	NS
High density	2	44.5 \pm 6.4	14.2 \pm 3.6	< 0.005
Decreased food	3	69.0 \pm 12.1	82.5 \pm 13.7	< 0.025
Increased competitors	3	92.0 \pm 21.9	58.3 \pm 21.2	< 0.020
Decreased competitors	4	48.5 \pm 15.2	125.2 \pm 51.2	< 0.050
Controls	10	84.1 \pm 34.1	84.8 \pm 33.4	NS

($N=4$). Other immigrating pairs or floaters that moved into the site were also removed during the post-manipulation period to minimize conspecific encounters.

Increased food and associated competitors

To test whether competitors directly inhibit access to food resources territorial pairs were presented supplemental food associated with a conspecific. In two experimental territories, eight *P. meandrina* colonies were added in conjunction with bottled adult *C. multicinctus*. Corals were spaced evenly around and less than 1 m beyond the territory perimeter with a bottled fish positioned between each coral head and the territory border. In this way, fish encountered a conspecific when feeding on supplemental corals. Three additional experimental sites were established to test for independent effects of the corals and bottled conspecifics. On these territories, eight coral heads ($N=2$) and eight bottled fish ($N=1$) alone were arranged in the same configuration as the combined presentation experiments.

RESULTS

Spatial and Temporal Stability of Territory Size

All territory residents formed heterosexual pairs with males ($\bar{X}=78.1$ mm SL) larger than their female mates ($\bar{X}=77.0$ mm SL, $N=39$; $P<0.01$, paired *t*-test). Territory area ranged from 33 to 275 m² ($\bar{X} \pm \text{SD}=90.3 \pm 54.2$ m², $N=45$). Smaller territories were held by fish in the deep coral-rich habitat (75.8 ± 28.9 m², $N=34$) than on the reef flat (205.8 ± 73.4 m², $N=5$; $P<0.001$, *t*-test). Territory

Table II. Activities ($\bar{X} \pm \text{SD}$) of five fish pairs given as proportion of total time budget

Activity	Males	Females
Forage	0.928 \pm 0.044	0.962 \pm 0.036
Chase	0.034 \pm 0.027	0.014 \pm 0.009
Shelter	0.030 \pm 0.037	0.020 \pm 0.028
Clean	0.008 \pm 0.008	0.004 \pm 0.006
Observation time (min)	1215	1200

area in the coral-rich habitat, which was the site of all experimental manipulations, was a normally distributed variable (Kolmogorov-Smirnov D-max test, Sokal & Rohlf 1981), thus changes in territory area in manipulation experiments were tested by the *t*-test for small sample size.

Undisturbed territories showed extreme temporal and spatial stability. No difference was found between pre- and post-manipulation size in 10 control territories (Table I). Typically, a zone between borders less than 1 m wide was the site of agonistic encounters and any minor spatial adjustments. Resident duration in territories for some pairs has exceeded 4 years with changes in area of less than 5%.

Activity Budget

The activity budget of *C. multicinctus* shows an extreme bias for feeding (Table II). Foraging involved travel between coral heads, inspection and consumption of coral tissue (Tricas, in press b), and composed more than 92% of the daily time budget for both sexes. Fish foraged continuously from first

Table III. Feeding rates ($\bar{X} \pm \text{SD}$) of fish pairs during pre- and post-manipulations of food and competitors

Experiment	Bites/5 min		<i>F</i> *	<i>P</i>
	Pre-manipulation	Post-manipulation		
Increased food				
Low density				
Males	64.1 ± 22.1	68.1 ± 20.9	0.62	NS
Females	62.3 ± 17.8	71.8 ± 20.4	10.21	< 0.002
High density				
Males	48.3 ± 22.0	43.8 ± 24.4	9.53	< 0.003
Females	48.4 ± 25.7	41.7 ± 24.0	13.24	< 0.0004
Decreased food				
Males	55.7 ± 18.3	66.2 ± 22.2	9.32	< 0.003
Females	59.4 ± 20.6	73.6 ± 20.0	22.31	< 0.0001
Increased competitors				
Males	64.7 ± 21.8	51.0 ± 24.6	16.82	< 0.0001
Females	65.2 ± 21.1	44.1 ± 27.8	32.97	< 0.0001
Decreased competitors				
Males	64.1 ± 18.9	50.9 ± 17.8	4.85	< 0.03
Females	63.0 ± 19.0	57.7 ± 22.9	0.25	NS
Controls				
Males	49.1 ± 19.2	49.6 ± 17.7	1.41	NS
Females	51.4 ± 21.0	51.5 ± 18.5	0.09	NS

