

The use of territorial gardening versus kleptoparasitism by a subtropical reef fish (*Kyphosus cornelii*) is influenced by territory defendability

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Many territorial herbivorous animals increase the productivity or quality of the prey community on their territory. However, this gardening tactic may be vulnerable to kleptoparasitism unless gardeners can exclude others from the patch. We investigated the influence of territory defendability on the decision of western buffalo bream (*Kyphosus cornelii*) to defend an algal garden or to leave their territories and invade those of conspecifics. Fish monitored while away from their territories did kleptoparasitize the gardens of conspecifics. We manipulated the structural complexity of territories through the addition of short or tall simulated vegetation. Increasing the height of simulated vegetation on the territory decreased the defendability of territories but increased their safety for fish; territories with tall vegetation were more easily invaded by conspecifics, but fish returned more rapidly to these territories after being disturbed. In a paired experiment, fish spent more time away from their territories (roving) when tall vegetation was added than when short vegetation was added. However, this effect was influenced by depth, with a greater difference between treatments on deeper territories, and by body size, with a greater difference for larger fish. These results support the prediction that territory-holding individuals faced with a trade-off between defending their own garden or kleptoparasitizing from others adjust their use of these tactics based on the defendability of resources. *Key words:* kleptoparasitism, Kyphosidae, resource defense, territorial gardening, western buffalo bream. [*Behav Ecol* 14:561–568 (2003)]

Many interactions among foraging animals are characterized by kleptoparasitism, in which some individuals use the investment of others in some way to reduce the costs of obtaining food (Barnard, 1984; Giraldeau and Caraco, 2000). These tactics include aggressive kleptoparasitism of items acquired by others (e.g., bald eagles, *Haliaeetus leucocephalus*; Hansen, 1986), joining successful foragers at discovered patches (e.g., spice finches, *Lonchura punctulata*; Giraldeau et al., 1994), eavesdropping on publicly available information regarding the likely location of resources (e.g., little brown bats, *Myotis lucifugus*; Barclay, 1982), and pilferage of resources that are left unguarded (e.g., kangaroo rats, *Dipodomys merriami*; Daly et al., 1992) or can be stolen before the defender detects the thief (e.g., kleptoparasitic spiders, *Argyrodes elevatus*; Vollrath, 1984). Many foraging groups are characterized by at least occasional kleptoparasitism, and understanding how its use changes with ecological and social conditions is an integral part of understanding social foraging systems.

Animals that engage in behaviors that result in the maintenance of food patches that are predictable and available may be particularly vulnerable to exploitation by kleptoparasites. Such behaviors include those of several marine organisms—including reef fish, limpets, and nereid polychaetes—that increase the biomass or productivity of the algal community on their territories by excluding other

grazers, removing inedible species of algae, and increasing the substratum available for edible algae (Branch et al., 1992). When this behavior occurs at a fixed site and benefits the individual grazer involved, it has been termed gardening (Branch et al., 1992). In terrestrial environments, the storage of food in caches or hoards similarly results in valuable patches that can benefit the owner but potentially can be pilfered.

Such costly behaviors can only persist if the net benefit to the gardening or hoarding individual exceeds the net benefit to others (Andersson and Krebs, 1978; McNamara et al., 1990). Among scatter-hoarding animals, the location of items may be better known to the hoarder than to others (see Hitchcock and Sherry, 1995), thus meeting this condition. Gardening of algae appears to be restricted to territorial species (Branch et al., 1992) that can largely exclude others from using their gardens. Nevertheless, because gardens or hoards represent valuable food patches, other foragers commonly attempt to exploit them. For example, eastern chipmunks (*Tamias striatus*) enter the burrows of absent conspecifics and pilfer seeds from the larders therein (Elliott, 1978), and pikas (*Ochotona princeps*) steal from the haypiles of conspecifics (McKechnie et al., 1994). Among algal-grazing fish, theft of food from gardens occurs, and not only when the territory-holder is absent. Western buffalo bream (*Kyphosus cornelii*, hereafter WBB) often invade the gardens of conspecifics while the territory holder is distracted by other invading fish (Hamilton and Dill, in press). Indeed, circumventing the territorial defenses of gardeners is thought to be an important factor in the formation of feeding groups by many nonterritorial reef fish (Foster, 1985; Hamilton and Dill, in press; Robertson et al., 1976).

In some cases, gardeners and kleptoparasites are of different species. Blue tang surgeonfish (*Acanthurus coeruleus*;

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Foster, 1985) and striped parrotfish (*Scarus iserti*; Robertson et al., 1976) forage in large "roving" groups, feeding from the algal turf defended by damselfish (Pomacentridae). In other cases, individuals of the same species play both tactics, although the use of the tactics may differ with condition. In WBB, use of the gardening tactic is more common among fish that are large and sexually mature (Moore, 1993), although these differences in condition may be consequences of the benefits of gardening.

