GROUP FORAGING BY A KLEPTOPARASITIC FISH: A STRONG INFERENCE TEST OF SOCIAL FORAGING MODELS

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Abstract. Animals that obtain food by using the investment of other foragers (kleptoparasites) often do so in groups. We tested whether group formation by a kleptoparasitic fish, the western buffalo bream (*Kyphosus cornelii*), fit the predictions of five social foraging models. Two aggregation economy models assumed that there was some benefit to grouping shared by group members, such as reduced predation risk or increased ability to gain access to resources. These models and a third, the dispersion (ideal free) economy model, assumed that kleptoparasites had perfect information regarding the quality of opportunities for kleptoparasitism. The other two models did not make this assumption. These producer–scrounger models assumed that some kleptoparasites (producers) discovered opportunities, while others used producers to reduce the costs of foraging. These last two models differed in whether foragers could estimate the state of current opportunities for kleptoparasitism. We compared typical group size, and the influence of group size on intake rate and the success of kleptoparasitic attempts, with the predictions of these models. We found that typical group size was larger during periods when opportunities for kleptoparasitism were poor than when good and that there was no influence of group size on the likelihood that the group was successful at kleptoparasitizing. Individual intake rate declined with group size for small group sizes, but increased with group size in large groups. However, large groups were rare. For small groups, only a producer–scrounger model allowing foragers to update their information could not be rejected. For large groups, neither that model nor the aggregation economy with foraging benefits model could be rejected. We compare these results with those of other studies of kleptoparasitic groups.

Key words: aggregation economy; dispersion economy; ideal free distribution; information; kleptoparasitism; Kyphosus cornelii; *producer–scrounger model.*

INTRODUCTION

Animals forage in groups for many reasons. These reasons include reduced time and energy expenditures searching for prey (Barnard and Sibly 1981, Pitcher et al. 1982), cooperative capture of prey (Packer and Ruttan 1988), and reduced predation risk (Dehn 1990, Wrona and Dixon 1991, Krause et al. 1998). Aggregations may also occur despite the absence of any benefit to grouping, as animals congregate in productive patches (Fretwell and Lucas 1970). In addition, animals that forage by exploiting patches or items discovered by others (kleptoparasites) may forage as groups to gain access to defended resources. Defense of resources by owners may be diluted if kleptoparasites invade en masse. For example, in several species of herbivorous reef fish, nonterritorial individuals band together in large groups when invading the algal gardens maintained and defended by other fish (Robertson et al. 1976, Foster 1985). Blue tang surgeonfish (*Acanthurus coeruleus*; Foster 1985) and striped parrotfish (*Scarus iserti*; Robertson et al. 1976) foraging in groups experienced higher per capita intake rates than solitary fish did when feeding off the algal garden defended by damselfish (Pomacentridae). Upon removal of territorial damselfish, group-foraging surgeonfish did not differ in intake rate from solitary fish, suggesting that the benefit to group foraging was in terms of increased access to territories (Foster 1985). A similar advantage to group foraging has been suggested for juvenile Common Ravens (*Corvus corax*; Marzluff and Heinrich 1991) and nonterritorial Sanderlings (*Calidris alba*; Myers et al. 1979). This "overwhelming" of territorial defenses has been compared to the capture of single, divisible prey by groups of predators (Packer and Ruttan 1988).

In other cases, however, kleptoparasites form groups despite decreasing mean intake rate with increasing group size. In a study on Parasitic Jaegers (*Stercorarius parasiticus*) kleptoparasitizing Common Terns (*Sterna hirundo*), members of groups of three or more were significantly less likely to acquire prey from terns than were solitary foragers, and the net energy intake rate of members of pairs and larger groups was lower than that of solitary birds (Bélisle 1998). Bélisle concluded that these birds form groups despite a lower mean intake rate for group foragers because there were rela-

tively few terns per jaeger, and multiple jaegers collected around each tern. In this case, groups formed in a dispersion economy (Giraldeau 1988, Giraldeau and Caraco 2000), such as that assumed in models of the ideal free distribution (IFD; Fretwell and Lucas 1970). In other systems, groups may form even though individual intake rate decreases with group size because some kleptoparasites use others to locate or otherwise reduce the costs of obtaining prey from hosts (Barnard 1984, Hamilton and Dill 2002).

We investigated why a subtropical reef fish, nonterritorial western buffalo bream (*Kyphosus cornelii* Whitley, Kyphosidae, hereafter WBB), sometimes occurs in foraging groups (or ''roving groups''; Horn 1989). Adult WBB are almost exclusively herbivorous, feeding on filamentous red algae (Rhodophyta; Clements and Choat 1997). Some WBB maintain and defend algal gardens, much like those of territorial damselfish (Berry and Playford 1992, Moore 1993, Hamilton 2001). Those that do not (and territorial fish foraging away from their territories) obtain approximately 40% of their total bites of algae by kleptoparasitizing these gardens (Hamilton and Dill 2003). WBB invade these territories singly or in small groups by swimming quickly through the territory, and, if successful, taking a bite from the algal garden before they are discovered and chased away by the territory holder (Berry and Playford 1992, Moore 1993).