* Sample sizes for each treatment are the same as in Table I. *df* = 1 for all *F* tests.

light until dark with no intrasexual differences between morning and afternoon feeding rates ($N = 51$, paired *t*-test). Females, however, fed more than their mates ($P < 0.05$, paired-*t* test), while males chased more conspecifics ($P < 0.05$, sign test). Because of these differences, all pre- and post-manipulation activities are analysed by sex. The small amount of time spent sheltering by adults is consistent with the lack of any observed predation on adults during the study. Fish spent a small portion of their time at cleaning stations of the wrasse, *L. phthiophagus*, which occurred within most territories. There were no differences between pre- and post-manipulation feeding (Table III) or defence (Table IV) activities for any of the 20 control fish.

Correlates of Territory Size

Total coral cover in territories ranged from 8% in the shallow habitat ($\bar{X} \pm \text{SD} = 13.2\% \pm 4.1$, $N = 5$) to 90% in the deeper coral-rich habitat ($50.4\% \pm 18.8$, $N = 32$). When data from all territories were pooled, area correlated only with measures of coral abundance (Table V). In con-

trast, territory size in the coral-rich habitat correlated with total food and male length, thus fish holding the largest territories in the coral-rich habitat controlled the most food. No relationship was found between female length or chase rates (by males, females or combined). First order partial correlation analyses (cf. Myers et al. 1979) that controlled for coral abundance and chase rates (a measure of intrusion pressure) did not change the significance of associations between territory size and any measured variable.

Experimental Manipulations

Increased food

In the two low-density food enhancements, fish pairs retained all of the original foraging area (Table I) and added a few supplemented coral heads beyond their borders. Feeding rates increased for females (Table III), while chases against intruding pairs increased for both sexes (Table IV). At higher densities of food enhancement, residents retained their original territory area for a few days until the extreme costs of defence against conspecific intruders (Table IV) resulted in

Table IV. Chase rates ($\bar{X} \pm \text{SD}$) of fish pairs during pre- and post-manipulations of food and competitors

Experiment*	Chases/5 min		G	P
	Pre-manipulation	Post-manipulation		
Increased food				
Low density				
Males	0.13 \pm 0.34	0.80 \pm 1.17	42.24	< 0.005
Females	0.12 \pm 0.33	0.63 \pm 1.04	27.11	< 0.005
High density				
Males	0.30 \pm 0.55	3.95 \pm 4.68	104.69	< 0.005
Females	0.28 \pm 0.58	3.81 \pm 4.95	105.75	< 0.005
Decreased food				
Males	0.20 \pm 0.48	0.18 \pm 0.50	0.58	NS
Females	0.25 \pm 0.54	0.15 \pm 0.46	5.61	< 0.025
Increased competitors				
Males	0.34 \pm 0.78	7.53 \pm 7.34	210.56	< 0.005
Females	0.17 \pm 0.46	7.72 \pm 8.33	210.45	< 0.005
Decreased competitors				
Males	0.0	0.04 \pm 0.19	6.25	< 0.025
Females	0.0	0.19 \pm 0.14	8.36	< 0.005
Controls				
Males	0.15 \pm 0.47	0.12 \pm 0.48	3.68	NS
Females	0.09 \pm 0.37	0.10 \pm 0.41	0.88	NS

* Sample sizes for each treatment are given in Table I.

Table V. Correlation coefficients for feeding territory size and measured variables

Habitat†	Percentage coral cover			Total food	Male length	Total chases
	<i>Porites lobata</i>	<i>Porites compressa</i>	All species			
All (37)	-0.592***	-0.356*	-0.453**	0.286	0.164	0.052
Coral-rich only (32)	-0.171	0.236	0.031	0.657***	0.324*	0.033

† Sample size for each habitat is given in parentheses.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

decreased feeding (Table III) and a contraction of territories (Table I). In spite of increased chase rates, territories contracted only after conspecific intruders successfully invaded and established small territories within the original borders (Fig. 1). This transition indicates that decreased territory size was due to increased costs of defence and the inability to displace intruders rather than a direct response to increased food resources.