In WBB, most fish that hold gardens at least occasionally leave theirs (Hamilton IM, personal observation). This time spent away from gardens may indicate that such fish are using a mixture of kleptoparasitism and gardening tactics to obtain food. If so, these fish provide an opportunity to test predictions regarding the use of alternative foraging tactics. Fish may leave their territories for other reasons, such as movement after a disturbance (see Itzkowitz, 1978) or avoiding predators. Because the location of a garden is fixed, gardening fish may be more easily and predictably found by predators than are roving fish. In WBB, gardens are in relatively shallow water and are conspicuous even from the air. Therefore, gardening fish may be at greater risk of predation from birds, particularly ospreys (*Pandion haliaetus*), which are known to capture them (Moore, 1993; Saunders and de Rebeira, 1993).

In this study, we followed roving gardening fish to determine whether they kleptoparasitized the territories of other gardeners, and we found that these fish indeed did so. We compared the feeding rates of territorial and roving fish to determine whether the foraging payoffs to each tactic were equivalent. We then used this system to test the prediction that fish would spend more time away from their territories when exclusivity of resource use is reduced, by manipulating the structural complexity of territories through the addition of simulated vegetation. Increasing structural complexity can reduce territory defendability by reducing territory holders' ability to detect intruders (Eason and Stamps, 1992). We therefore predicted that use of the gardening tactic would decrease when structural complexity was increased. This could be manifested as a decrease in garden maintenance and defense, an increase in the use of the kleptoparasitic roving tactic, or both. We also predicted that if territories can be more easily invaded when structural complexity is increased, roving fish should invade these territories more frequently. Roving fish should also invade in smaller groups when complexity is increased, because the net benefit of joining a group would be lower relative to solitary foraging. We also used this manipulation to address an alternative hypothesis: that time spent away from territories is a result of avoidance of short term increases in predation risk. We expected that our manipulation of territory defendability would also decrease the riskiness of the territorial tactic. Increasing structural complexity has been shown to reduce the perceived riskiness of a habitat for a variety of fish (e.g., Eklov and Persson, 1996; Gotceitas, 1990; Lonzarich and Quinn, 1995; Pettersson and Bronmark, 1993). Therefore, if fish are leaving territories to avoid predators, we expected them to spend more time on their territories when structural complexity was increased—the opposite of the prediction of our defendability hypothesis.

METHODS

Study species

The western buffalo bream is a medium-sized subtropical reef fish endemic to the eastern Indian Ocean along the coast of Western Australia. Adult WBB are almost exclusively herbivorous, browsing on filamentous red algae (Clements and

Choat, 1997). In some regions, some larger fish defend algal gardens (Berry and Playford, 1992; Moore, 1993), which are conspicuous patches of closely cropped red algae (less than 2 cm), in contrast to the taller seagrasses, *Sargassum*, and coralline red algae of unbrowsed areas. These patches of algae are roughly elliptical when density is low or polygonal when density is high (mean \pm SD size of territories at five bays on Rottneest Island in 1999 and 2001: length, 4.37 ± 1.00 m; width, 3.13 ± 0.75 m; elliptical area, 11.04 ± 4.57 m², $n = 36$). Gardens are defended from competitors, including conspecifics and, to a lesser degree, other herbivorous fish, particularly other members of the family Kyphosidae (e.g., *K. sydneyanus*, *Girella zebra*, and *Microcanthus strigatus*) and damselfish (*Parna mccullochi*, *P. occidentalis*, *Pomacentrus milleri*, and *Stegastes obreptus*). Gardens are also weeded. Strings of brown algae introduced to territories are quickly removed by the resident fish (Moore, 1993).

Only a single fish defends each garden. These fish may be of either sex and often have developed gonads (Moore, 1993). However, neither mating nor eggs have ever been observed on the territories (Berry P, personal communication; Hamilton IM, personal observation). Territorial vacancies appear to be filled by fish immigrating from elsewhere rather than by movement of neighboring fish (Moore, 1993).

WBB that do not garden typically band together in large groups (50 or more individuals) when not foraging. When foraging, these roving fish are generally solitary, feeding mostly on floating clumps of red algae and the defended and undefended territories of conspecifics and of damselfish. However, they may form pairs or small groups (Hamilton and Dill, in press), and have occasionally been observed invading the territories of conspecifics in groups of 30 or more individuals (Hamilton IM, personal observation).

In this paper, individual fish that at least sometimes defend a territory are referred to as territory-holders. When they are defending their territories, we refer to them as using the territorial tactic. When territory-holders and other fish are not on territories, we refer to them as using the roving tactic.