We compared typical group size (Jarman 1974) of WBB and the effects of group size on two measures of intake (intake rate and probability of feeding when invading) with the predictions of five simple group-foraging models: a dispersion (ideal free) model, two models that assume a benefit to aggregation, and two producer–scrounger models. This approach is similar to that used by Bélisle (1998). However, we included differences in the quality of opportunities for kleptoparasitism in our models, because the cost of attempting kleptoparasitism changes with the behavior of the territory holder. These models and their predictions are outlined below.

The models

We begin with the following scenario. Roving WBB invade territories of conspecifics, the location and general characteristics of which are known to these kleptoparasites. For each territory, we assume that the roving fish using it have few other foraging alternatives (the resources available from using these alternatives, such as feeding on floating algae or invading other nearby territories, are included in the models as the variable y). For the focal territories used in this study, this assumption was met. These territories were isolated or in small groups (range of territories within 10 m radius of the center of the territory, 4–13 in 2001; I. M. Hamilton, *unpublished data*) on rocky outcrops. Although some roving fish did move among outcrops within a 15-min observation period, many roving fish

used the same outcrops for feeding for periods of at least several weeks (I. M. Hamilton, *personal observation*). In other areas, however, large numbers of WBB territories occupy large limestone platforms (e.g., Berry and Playford 1992), and fish may have more choice among foraging options.

On a territory, there is a large number of opportunities for invasion, π_t, which differ in quality, over a given time period. For simplicity, we divide these into intrinsically ''good'' and ''poor'' opportunities. Good opportunities for kleptoparasitism are those in which the territory holder is engaged in some task other than being vigilant against intruders or is otherwise unable or unwilling to defend the territory. Poor opportunities are those in which the territory holder will defend the territory. The cost of invading during a good opportunity is assumed to be lower than during a poor opportunity. The success of an invader may also be higher in good opportunities. Over a given period of time, the number of good opportunities on a given territory is π_g and that of poor opportunities is $\pi_p = \pi_t - \pi_g$. We assume that intrinsic opportunity quality is not under the control of the invading kleptoparasites, but that the fitness payoffs to invading during a particular opportunity type are influenced by the behavior of others. The terms used in all models are listed in Table 1.

Dispersion economy

In a dispersion economy, individuals disperse among opportunities such that no individual can do better by choosing a different foraging tactic. We assume that a roving fish arriving at territory can choose between two tactics. The first of these is to invade the territory, receiving F_i resources, divided by the N_i fish that choose to invade, and paying an invasion cost of c_i, which is also divided among all fish. In all of the models presented, fish are assumed to be competitively equal; that is, resources are divided equally among all fish using a given tactic. The fitness payoff to a fish choosing to invade during an opportunity of type i is therefore $(F_i - c_i)/N_i$. The second tactic is to continue foraging. Roving WBB that choose not to invade a given territory may be able to find some food elsewhere, on neighboring defended or undefended territories or by feeding on floating algae. The resources available to a fish that does not invade the territory are y, which we assume is divided equally among the $N - N_i$ fish that choose not to invade (although the general prediction relating group size to opportunity quality does not depend on the resource being divided among fish that do not invade the territory). At equilibrium, the fitness payoffs to the two tactics are equal, i.e., $y/(N - N_i) = (F_i - c_i)/N_i$.

The equilibrium group size is simply $N_i^* = N(F_i - c_i)/(y + F_i - c_i)$. Assuming that $c_g < c_p$ (or $F_g > F_p$), $N_g^* > N_p^*$, that is, groups should be larger during good opportunities than poor ones. This is because the net

TABLE 1. List of terms used in the models.

Term	Description
π_t	Total number of foraging opportunities on a territory over time t.
π_g	Number of "good" foraging opportunities over time t.
π_p	Number of "poor" foraging opportunities over time t.
F_i	Richness of patch available during opportunity type i (g, good opportunities; p, poor opportunities).
N	Total number of foragers (roving fish).
N_i	Number of foragers choosing to invade during opportunity type i.
c_i	Cost of invading during opportunity type i.
y	Resources available to fish that do not invade territory.
$\hat{\gamma}$	Stable group size in aggregation model.
λ	Rate of discovery of foraging opportunities in producer–scrounger model ($\lambda N_i[1 - q]$ = rate of invasion).
a	Finder's share. Resources used exclusively by producer upon discovery of an opportunity.
A	Resources shared by producer and all scroungers.
Ω_p, Ω_s	Fitness payoffs to producing and scrounging, respectively.
q	Proportion of foragers scrounging.
γ^*	Expected group size in producer–scrounger models.
x	Probability that observing a good opportunity indicates that current opportunity is good.

benefits of kleptoparasitizing are greater during good opportunities. Group size should not change with the proportion of opportunities that are good (π_g/π_t) because fish are basing the decision only on the quality of the current opportunity. However, this system may also be described by a sequential game in which the discounted expected payoffs from future invasions (or from leaving the territory in the future) influence these decisions. Because of this, we expect that the probability of encountering good and poor opportunities in the future may influence group size, and finding such a relationship does not necessarily falsify the hypothesis whereby groups form within the context of a dispersion economy.