Decreased food

Territory area increased in all three food reduction experiments (Table I). The two-step reduction experiment resulted in sequential 20% and 40% increases in original area. Feeding also increased for both sexes (Table III). Surprisingly, chase rates did not increase during territory expansion and, in fact, decreased among females (Table IV). The lack of increased aggression was due to increased time

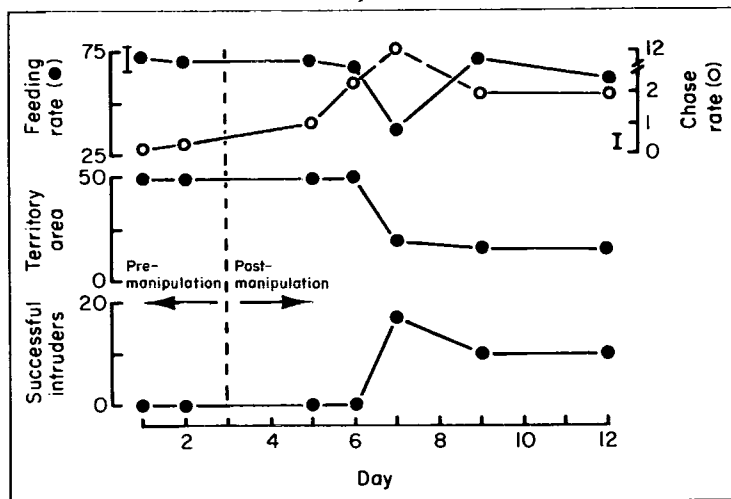


Figure 1. Changes in activity budgets, territory area and number of intruders for high-density food enhancement (experiment 2). Feeding (bites/5 min) and chase (chases/5 min) rates are averaged for the experimental pair. Territory area in m². Successful intruders: number of *C. multicinctus* that successfully defended areas within borders of original territory. Dashed vertical line indicates addition of supplemental coral and start of post-manipulation period. Vertical bars near feeding and chase rate ordinates indicate 95% confidence limits of pooled pre-manipulation data.

feeding, gradual encroachment by fish into territories of smaller neighbouring pairs, and qualitatively more vigorous (but not more frequent) agonistic interactions by the male. The territory in which non-food substrate was covered did not change in size and affirms that territory expansion by experimental fish was not a response to the food covers.

Increased competitors

Within 1 day after introduction of bottled conspecifics, all three experimental pairs contracted territories to borders set by the locations of bottled intruders (Table I). Residents spent most of their time travelling between bottles to display and attack the intruders. As a result, chase rates abruptly increased while feeding rates decreased for both sexes and persisted for the following 2-week period (Tables III and IV). Two pairs retained their retracted borders for the full experimental period while the third began to habituate to the model-bottle stimuli after a few days and then expanded one inter-bottle segment of the contracted territory into that of a smaller neighbour pair. The territory in which empty bottles were placed did not change in size and affirms that territory contraction by experimental fish was not a response to the holding bottles.

Decreased competitors

Within a few hours after removal of contiguous neighbours, experimental fish began to forage beyond their original territories, and foraging area increased between 81 and 364% in less than 2 days (Table I). Feeding rates declined among males while females fed at pre-manipulation rates for the 2-week post-manipulation period (Table III). Although observers were successful in removing most immigrating conspecifics, some confrontations were recorded and are seen as post-manipulation chases (Table IV). These encounters, however, had negligible influence on their spatial use.

Increased food and competitors

When corals alone were added beyond territory boundaries resident pairs expanded their territories to include new corals. After 3–4 days, some added colonies were defended and used exclusively by the pair. These experiments show that fish will increase their defended area to include more food. When conspecifics alone were placed around the border, territory size did not change although fish were very aggressive at their borders towards bottled fish. This experiment showed that territory residents do not increase their defended area as a result of attraction to conspecifics, although activities may be altered. The concurrent presentation of

corals and bottled competitors did not produce changes in territory size. Experimental fish moved rapidly between corals (both indigenous and added), fed by quick, intense bites, and were highly aggressive towards bottled fish and neighbours. Despite the intense competition, fish did not prevent neighbours from feeding on added corals as observed for some colonies when food was added alone. These experiments demonstrate that the continuous presence of conspecifics can inhibit access and control of food.

DISCUSSION

Chaetodon multicinctus: a Territorial Energy Maximizer

The coral-rich habitat at Puako is composed of three primary corals that are distributed relatively evenly across the reef. The coral tissues cropped by *C. multicinctus* are a renewable food resource that supply long-term energetic and nutritional requirements, and exhibit extreme longevity (Connell 1973; Maragos 1977). These characteristics collectively make corals an economically defensible food resource (sensu Brown 1964) that promotes the evolution of territorial social systems among coral-ivorous reef fishes (Tricas 1985). For *C. multicinctus*, undisturbed territories are highly stable in space and time.