Study site

This study was conducted from the University of Western Australia Department of Zoology Research Station at Rottneest Island, Western Australia (32°00' S, 115°30' E), from February–April 2001. Rottneest Island is located in the Indian Ocean, 19 km west of Fremantle in southwestern Western Australia. Experiments were conducted at three sites on the western half of the island: Little Armstrong Bay on the north side of the island, and Kitson Point and Mary Cove on the south.

Comparison of territorial and roving fish

One hundred and nine roving fish (40 in Little Armstrong Bay, 27 at Kitson Point, and 42 in Mary Cove) were each followed by a snorkeling observer. Individual fish could be identified by patterns of scarring, and only one follow per individual was made. The observer remained several meters away from the fish at all times and followed it until it was lost from view or returned to a territory, for a maximum period of 15 min. During this time, the observer recorded the number of bites taken by fish from gardens and undefended areas, and whether the owner of each invaded garden chased the invading fish. If, during the observation period, a fish returned to a garden and defended it, the fish was recorded as a territory holder.

We compared the feeding rates (bites per minute) of territorial and roving fish in the three bays using a mixed-

model two-factor ANOVA, with foraging tactic as a fixed effect and site as a random effect in the model. We also compared the total rates of agonistic interactions (chasing or being chased) with conspecifics and damselfish for the two tactics with a similar model. Feeding rates of territorial fish were obtained by using the six observations on focal territorial fish made during territory watches (described below). We recorded the rate at which bites were taken by the territory-holder per minute that it was present on its territory, and used the means of all six observations in our analyses. We also conducted this analysis by randomly selecting one observation per territorial fish. The results of these two analyses were qualitatively the same, and we present only the results of the former. Many roving fish swam out of view quickly, whereas most territorial fish spent some time away from their territories and observers. To account for possible differences in observation duration between all territorial and all roving fish, only data from fish that were followed for more than 240 s were used.

We compared the likelihood of feeding during the observation period between roving fish that were known to be gardeners and other rovers by using logistic regression. For roving fish that fed, the proportions of feeds taken from territories were compared between those owning a garden and other rovers and among sites using a two-factor ANOVA. Only fish that were followed for less than 600 s were used in these analyses, so that the mean duration of follows for the two types of roving fish were approximately equal.

Disturbance experiment

To measure the effects of structural complexity on return time after disturbance, we randomly selected 12 territories each at Kitson Point and Mary Cove, and six at Little Armstrong Bay. Territories were randomly assigned to one of two simulated vegetation treatments. Those in the short vegetation treatment were manipulated by adding an 80-cm length of rope attached to two 1.5-kg dive weights; thirty 10-cm-long, 1-cm-wide fronds of black plastic were tied to each rope. The tall vegetation treatment was identical, except that the fronds of black plastic were 30 cm long. The tall vegetation treatment was of similar height to the *Sargassum*, coralline red algae, and seagrasses found in undefended areas and in the “hedgerows” that separate adjacent territories.

Ropes were extended to their full length and placed in the center of each territory so that the fronds floated up into the water column. Fish were then left to acclimate for at least 30 min before the start of the experiment. Previous observations indicated that fish returned to their territories and began defending them and/or feeding within 5 min after disturbance (Hamilton IM, personal observation). Each fish was then rapidly approached twice by a snorkeler, separated by at least 15 min. The snorkeler attempted to maintain a constant speed and approach the fish side on. In all cases, fish left their territories on approach. We recorded the time from when the fish crossed the boundary between its garden and adjacent gardens or undefended areas on leaving to when it crossed on returning. The log-transformed mean times that fish were away from their gardens were compared between treatments and sites with a mixed model two-factor ANOVA, with site as a random effect and treatment as a fixed effect.

Focal territory observation

Focal territories were manipulated by adding structural complexity to assess the effects of this manipulation on the decision of the territory holder to defend or kleptoparasitize. At each site, six territories that were not used in the previous

experiment were selected for observation. One of the territories in Little Armstrong Bay was permanently abandoned before any observations had occurred; therefore, results from a total of 17 territories are reported. A fish's territory was defined as the area enclosed by the reef edge and the hedgerows that separate adjacent gardens (Berry and Playford, 1992).

To manipulate complexity, simulated vegetation was added to each territory as described above. For each territory, we conducted three trials with the tall vegetation treatment and three with the short vegetation treatment, presented in random order. After vegetation was added, fish were allowed to acclimate for at least 30 min before observation. Territories were then observed for 15 min by a snorkeling observer, who remained at least 3 m from the territory. For each territory, the location of the observer was the same for all watches, so that any possible disturbance resulting from observation should be the same in both treatments.