Aggregative foraging or antipredator benefits

The general aggregation economy, or Allee-type IFD model (Fretwell and Lucas 1970, Pulliam and Caraco 1984, Clark and Mangel 1986, Giraldeau 1988, Giraldeau and Caraco 1993, Higashi and Yamamura 1993), assumes that foragers have perfect information about the distribution of opportunities and that they gain some fitness benefit shared by all group members over at least some range of group sizes. Therefore, the fitness of a forager increases initially with group size, peaks at some "optimal" group size and then decreases. Given free entry of foragers into the group, group size should continue to increase until individuals can do no better by joining a group than if they were on their own (the stable group size, $\hat{\gamma}$; Giraldeau 1988). However, because groups are likely to break up (e.g., because of disturbance by predators or other factors), groups smaller than $\hat{\gamma}$ are also likely to be observed in observational studies.

If the shapes of the functions relating fitness to group size are the same for good- and poor-quality opportunities, then the predictions of these models should be similar to those of the dispersion model, except that typical group size should be larger, because there is a benefit to grouping (Bélisle 1998). If the benefits to

grouping change with the quality of opportunities, the predictions of the aggregation model will depend on exactly how these benefits change. For example, if there is more of an aggregative benefit during poor opportunities than good ones, groups could be larger during poor opportunities than during good ones.

We considered two possible benefits for group-foraging WBB. The first is reduced predation risk. Because territories are in relatively shallow water, where the risk of predation from Ospreys (*Pandion haliaetus*) is likely to be higher (Poole 1989), roving fish may move into a riskier habitat when kleptoparasitizing. Therefore, they may gain some benefit from doing so as a group. If group foragers benefit from dilution of predation risk, the qualitative predictions regarding group size and the effects of group size on intake rate are generally the same as for the dispersion model. However, the benefit to grouping would likely be higher on shallow territories because risk from Ospreys is highest there. Therefore, groups should be larger in shallows.

If grouping allows roving WBB to overwhelm territory holders, as appears to be the case for several other nonterritorial animals, then the intake rate of group members should be equal to or greater than that of solitary fish when invading defended territories, for groups smaller than $\hat{\gamma}$. Because the group size predictions of the aggregation model depend on the shapes of the functions relating group size and fitness, which we assume differ if the benefit is in terms of overwhelming, we do not set out any specific prediction regarding how typical group size changes with opportunity quality.

First invader creates opportunities for others (producer–scrounger model)

Whereas the previous models assume that individuals have perfect information about the opportunities for kleptoparasitism, and must decide whether to invade the territory or move on, this model assumes they

have no information, other than the likelihood of encountering a good opportunity. Therefore, we begin with the assumption that a set of N fish has decided to invade the territory (see below for a discussion of the size of N) and must decide between initiating the invasion and following others. A fish that initiates an invasion creates lower cost opportunities for invasion for others, because they can feed while the first fish is chased. Thus the population is divided into fish that initiate invasions (producers) and those that follow (scroungers). Producers must have priority of access to resources for this to be stable.

The rate-maximizing producer–scrounger model we use here is based upon that of Vickery et al. (1991). The proportion of the N kleptoparasites in the population that scrounges is q, while the remainder produces. Producers discover opportunities at the rate λ (so that the rate of discovering an opportunity of type i is $\lambda\pi_i/\pi_t$). They take a of the F_i items of food discovered before being joined (the finder's share), but pay c_i (the cost of producing, i.e., being chased by the defending fish). The remaining $A = F_i - a$ items are shared with all scroungers in the population. The fitness of a producer, Ω_p, is given by $(\lambda\pi_g(a + A/(qN + 1) - c_g) + \lambda\pi_p(a + A/(qN + 1) - c_p))/\pi_t$, while the fitness of a scrounger, Ω_s, is given by $\lambda N(1 - q)(\pi_g A/(qN + 1) + \pi_p A/(qN + 1))/\pi_t$. At the equilibrium proportion of scroungers, q^*, $\Omega_p(q^*) = \Omega_s(q^*)$, which is $A\pi_t/(\pi_g(F_i - c_g) + \pi_p(F_i - c_p)) - 1/N$. Group size, γ^*, is $q^*N + 1$ if all scroungers follow one producer. It is likely that scroungers will be able to follow more than one producer at any time, so group sizes may be smaller than this. In this model, $\partial_{q^*}/\partial_{\pi g} < 0$ if $c_g < c_p$, as is assumed. That is, the number of scroungers (and thus, group size) should decrease as the proportion of good opportunities for kleptoparasitism increases. Because roving fish know only the likelihood of encountering a good or poor opportunity, group size should not differ between opportunity types.