Although corals may be a temporally and spatially stable resource, they are a low energy food (Tricas 1985, in press b). As a result, both sexes invest more than 90% of their time budget feeding. Hourigan (1987) found a similar proportion of time spent feeding by *C. multicinctus*, and over 90% for the omnivorous corallivore *Chaetodon quadrimaculatus*. The time invested in benthic feeding by these corallivorous butterflyfishes is extreme compared with the 9% reported for the herbivorous redlip blenny, *Ophioblennius atlanticus*, (Nursall 1981), 23% for the herbivorous reef damselfish, *Parma victoriae* (Norman & Jones 1984), 70% for the striped parrotfish, *Scarus croicensis* (Robertson et al. 1976), and 77% for carnivorous female hogfishes of the genus *Bodianus* (Hoffman 1983).

The well-defined borders among neighbouring pairs are maintained primarily through displays and passive advertisement during foraging, thus overt aggression among neighbours was infrequent. The low levels of agonistic interactions among *C. multicinctus* and other chaetodontids are

a result of individual familiarity, and agonistic bouts reinforce their territorial behaviour (Reese 1975). This 'dear enemy' phenomenon provides mutual stimulation for the maintenance of territories between neighbours but reduces time and energetic costs of defence and the risk of injury (Wilson 1975).

Spawning, diurnal sheltering, and cleaning comprise the remaining fraction of the time budget. Courtship is brief, gametes are shed seasonally by pairs into the water column at sunset, and there is no parental care (Lobel 1978; Tricas, in press a). The lack of any observed predation on adults, the long duration of territory residency, and the small proportion of time spent sheltering indicate that predation pressure on adults is not a major influence on their daily activity budget. The small time investment in spawning and sheltering further indicate that the primary function of the territory is to defend food resources rather than spawning sites or shelter as reported for other reef fishes (e.g. Warner & Hoffman 1980).

Because *C. multicinctus* feeds almost continuously and spends relatively little time at other activities, it can be classified as an energy maximizer whose foraging is constrained by time (Schoener 1983). The foraging time constraint was demonstrated in numerous experiments where increased defence costs resulted in decreased feeding. It is not possible, however, to reject the coexistence of a processing constraint (Belovsky 1981; Schoener 1983) since this species has a very long gut (Motta 1988) that becomes packed with coral tissue early in the day (Hobson 1974; Tricas, personal observation).

Determinants of Territory Size

Ecological correlates

The inverse relationship between territory size and coral abundance for the Puako population is not surprising in view of the extremes in coral abundance between the two habitats and the obligate dependence of *C. multicinctus* on coral food. The size of fish territories on the food-poor reef flat averaged almost three times that of territories in the deeper coral-rich habitat similar to that reported for the corallivorous butterflyfish, *C. trifasciatus*, on the Great Barrier Reef (Sutton 1985). When compared with experimental treatments (discussed below), correlation analyses have

limited value for predicting responses to increased or decreased food resources. In contrast, the correlation between male length and territory size within the preferred coral-rich habitat is probably related to fighting ability, and is perhaps even more important to advertisement since undisturbed territories are normally maintained by patrolling borders with infrequent overt aggression.

Food abundance

The increase in territory size associated with food reduction indicates that fish could assess changes in food availability and make compensatory responses as reported for other fishes (Slaney & Northcote 1974; Hixon 1981). Three similar food coral reduction experiments were performed on territories of *C. multicinctus* where 37–57% of original *P. lobata* corals were covered (Hourigan 1987; Hourigan et al. 1988). In those manipulations, territories also expanded, but much more rapidly, chase rates increased, and feeding rates decreased. It is likely that the expansion represents a response to insufficient resources since all food energy comes from within the feeding territory and daily energy intake is not much in excess of daily energy requirements for *C. multicinctus* (Hourigan 1987).

In contrast to the food reduction experiments, fish did not decrease territory size when food supply was increased and accompanied by moderate increases in defence costs from attracted conspecifics. Residents were unsuccessful, however, in attempts to maintain original borders at levels of food enhancement that attracted large numbers of competitors. Although untested, there is no evidence to suggest that fish would have decreased their foraging territories had competitor intrusions been eliminated in conjunction with increased food. In fact, foraging area greatly increased when neighbouring conspecifics were removed (see below). In this territorial system, fish forage over the largest area that they can successfully defend against intruders.