During this time, we recorded the total length of time the fish was on its territory, defined as the water column above and within the boundaries described above. If a fish crossed the boundary of its territory, but remained within an estimated 2 m distance and had an unbroken line of sight to its garden, we considered it to be still on its territory; this happened rarely, as most fish that crossed these boundaries disappeared from view. Fish were considered to be off their territory if (1) they were in a position in which they were unable to see their territory, (2) they were more than 2 m from the boundaries of their territory, or (3) they were observed feeding on an adjacent territory.

We also recorded the number and size of groups of roving fish that crossed into the territory. Fish were considered to be in a group if they were within two body lengths of one another and swimming in the same direction when they entered the garden. The tolerance of the gardener to roving fish was qualitatively recorded on a scale from one to four as follows: (1) chase invader, (2) approach and signal to invader, usually by leaning to one side, (3) approach, (4) ignore invader. We defined a “tolerance index” for each individual, which was the mean tolerance toward solitary roving fish invading its territory. We did not include invasions by larger groups or neighboring gardeners in the calculation of tolerance because we expected that territorial fish might differ in their tolerance toward such fish. A high value of the tolerance index indicates greater tolerance toward invading fish.

We used several measures to estimate the loss of algae to roving fish on manipulated territories. These were the number of bites taken by roving fish per minute that the territory was defended, the overall bite rate (including undefended periods), the number of bites taken per invasion, the number of groups invading per minute that the territory was defended, the overall invasion rate, and group size. These measures allowed us to examine effects of the manipulation on the defendability of the territory (i.e., the loss of algae per invading group) and on the rate of loss of territorial resources to roving fish.

To examine the influence of treatment on the behavior of gardening fish, we compared the mean log-transformed time spent away from the territory and mean tolerance index between tall and short vegetation treatments. Time away was used as a measure of the proportion of time that gardening fish spent using the roving tactic. We used tolerance as a measure of the willingness of territorial fish to defend their territory.

The experiment was of a paired design, and we tested for effects of treatment, and interactions between treatment and site, body size, and territory depth on these eight measures (bite rate while territories occupied, overall bite rate, bites per

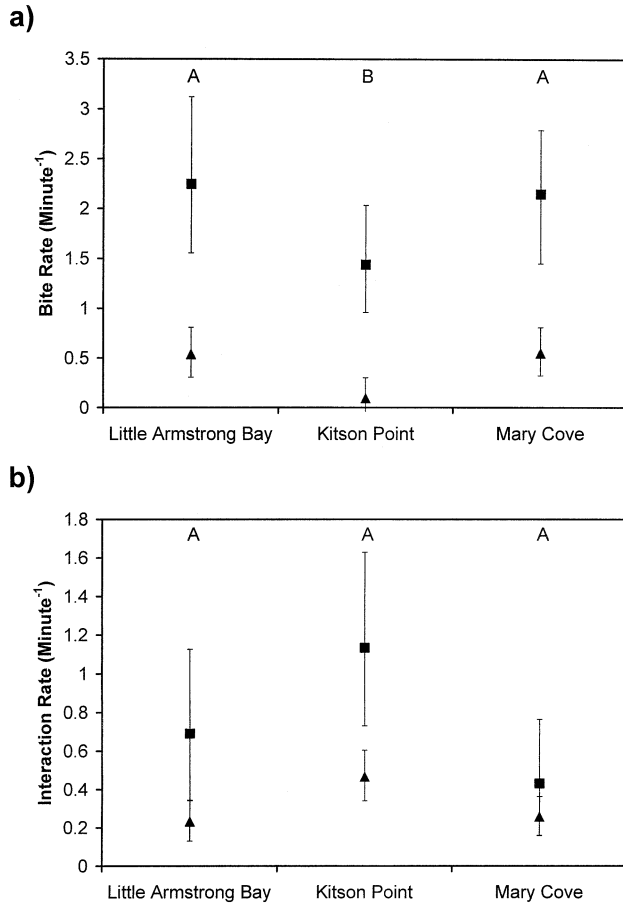


Figure 1 Number of bites (a) and agonistic interactions with conspecifics (b) per minute of observation for the two foraging tactics (territorial and roving) of western buffalo bream at three sites at Rottnest Island. Error bars are 95% confidence intervals. Territorial fish (squares) fed significantly more frequently than roving fish (triangles) at all sites. The overall rates of interactions with others did not differ significantly between territorial and roving fish. The rates of feeding and agonistic interactions letter did not differ significantly among sites denoted by the same letter, using Tukey's HSD test for multiple comparisons. There were no significant interactions between tactic and site.

invasion while occupied, invasion rate while occupied, overall invasion rate, invading group size while occupied, time spent away from the territory, and tolerance toward invaders). Preliminary comparisons indicated that the effect of vegetation treatment on any of these measures did not differ between Kitson Point and Mary Cove. In addition, these sites were sufficiently close together that roving fish could swim between them. Therefore, we pooled these two sites into a "south" site, allowing us to enter site into the multiple regression model as a binary dummy variable. Other variables entered into the model were the length of the territory-holder and the depth of the deepest point on the territory. We included body length because we expected the ability to defend a territory to be correlated with size. We included depth in the model because territory productivity and safety may be correlated with depth. Because we did not capture territorial fish, we estimated fork length from videotapes of the territorial fish swimming next to and parallel with an object of known length. Depth of the territory was measured relative to chart datum using tide height data obtained from the National Tidal Facility (Flinders University, South Australia).