Producer–scrounger model with updated information

In this modification of the above model, we assume that individuals that have decided to invade have an estimate of the probability that the current opportunity is good. For example, fish may observe the reaction of a territory-holder to the previous invasion. From Bayes' theorem, it follows that, after observing j invasions, $\pi_{g(j+1)}/\pi_t = \pi_{gj}x/[\pi_{gj}x + \pi_{pj}(1 - x)]$ if the previous group was tolerated, and $\pi_{g(j+1)}/\pi_t = \pi_{gj}(1 - x)/[\pi_{gj}(1 - x) + \pi_{pj}x]$ if the previous group was resisted. The probability that the current opportunity matches that observed by the fish is x. The payoffs to the two tactics are as above, except with the updated information. The stable proportion of scroungers after an observation indicative of a good opportunity is:

$$q^*_{j=g} = \{\pi_p(F - NA - c_p)[(1 - x)\pi_p + x\pi_g]$$
$$+ (F - NA - c_g)x\pi_g\pi_t\}$$
$$\div \langle N\{(F - c_p)[(1 - x)\pi_p + x\pi_g]$$
$$+ (F - c_g)x\pi_g\pi_t\}\rangle$$

and after a poor opportunity is

$$q^*_{j=p} = \{\pi_p(F - NA - c_p)[x\pi_p + (1 - x)\pi_g]$$
$$+ (F - NA - c_g)(1 - x)\pi_g\pi_t\}$$
$$\div \langle N\{(F - c_p)[x\pi_p + (1 - x)\pi_g]$$
$$+ (F - c_g)(1 - x)\pi_g\pi_t\}\rangle.$$

The proportion scrounging, q^*, and therefore group size, is predicted to be greater after an observation indicative of poor opportunities, as long as $c_g \leq c_p$ and $x > 0.5$. If $x < 1$, this proportion should also decrease as good opportunities become more common, after observing either quality of opportunity.

Both of the producer–scrounger models can be modified to incorporate some of the assumptions of the dispersion and aggregation models, namely, that patch encounter rate of producers is influenced by the presence of others and that foragers may leave the territory altogether. To incorporate this possibility, we allowed fish that left to receive a payoff of $y/(N - N_i)$, as in the dispersion model. For fish that stayed, interference among producers reduced the patch encounter rate to $\lambda_i = \lambda/(N_i(1 - q))^m$. For simplicity, we set $m = 1$, which implies strong interference at territories. In this case, the equilibrium number of fish that are expected to stay at the territory is: $N_i = (\lambda NA - y)/(\lambda A + yq^*)$. The equilibrium number of scroungers, q^*, is the same as in the previous models (substituting N_i for N). N_i is larger when territories tend to be easily invaded (that is, when a large proportion of foraging opportunities are good) and, in the updated information model, after observations of good opportunities. Interestingly, despite this, the general predictions regarding group size remain the same as in the original models. Group size should decrease with an increasing proportion of good opportunities and should increase in poor opportunities in the updated information model.

We used several tests to distinguish among these models (Table 2). First, did the typical group size for roving WBB invading a given territory decrease when that territory was temporarily unoccupied? All opportunities for kleptoparasitism on an unoccupied territory are good, because invaders will not be resisted. The dispersion model predicts that groups should be larger during these good opportunities. If there were foraging or antipredator benefits to aggregating, typical groups could be larger, smaller, or the same size when invading occupied and unoccupied territories, depending on how fitness changes with group size in each; therefore, we could not use this test to reject this model. Both pro-

TABLE 2. Predictions of five group foraging models and observations from western buffalo bream groups at the University of Western Australia Department of Zoology Research Station at Rottnest Island, Western Australia, Australia.

Comparison	Dispersion	Aggregation (predation)	Aggregation (foraging)	Producer–scrounger	Producer–scrounger (updated)	Observed
Group size on occupied vs. unoccupied territories	↓	↑↓ or 0	↑↓ or 0	↑	↑	↑
Group size with increasing depth	0	↓	0	0	0	0
Group size during good vs. poor opportunities	↑	↑	↑↓ or 0	0	↓	↓
Change in group size with proportion of good opportunities	none†	none†	none†	↓	↓	↓‡
Change in intake rate with group size when smaller than stable group size	↓	↓	↑ then ↓	↓	↓	↓ then ↑

Notes: For predictions and observations, ↑ indicates increases, ↓ indicates decreases, 0 indicates no change.
† Assuming that fish only invade the territory once.
‡ For poor opportunities only.

ducer–scrounger models predict that groups should generally be small when most opportunities are good; therefore, groups should be smaller when invading unoccupied territories.

If there are benefits to grouping that are not related to invading territories (such as avoiding predators), the predicted relationship between group size and territory occupancy depends on whether and how these benefits differ with territory occupancy. One indication that these other benefits influence group size of WBB would be if territory occupancy were correlated with group size in other species of fish, which are not excluded from the patch by territory-holding WBB. Therefore, we also compared the typical group sizes on occupied and unoccupied territories for a related herbivorous fish that does not compete with WBB for food, the silver drummer (or common buffalo bream, *K. sydneyanus* Günther). *K. sydneyanus* are much less likely to be attacked by territory holders (I. M. Hamilton, *unpublished data*) than are WBB.

Second, we examined the influence of intrinsic territory riskiness on grouping by WBB. WBB fish tended to react to even nonpredatory birds flying over them by moving close to the substrate, suggesting that these fish perceive the risk from aerial predators to be high (I. M. Hamilton, *personal observation*). This risk should be highest on shallow territories, so we expected that groups should be larger on shallow territories if grouping confers antipredator benefits. Therefore, we tested whether there was a significant negative correlation between typical group size and the depth of the deepest point of the territory being invaded. No other model predicts a relationship between group size and water depth.