The defence of excess food by energy maximizers like *C. multicinctus* has both short- and long-term selective advantages. Exclusive access to extra food could increase daily energy intake through accelerated feeding on a higher self-renewing crop, or function as a hedge against unpredictable decreases in live coral (Myers et al. 1981; Lima 1984), which on Hawaiian reefs is associated primarily with winter storms (Dollar 1982; Walsh 1983). For

female fishes, increased food supply may directly increase reproductive output through increased fecundity (Tyler & Dunn 1976; Hirschfield 1980). Furthermore, energy partitioned to growth may provide size-related benefits where large males control the largest territories with the most food and have the largest female mates. This would increase reproductive output for both sexes since female fecundity increases rapidly with body length (Tricas 1986).

Competitor abundance

Fish adjusted territory size as an inverse function of competitor abundance and related costs of defence. Removal of neighbouring pairs resulted in foraging far beyond original borders similar to that reported for other fishes (Nursall 1977; Larson 1980; Norman & Jones 1984) and indicates that conspecifics often constrain territories below some larger size. The importance of conspecifics in limiting territory area is also supported by the reciprocal experiments in which territory area decreased rapidly following increased intrusion rates with bottled fish. While decreased intruder pressure has been demonstrated to increase territory size in reef fishes (Norman & Jones 1984), it is difficult to simulate increased competitor density in more natural ways since introduced fish are very likely to be chased away by territory holders (e.g. Nursall 1977).

Further evidence that competitors directly inhibit access to food resources was provided by the experiments in which additional food was presented in association with competitors. These showed that the presence (or advertisement) of a conspecific near a food coral was sufficient to disrupt normal access to food resources independent of any intruder-induced decrease in food availability. The lack of inclusion of new coral heads in their territory was due to residents spending large amounts of time displaying at bottled conspecifics and little time spent feeding on the associated coral heads.

Models of Territory Size

The major condition of the competitor constraint hypothesis, that increased food must attract additional food competitors (Myers et al. 1979), was met in this system. Food manipulation experiments show that fish adjust territory size according to defence costs against intruders rather than food supply. Therefore, in extreme cases of food in-

creases, the competitor constraint hypothesis is supported. Although territory size increased when food supply was reduced, increased food supply alone did not cause a decrease in defended area. Thus, the major prediction of the food maintenance hypothesis, that territory size is adjusted inversely to food abundance, is not supported. That hypothesis may be more appropriate for animals with a time minimization strategy or perhaps energy maximizers with spare time due to a processing constraint where the defence of extra food would have no value.

The critical assumptions of Hixon's (1980) model for an energy maximizer operating under a time constraint are met by the *C. multinctus* system. Food is evenly distributed, immobile, continuously renewing, and harvested at a sustainable yield. Territory size was predicted to decrease with increased food abundance because of an increase in time required to consume the daily production of food. In the low-density food enhancement experiments, fish increased their feeding rates to consume additional food while territories remained unchanged in size. In addition, fish accommodated the increased food supply concurrently with a moderate increase in time allocated to defence. Thus, it appears that *C. multinctus* is not as tightly constrained by trade-offs between time allocated to feeding and defence as required by the model. The decrease in territory size seen in the high-density food enhancements was not a direct response to increased time required to consume the daily production of food, but rather was due to increased time spent chasing intruders attracted to the supplemental food resources. While these responses may be inconsistent with the original prediction set where food and competitors were assumed to vary independently, they are in general agreement with predictions for systems where food and competitor abundances covary in such a manner or foraging efficiencies change with food abundance (Schoener 1983; Hixon 1987).

Ebersole (1980) modelled the effects of food supply and attracted competitors (his equation set 5 for insectivorous birds). At a given food density, territory size was determined by the total time that could be spent foraging in the territory (a constraint similar to Hixon's model), and was influenced by both travel time to a central nest (ignored for the present system) and time spent in defence of the territory perimeter. The model predicts that territory size should vary inversely

with competitor abundance and also food supply if accompanied by covarying levels of attracted competitors. This model can account for decreased territory size when defence costs are independently high or vary directly with increased food supply. However, the prediction that territory size should vary directly with food abundance if competitor intrusion rates remain constant failed when food supply was decreased. It is unlikely that lowered defence costs which accompanied food reduction were responsible for the increase in area especially when Hourigan's (1987) and Hourigan et al.'s (1988) extreme food reduction experiments for *C. multinctus* (increased territory area at increased defence costs) are considered. It is more probable that territories expanded because food was reduced below a level that could provide energy requirements for the pair. Both deterministic models would benefit from explicit functions to account for responses to food decreased below some minimum supply level, and strategies for the maintenance of surplus food resources in the non-breeding season for energy maximizers.

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