Table 1

The influences of site and length of simulated vegetation added to territories on the time that gardening western buffalo bream spent away from manipulated territories after being disturbed by a rapidly approaching snorkeler

	Mean time away (s)	95% confidence intervals	N
Treatment			
Short vegetation ^a	17.43	13.13–24.02	15
Tall vegetation ^b	12.44	8.87–15.67	15
Site			
Little Armstrong Bay ^a	19.33	12.63–29.33	6
Kitson Point ^a	12.33	9.79–17.16	12
Mary Cove ^a	13.84	9.78–19.41	12

Categories within a factor (treatment or site) that are followed by the same letter were not significantly different in multiple comparisons with Tukey's HSD test.

For each of these eight behavioral measures, we constructed multiple regression models by using the difference between tall vegetation and short vegetation as the dependent variable, and all combinations of territory depth, size, and site and all interactions among these, restricted so that no interaction could be included without all of its components also included, as independent variables. We compared Akaike's information criteria (AIC) of all possible models. The model with the lowest AIC was considered the most parsimonious. We used the variables retained in the model with the lowest AIC to construct repeated-measures ANCOVAs and used these to test for an effect of the experimental treatment on each dependent variable.

RESULTS

Comparison of territorial and roving fish

Territorial fish fed at a significantly higher rate than did roving fish ($F_{1,2,082} = 5399.6$, $p < .005$) (Figure 1a). Feeding rate also varied among sites, ($F_{2,2} = 29.75$, $p < 0.05$) with all fish feeding at a lower rate at Kitson Point than at Little Armstrong Bay or Mary Cove. The interaction between site and tactic did not significantly influence feeding rate ($F_{2,85} = 0.12$, $p > .85$). Territory-holders observed while on their gardens were not involved in significantly more agonistic interactions per minute than were roving fish observed while roving ($F_{1,2,006} = 12.98$, $p > .05$) (Figure 1b). The rate of agonistic interactions did not vary significantly among sites ($F_{2,2} = 4.50$, $p > .15$) or with the interaction between site and tactic ($F_{2,84} = 1.71$, $p > .15$).

Eighteen of the 109 roving fish that were followed defended a garden, including two fish used in focal territorial observations. Both of these fish fed off other WBB territories. Seventy-seven fish, including 15 that defended a garden, were followed for less than 600 s and were used for comparisons. Fish that held gardens did not differ in their behavior from other roving fish. When gardening fish were away from their territories, 40% of observed fish fed, whereas 50% of a random selection of roving fish (which may have included some territory-holders) fed. This difference was not significant (Wald $\chi^2 = 0.17$, $df = 1$, $p > .68$). Roving fish were equally likely to feed during the observation period at the three sites (Wald $\chi^2 = 1.30$, $df = 2$, $p > .5$), and the interaction between site and type of roving fish did not significantly influence the proportion of fish feeding (Wald $\chi^2 = 0.44$, $df = 2$, $p > .8$).

Both types of roving fish took food from territories, as well

Table 2

Adjusted mean values of eight measures of territory defendability, loss of algae to roving fish, and territorial defense after the addition of tall or short simulated vegetation ($n = 17$)

Variable	Short (mean)	Tall (mean)	Difference (mean)	Difference +1 SE	Difference -1 SE
Bites per minute	0.051	0.110	0.059	0.076	0.042
Overall bites per minute	0.051	0.158	0.107	0.141	0.073
Bites per invasion	0.051	0.117	0.066	0.091	0.041
Invasions per minute	0.756	0.839	0.083	0.174	-0.003
Overall invasions per minute	0.445	0.522	0.077	0.191	-0.017
Group size	1.41	1.45	0.04	0.12	-0.04
Time away (s)	39.61	57.89	18.28	28.34	9.68
Tolerance score	2.08	2.26	0.18	0.28	0.08

Statistical tests (Tables 3 and 4) were performed on the differences between treatments. Reported values are back-transformed from ln-transformation when appropriate.

as bites from undefended areas or floating algae. Although fish known to hold a garden took a smaller proportion of their food from the territories of other fish than did other roving fish (least-squares mean \pm SE: gardeners, $33 \pm 19\%$, $n = 6$; unknown roving fish, $43 \pm 9\%$, $n = 31$), this difference was not significant ($F_{1,2,92} = 0.79$, $p > .4$). This proportion did not differ significantly among sites ($F_{2,2} = 0.15$, $p > .85$) or with the interaction between site and type of roving fish ($F_{2,31} = 0.41$, $p > .45$).