Third, we tested whether groups were larger during good or poor invasion opportunities, when the territory holder was present. The dispersion model and the aggregation model with antipredator benefits predict that groups should be larger during good opportunities. The basic producer–scrounger model predicts no change in group size with opportunity quality, while the produc-

er–scrounger model with updated information predicts that groups should be larger during poor opportunities. If there were aggregative benefits to foraging, typical group size could be larger, smaller, or the same size during good opportunities as during poor ones, depending on how intake rate changes with group size in each; therefore, we again could not use this test to reject this model. We tested the effects of opportunity quality on group size by comparing the typical group size of invasions when the previous invasion on that same territory had been resisted and when it had not. We used the reaction to the previous invasion for two reasons. First, it is a plausible measure by which roving WBB might assess the quality of the current opportunity. The previous invasion could be no more than 15 min earlier and in most cases was only a few seconds prior to a current invasion. Therefore, it should be a reliable indicator of current opportunity quality. Second, the reaction of the territory holder may be influenced by group size, so using the reaction to a particular invasion as a measure of the opportunities for that invasion would be circular.

Fourth, we tested whether group size decreased as the proportion of opportunities that were good increased by testing whether typical group size for fish invading occupied territories decreased with increasing proportion of invasions tolerated on a given territory, controlling statistically for the frequency of invasions. The dispersion and aggregation models predict no change in group size with increasing proportion of good opportunities, while the producer–scrounger models both predict that group size should decrease when the proportion of opportunities that are good increases.

The final test was whether the intake rate of the average group member increased with group size over at least some group sizes. Only the aggregation model for foraging benefits makes this prediction. At equilibrium, fitnesses should be equal across all group sizes for all models. However, if groups occasionally break up, so that group sizes smaller than equilibrium are observed, fitness should increase with group size over some range

of group sizes for the aggregation models and decrease with group size for the others. Because we only measured intake rate and feeds per invasion, this increase would only be detectable if the fitness benefit were in terms of intake rate (rather than survival).

METHODS

Study site and species

This study was conducted at the University of Western Australia Department of Zoology Research Station at Rottnest Island, Western Australia, Australia (latitude, 32°00′ S; longitude, 115°30′ E) from February through April 1999 and 2001. Rottnest Island is located in the Indian Ocean, 19 km west of Fremantle in southwestern Western Australia. Observations were conducted in five bays on the western half of the island.

The WBB is a subtropical reef fish endemic to the eastern Indian Ocean along the coast of Western Australia (Hutchins and Thompson 1995). In some regions, larger fish maintain elliptical or polygonal algal gardens on limestone platforms (area, 11.04 ± 4.57 m²; mean $\pm$ 1 SD), defending these against other herbivorous fish (Berry and Playford 1992, Moore 1993, Hamilton 2001). In this paper, a fish's territorial garden is defined as the area enclosed by the reef edge and the ''hedgerows'' of brown algae, coralline red algae, or seagrass that separate adjacent algal gardens (Berry and Playford 1992) and the water column immediately above it. Fish that do not defend territories, and those that do but are temporarily off their territories, forage solitarily or in small groups and feed on floating clumps of red algae and the defended and undefended territories of conspecifics or, occasionally, those of damselfish (*Parma mccullochi*, *P. occidentalis*, *Pomacentrus milleri*, and *Stegastes obreptus*).

Several characteristics make these fish amenable for testing simple group-foraging models. When not feeding, they aggregate in large groups in deeper water immediately adjacent to foraging areas. Because they remain in proximity to the territories from which they feed, they may be able to monitor the availability of opportunities for kleptoparasitism. Most of the members of roving groups are nonreproductive (Moore 1993). Therefore, group formation is unlikely to be influenced by mating considerations. WBB larvae are pelagic (Rimmer 1986), and it is therefore unlikely that group members are closely related. As well, groups of roving WBB are free-entry; that is, current group members generally do not resist attempts by others to join, and competition among roving WBB is by scramble only (I. M. Hamilton, *personal observation*). Finally, the stability of group membership is low. Groups often change size between invasions, and the turnover rate in groups appears to be high (I. M. Hamilton, *personal observation*). Therefore, it is likely that the size of a group invading a territory will reflect the costs and benefits of the current invasion.

Territory observations

Thirty-six territories (19 in 1999 and 17 in 2001) were randomly selected for observation. Different territories were used in each year. Territories used in 2001 were used in an experiment in which their defendability was manipulated (Hamilton and Dill 2003) for the first six of 10 observation periods. These manipulations had significant effects on the behavior of the territory holder, but did not appear to influence the behavior of roving fish (Hamilton and Dill 2003). All of these territories received the same number of replicates of each manipulation in random order.

For each territory, we conducted 10 observations of 15 min duration. During this time, we recorded the presence of the territorial fish on the territory. If a fish crossed the boundary of its territory, but remained within an estimated 2 m of the garden and had an unbroken line of sight to its territory, we considered it to be still on its territory. We used the 2 m limit because preliminary observation suggested that fish that remained close to the territory and were not feeding off adjacent territories were able to quickly return if invaded. Fish were considered to be off their territory if (1) they were in a position where they were unable to see their territory, (2) they were more than 2 m from the boundaries of their defended garden, or (3) they were observed feeding off an adjacent territory.

We also recorded the number and size of groups of roving fish that crossed the boundaries of the garden. Fish were considered to be in a group if they were within two body lengths of another fish swimming in the same direction when they entered the defended garden. The tolerance of the territory holder to roving fish was qualitatively recorded on a scale from 1 to 4 as follows: (1) chase invader, (2) approach and signal invader, usually by leaning to one side, (3) approach invader, or (4) ignore invader. The number and size of groups of roving fish that entered the territory while the territory holder was away was also recorded. In all cases, we recorded the number of roving fish per group that fed.

Observations of focal roving fish

One hundred and nine roving fish at three of the bays (40 at Little Armstrong Bay, 27 at Kitson Point, and 42 at Mary Cove) were each followed by snorkelling in 2001. Individual fish could be identified by patterns of scarring, and only one follow per individual was conducted. 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 measured the number of bites taken by the fish from the occupied territories of WBB and damselfish, unoccupied territories and undefended areas, as well as the number of territories invaded, the reaction of the ter-

ritorial WBB or damselfish, group size during invasions, and bites taken per invasion, as defined above.

Statistical analyses

For all analyses of focal territories, we used typical group size (Jarman 1974) as our measure of the size of groups:

$$\sum_{j=1}^{n} \gamma_j^2 \bigg/ \sum_{j=1}^{n} \gamma_j$$

where γ_j is the group size of the jth observation (out of a total of n observations) during an observation period. This measure of group size is considered to be more appropriate for depicting the social context of the average individual invading that territory than is mean group size (Giraldeau 1988). For analyses of focal roving fish however, we followed the same individual over time. Thus, the more appropriate measure of the group size experienced by focal roving fish was the mean size of groups in which they invaded territories.

To test the influence of territory occupancy on group size, we calculated the typical group size of roving WBB and silver drummers for each territory when it was occupied and when it was unoccupied. These were compared using a Wilcoxon signed rank test in JMP 4.0 (SAS Institute 2001), with rejection level adjusted for the multiple comparisons to 0.025 ($\alpha = 0.05/2$). We employed the Bonferroni correction because we separately compared the typical group sizes of WBB and silver drummers. To test the hypothesis that group size was correlated with depth, we used a multiple regression with depth and rate of invasions while unoccupied as independent variables and typical group size while the territory was unoccupied as the dependent variable. Depth of the territory was defined as the depth of the deepest point on the territory, measured relative to chart datum using tide height data obtained from the National Tidal Facility (Flinders University, South Australia). Typical group sizes were log transformed.

We calculated the typical group size for each territory and observation period for those observations for which the previous invasion had been resisted (1–3 on the tolerance scale above, *Territory observations*; poor opportunities) or tolerated (4 on the tolerance scale; good opportunities). To test if group size was greater in good opportunities than in poor ones, we compared the mean typical group sizes during all good and all poor opportunities on each territory with a Wilcoxon signed-ranks test. We tested whether tolerance towards the previous invasion was correlated with tolerance towards the current invasion using a Cochran-Mantel-Haenszel (CMH) test, stratified by territory.

To examine the influence of the distribution of good and poor opportunities on typical group size within territories, we used ANCOVA, with territory included as a random effect and log-transformed typical group size for each observation period as the dependent variable. We compared groups for which the previous invasion was tolerated separately from groups for which the previous invasion was resisted. There were a total of 10 observation periods per territory. For some observation periods, all groups were preceded by invasions that were resisted. For others, all groups were tolerated. Therefore, sample sizes for these two comparisons are not equal. Covariates in the model were the proportion of invasions that were tolerated and the number of invasions while occupied.

We also examined the influence of group size on intake. For focal nonterritorial fish, we calculated mean group size for all invasions in which that fish had taken part, the number of territories invaded per minute (invasion rate), the number of times per minute the fish was chased by territorial WBB or damselfish, and its mean intake rate (including bites taken away from territories). Using a general linear model (GLM), we compared intake rates among sites and group sizes. Site was included as a fixed categorical variable and group size and mean number of chases per minute as covariates. The relationship between intake rate and group size appeared nonlinear, so the square of group size was also included in the GLM. We also used a similar GLM to compare invasion rates among sites and group sizes. All interactions among effects were initially included in the model, but removed if not significant.

For focal territories, we calculated the proportion of all invasions by groups of 1, 2, 3, 4–5, 6–10, 11–15, and 16–20 individuals in which at least one member successfully fed. We also calculated the probability that the average fish involved in these invasions fed (total number of fish feeding/total number of fish observed). We compared these probabilities between solitary fish and each group size using Wilcoxon signed-ranks tests adjusted for multiple comparisons using a Bonferroni-corrected $\alpha = 0.0083$ (0.05/6).