Return after disturbance

Fish returned significantly sooner after disturbance when tall vegetation was added to their territories than when short vegetation was added ($F_{1,2,80} = 14.94$, $p < .05$) (Table 1). There was not a significant effect of site on the time that fish spent away from their territories in this experiment ($F_{2,2} = 5.00$, $p > .15$) (Table 1). The interaction between these factors also did not significantly influence time to return ($F_{2,24} = 0.36$, $p > .70$).

Territory defendability

The rate at which bites were taken from defended focal territories by roving fish was greater when tall vegetation was added than when short vegetation was added (Table 2). This difference was significant in repeated-measures ANCOVA (Table 3). However, there was also an effect of the interaction between site and depth on this difference (Table 3). At the south site, there was little change in this difference with depth, whereas at Little Armstrong Bay, the difference in bite rate between treatments decreased with increasing depth. The main effects of depth and site were also significant in the model (Table 3). Including both occupied and unoccupied periods, the overall rate at which bites were taken from territories was significantly greater when tall vegetation was added to the territories (Tables 2 and 3). This difference was greater at Little Armstrong Bay than at the south site (Table 3). No other effects were significant in this model.

The difference in bites removed by roving fish arose largely because each group of roving fish was more likely to feed when invading territories with tall vegetation (Tables 2 and 3). The effect of treatment differed among sites and with the interaction between depth and site; however, these differences were marginally not significant (Table 3). For both occupied territories and for the observation period as a whole, the rate of invasion was slightly higher when tall vegetation was added, but not significantly so (Tables 2 and 3). The rate of invasions (including both occupied and unoccupied periods) was

higher for the tall treatment than for the short one at Little Armstrong Bay, and slightly lower for the tall treatment at the South site; this difference was not significant for either occupied territories or the entire observation period (Table 3). The sizes of groups invading occupied territories did not differ significantly among treatments (Tables 2 and 3).

Unexpectedly, territories were invaded more frequently when occupied than when unoccupied. This difference was significant in a repeated measures ANOVA, with site included as a main effect ($F_{1,13} = 15.9443$, $p < .005$). This difference was not significantly influenced by site ($F_{1,13} = 0.04$, $p > .8$).

Territory defense

Overall, there was a significant effect of the manipulation on the time that fish spent away from their territories (Table 4). Territory holders spent more time away from the territory when tall vegetation was added than when short vegetation was added (Table 2). However, this effect was also influenced by the body size of territory holders and the depth of the territory. The effects of vegetation height on the time spent away from the territory were greater for larger fish and those on deeper territories (Figure 2). The tolerance of territory holders towards invaders did not differ significantly between treatments (Table 4), although there was a trend for territory holders to be more tolerant when tall vegetation was added (Table 2).

DISCUSSION

The defense of resources typically involves trade-offs, because time and energy allocated to defense often cannot be allocated to finding food (Ydenberg and Krebs, 1987), avoiding predators (Martel and Dill, 1993), or gaining mates (Dunn and Robertson, 1993; Soukup and Thompson, 1997). Territory-holding WBB face a trade-off between using their own algal garden and kleptoparasitizing those of others. In this study, we found that changes in the ecological characteristics of algal gardens that made them more difficult to defend influenced how fish allocated time between these behaviors. In our experiments, algae was lost to roving fish at a greater rate when tall vegetation was added to territories than when shorter vegetation was added. This was because each invading fish was more likely to successfully remove algae when tall vegetation was added. When tall simulated vegetation was added, territory-holders did not become less aggressive to invading fish. However, territory-holders of mean length on territories of mean depth spent more time away from their territories, as predicted based on the defendability hypothesis.