RESULTS

Observed invasions generally involved one or two roving fish, and groups of five or more were rare (Fig. 1). Changes in group size with occupancy and opportunity and the influence of group size on intake rate are summarized in Table 2. Typical group size for western buffalo bream invading territories of conspecifics was greater when those territories were occupied than when unoccupied (median [interquartile range] on occupied territories, 3.11 [2.28–4.96]; on unoccupied territories, 1.45 [1.00–1.86]; Wilcoxon signed-ranks test, $T = 225.5$, $n = 33$, $P < 0.001$). By comparison, *K. sydneyanus* rarely formed groups regardless of territory occupancy (occupied, 1.00 [1.00–1.68]; unoccupied, 1.00 [1.00–1.75]; Wilcoxon signed-ranks test, $T = -1.5$, $n = 10$, $P > 0.9$). WBB group size did not change significantly with depth ($\beta \pm 1$ SE $= -0.16 \pm 0.13$, $F = 1.46$, df $= 1, 33$, $P > 0.2$, power $= 0.09$). For a biologically significant effect of depth of 0.31 (equiv-
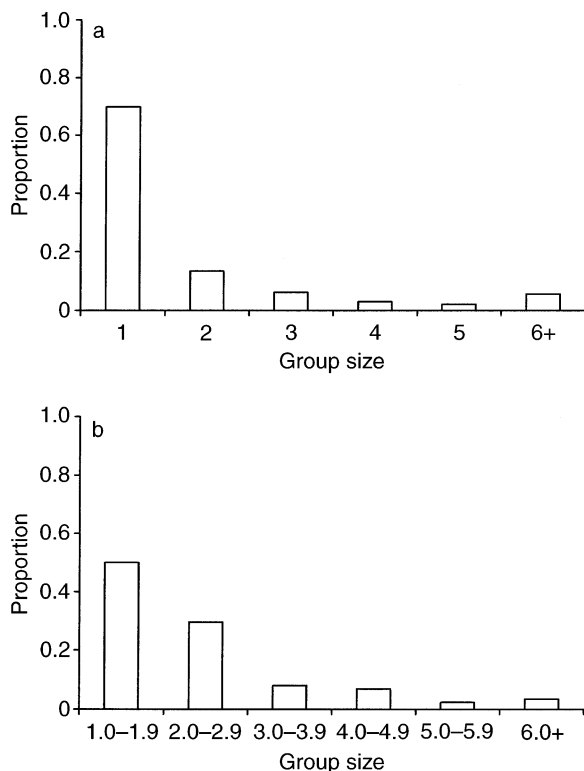
FIG. 1. Frequency distribution of observed western buffalo bream group sizes as a proportion of all observations during (a) focal territory watches and (b) watches of focal roving fish. Data in (b) are the mean group sizes experienced by each fish. The study was conducted at the University of Western Australia Department of Zoology Research Station at Rottnest Island, Western Australia, Australia.

alent to pairs on the shallowest territories and solitary fish on the deepest), the power of this test would be 0.97.

Tolerance towards the previous group was a good measure of tolerance towards the current group; a group that was tolerated was significantly more likely than expected by chance to be preceded by another group that was tolerated (CMH test, $\chi^2 = 3364.8$, $P < 0.001$). Pooling all territories, 93.2% of all invasions that were resisted were preceded by an invasion that was resisted, while 96.3% of invasions that were tolerated were preceded by another invasion that was tolerated. Typical group size was significantly greater if the previous group was resisted than if it was tolerated (median [interquartile range] if resisted, 2.28 [1.88–2.91]; if tolerated, 1.54 [1.36–1.99]; Wilcoxon signed-ranks test, $T = 241.5$, $n = 33$, $P < 0.001$).

The producer–scrounger models predict that typical group size should decrease as the proportion of good opportunities for kleptoparasitism (the proportion of invasions tolerated) increases, controlling for the rate of invasions. Typical group size when the previous group had been resisted decreased significantly with increasing proportion of invasions tolerated during that

period ($\beta \pm 1$ SE $= -0.58 \pm 0.27$, $F = 4.54$, df $= 1$, 182, $P < 0.05$) and increased with the overall number of invasions in an observation period ($\beta \pm 1$ SE $= 0.49 \pm 0.09$, $F = 32.17$, df $= 1$, 182, $P < 0.001$). The typical group size when the previous group had been tolerated was not significantly influenced by the proportion of invasions tolerated ($\beta \pm 1$ SE $= 0.38 \pm 0.31$, $F = 1.44$, df $= 1$, 125, $P > 0.2$), but did increase significantly with the rate of invasion ($\beta \pm 1$ SE $= 0.25 \pm 0.08$, $F = 8.35$, df $= 1$, 125, $P < 0.005$).

The relationship between mean group size and intake rate in 2001 was nonlinear (Fig. 2). Intake rate decreased with increasing group size ($\beta \pm 1$ SE $= 0.29 \pm 0.11$, $F = 6.23$, df $= 1$, 82, $P < 0.025$) and increased with the square of group size ($\beta \pm 1$ SE $= 0.05 \pm -0.02$, $F = 8.46$, df $= 1$, 82, $P < 0.005$). Thus, for fish that typically fed in the largest observed groups (mean group size ≈ 7), intake rate was approximately the same as for solitary fish (Fig. 2). Intake rate was significantly influenced by site ($F = 3.93$, df $= 2$, 82, $P < 0.025$), with fish at Kitson Point feeding at a lower rate than fish at Mary Cove (Tukey's HSD). Feeding rate was not significantly influenced by the rate at which fish were chased ($\beta \pm 1$ SE $= -0.10 \pm 0.14$, $F = 0.50$, df $= 1$, 82, $P > 0.4$). There was a significant interaction between site and group size on the rate at which roving fish invaded territories ($F = 4.58$, df $= 2$, 82, $P < 0.05$). At Kitson Point, groups were significantly more likely to be chased as group size increased ($t = 3.03$, df $= 82$, $P < 0.005$), whereas at the other sites there was not a significant relationship between group size and invasion rate.