Table 3
Repeated-measures ANCOVA tables for six measures of territory defendability and loss of algae to roving fish

	<i>F</i>	Numerator df	Denominator df	<i>p</i>
Bites per minute occupied				
Treatment	13.24	1	13	<.005
Treatment × site	12.44	1	13	<.005
Treatment × depth	5.11	1	13	<.05
Treatment × site × depth	5.31	1	13	<.05
Overall bites per minute				
Treatment	9.86	1	11	<.01
Treatment × site	6.53	1	11	<.05
Treatment × depth	1.57	1	11	>.2
Treatment × size	2.67	1	11	>.1
Treatment × site × depth	2.77	1	11	>.1
Treatment × site × size	2.40	1	11	>.1
Bites per invasion				
Treatment	7.05	1	13	<.025
Treatment × site	4.39	1	13	>.05
Treatment × depth	2.19	1	13	>.15
Treatment × site × depth	3.21	1	13	>.05
Invasions per minute occupied				
Treatment	0.92	1	12	>.35
Treatment × site	0.41	1	12	>.5
Treatment × depth	0.25	1	12	>.6
Treatment × size	1.77	1	12	>.2
Treatment × site × depth	4.63	1	12	>.05
Overall invasions per minute				
Treatment	0.64	1	15	>.4
Treatment × site	5.70	1	15	<.05
Group size				
Treatment	0.22	1	15	>.6
Treatment × size	3.81	1	15	>.05

Treatment refers to the difference in the response variable between tall and short vegetation treatments.

Alternatively, fish could have spent more time away from territories with tall vegetation because such territories were perceived as holding poorer quality resources or because tall vegetation could provide cover for underwater predators. However, the results of our disturbance experiment do not support these hypotheses. On disturbance, fish returned more quickly to territories with tall vegetation, suggesting they were perceived as either safer or more valuable than those with short vegetation.

We were unable to follow focal territory-holders while they were away from their territories during the experiment. However, other territory-holders, and some of the focal territory-holders observed at other times, used kleptoparasitism. Thus, although we cannot conclusively say that focal fish switched to kleptoparasitism when tall vegetation was added, it did result in a switch to greater use of a tactic that would allow the use of kleptoparasitism.

Similar movements away from the territory have been observed in several damselfish in which all individuals hold territories (Bartels, 1984; Itzkowitz, 1978). It has been suggested that damselfish travel away from their territories for several reasons, including short forays for feeding, and longer ones for courtship and the establishment of new territories after disturbance (Bartels, 1984). Our observations indicate that foraging is an important component of extraterritorial movements in WBB. Forays by WBB were generally of short duration and often involved feeding from defended and undefended areas (Figure 1). Territory-holders

are generally sexually mature (Moore, 1993); however, those followed while roving never engaged in apparent courtship behavior (Hamilton IM, personal observation). Although feeding is clearly important, the intake rate from roving was much lower than that from gardening (Figure 1). This may be owing in part to the inclusion of small nonterritorial fish in the roving category, but our comparisons of roving fish that

Table 4
Repeated measures ANCOVA table for two measures of territorial defense by territory-holders

	<i>F</i>	Numerator df	Denominator df	<i>p</i>
Time away				
Treatment	5.55	1	12	<.05
Treatment × site	1.95	1	12	>.15
Treatment × depth	5.78	1	12	<.05
Treatment × size	10.10	1	12	<.01
Treatment × site × depth	2.22	1	12	>.15
Tolerance score				
Treatment	3.11	1	15	>.05
Treatment × site	1.49	1	15	>.2

Treatment refers to the difference in the response variable between tall and short vegetation treatments.

hold gardens and unknown roving fish indicate that the foraging behavior of these groups are similar. Because the expected intake rate from roving is relatively low, this suggests that there are other benefits to roving, in addition to gaining foraging opportunities.

As suggested for damselfish (Bartels, 1984), territory-holding WBB may be able to gain information on the quality and availability of neighboring territories from their forays. We did not observe territory switching by these fish, and individuals have been observed on the same territory for periods of up to several years (Berry and Playford, 1992). However, one focal territory was abandoned, and vacancies created by removing territory-holders are quickly filled by other large fish (Moore, 1993), suggesting that fish may occasionally move among territories.

Another possible benefit from such movement is avoidance of predators. However, this alone cannot explain our observations. Fish temporarily left their territories after the close approach of a snorkeler, but returned more quickly when tall vegetation was present. If fish were leaving territories to avoid predators, we would expect them to allocate less time to foraging away from safe valuable territories. Instead, we found that focal fish in territory watches spent more time away from the territory when tall vegetation was added, suggesting that, at least for large fish on deeper territories, the additional benefit of safety (or increased value relative to risk of mortality) did not compensate for the reduced defendability of the territory.

Although fish generally spent more time away from their territories when complexity was increased, as predicted by the defendability hypothesis, this effect was itself influenced by the depth of the territory, so that, on shallow territories, some fish spent more time on their territory when complexity was high (Figure 2b). Deeper territories receive less light and, therefore, probably differ in both the productivity of algae and the algal community present. If territories in deeper water were less valuable, the net benefits to remaining on the territory when defendability was decreased may have been lower there than on shallow productive territories. Although we did not find support for the hypothesis that movement away from the territory was solely the result of predator avoidance, the safety of territorial foraging may still influence the decision to use kleptoparasitism. Risk of predation from birds, such as ospreys, is likely higher in shallow water, whereas risk from underwater predators, such as Australian sealions (*Neophoca cinerea*), bottlenose dolphins (*Tursiops aduncus*), and western wobbegongs (*Orectolobus* sp.), may be lower in shallows. The relative risk to territorial WBB from aerial and underwater predators is unknown. However, their behavior suggests that the perceived risk of predation from aerial predators was high; fish tended to react to even nonpredatory birds flying over them by moving close to the substrate (Hamilton IM, personal observation). If this risk is high, fish on shallow territories may have accepted reduced defendability of territories because of the increased safety afforded by the vegetation.

We also found that larger fish spent more time away from their territories when tall vegetation was added than did smaller fish. Smaller fish may be more vulnerable to predators, particularly gape-limited underwater predators and birds. Larger fish may also gain more from kleptoparasitism if they are better able to successfully invade the territories of others.

The producer-scrrounger model and similar models of kleptoparasitism predict that the use of kleptoparasitism should increase when foragers are less able to defend or exclusively use resources they produce (Barnard, 1984; Hamilton, 2002; Vickery et al., 1991). This prediction has been supported in tests with flocks of spice finches (Giraldeau

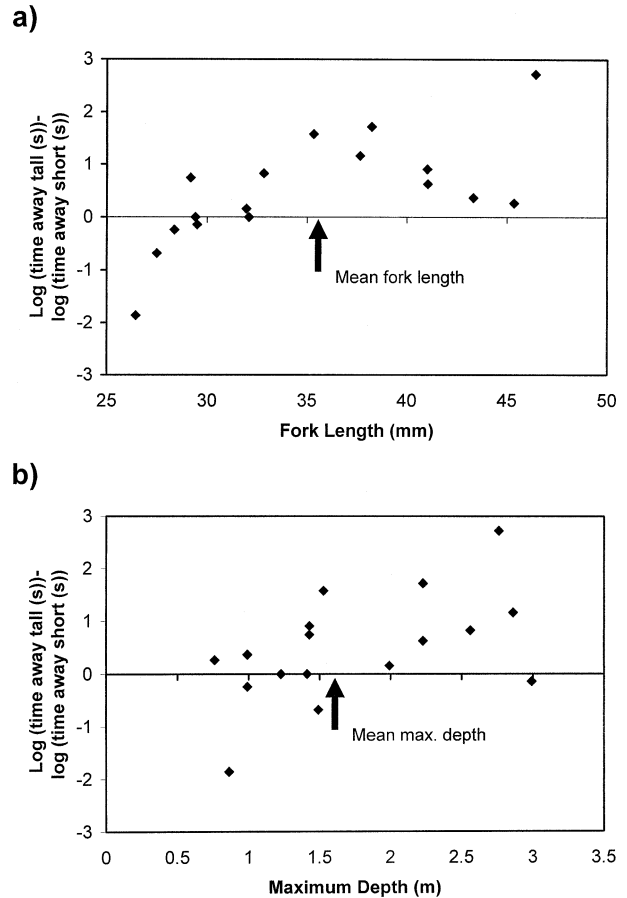


Figure 2 Interactions between body size (a) and territory depth (b) and the effect of the height of simulated vegetation on the time that gardening western buffalo bream spent away from their territories during observations. The difference in the mean log-transformed time spent away between tall and short treatments increased with increasing fork length of the gardening fish and with increasing depth of the deepest point on the territory. At the mean fork length and mean depth, the difference between tall and short vegetation treatments was significantly greater than zero.

and Livoreil, 1998). These models describe systems in which the ability of resource owners to exclusively use resources is an attribute of prey patches in general, rather than of a specific patch, as in our study. Our study suggests that the general prediction that the use of kleptoparasitism increases when resources are difficult to defend is applicable to a wide range of kleptoparasitic systems.

Our system differs from those assumed in producer-scrrounger models in another important way. By switching to roving, gardening fish increase the availability of food to other roving fish in the short term, because the garden is undefended. Despite this, the rate of invasions by roving fish was much lower when gardens were undefended. This may be because gardening fish chose to leave their territories only when the likelihood of being invaded was low, or because roving fish used the presence of a territorial fish as a cue that the territory was productive or safe to invade (i.e., the absence of the owner may have been owing to a predatory attack or a short-term increase in riskiness). In the longer term, increasing use of kleptoparasitism by territory-holders would likely result in reductions in the maintenance of territories and in their value to those territory-holders and to roving fish. This suggests the potential for indirect interactions between

factors influencing the relative uses of gardening and kleptoparasitism, such as territory complexity, the quality of algae, and possibly predation risk, and the growth and behavior of other herbivores (and their predators) on reefs where facultatively territorial herbivores are present.

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