Group size did not significantly influence the probability that at least one fish per group fed when invading occupied focal territories (Fig. 3a; 2 vs. 1, $T = -96.5$, $P < 0.05$; 3 vs. 1, $T = -6$, $P > 0.8$; 4–5 vs. 1, $T = -15.5$, $P > 0.7$; 6–10 vs. 1, $T = -10$, $P > 0.7$; 11–15 vs. 1, $T = 5$, $P > 0.8$; 16–20 vs. 1, $T = -8.5$, $P > 0.4$). However, the probability that a given individual fed was lower for individuals foraging in groups than
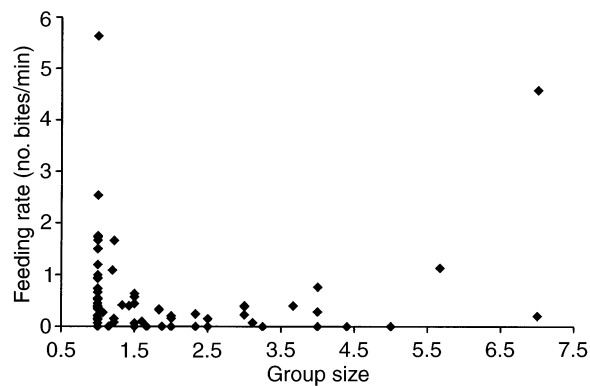

FIG. 2. The relationship between group size and intake rate for focal roving fish. The relationship between ln-transformed intake rate and group size is significantly nonlinear. $R^2 = 0.18$.
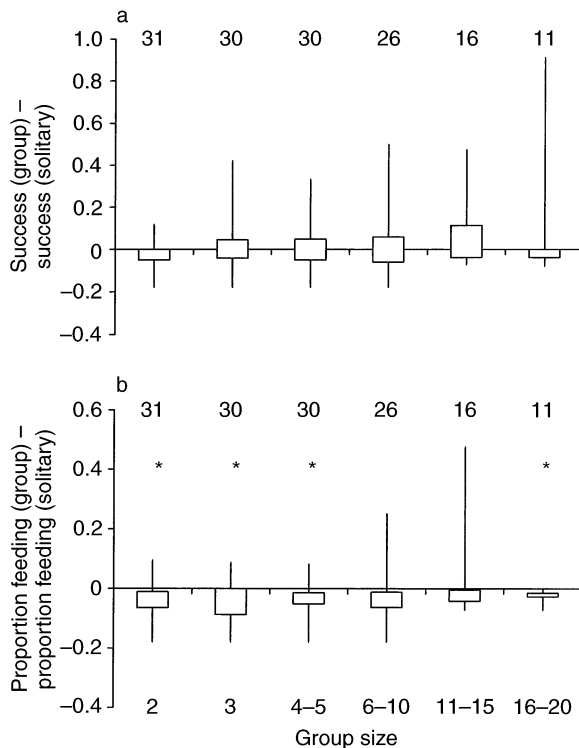
FIG. 3. The effects of group size on the success of groups invading focal territories. Boxes represent quartile ranges; bars represent ranges. Sample sizes appear above the bar for each comparison. (a) The difference in the probabilities that groups and solitary fish were successful (i.e., at least one fish in the group fed). (b) The difference in the probabilities that individuals in groups and solitary fish fed. Significant differences as assessed by Wilcoxon signed-ranks tests with α = 0.0083 (0.05/6) are indicated by asterisks.

for solitary invasions (Fig. 3b). For all group sizes except 6–10 and 11–15, this difference was significant (Fig. 3b; 2 vs. 1, $T = -141.5$, $P < 0.005$; 3 vs. 1, $T = -122$, $P < 0.005$; 4–5 vs. 1, $T = -140$, $P < 0.001$; 6–10 vs. 1, $T = -88$, $P < 0.01$; 11–15 vs. 1, $T = -33.5$, $P < 0.05$; 16–20 vs. 1, $T = -27.5$, $P < 0.005$).

DISCUSSION

Of the five models that we presented, our results from smaller groups best support the predictions of the producer–scrounger model with updated information (Table 2). In this model, some fish use the efforts of others to reduce the costs of obtaining food, but can use some cue to update their estimate of the quality of opportunities for kleptoparasitism. One potential cue, which we used as our estimate of opportunity quality, is the reaction of the territory holder to the previous group. This is a good, but not perfect, measure of the likelihood that the current group will be chased. However, other cues, such as the location of the territory holder on its garden or behavior of the territory holder, could have been used. Typical group size was negatively correlated with our estimate of opportunity quality, which

was not predicted by the dispersion model, the aggregation model with predation risk benefits, or the classical producer–scrounger model. We were able to reject the aggregation model with foraging benefits for small groups because the intake rate of fish foraging in these groups was lower than that of fish foraging alone (Fig. 2). These groups were no more successful at gaining access to resources than were solitary fish, and, within groups, there was intense competition for resources.

That kleptoparasites may exploit opportunities created by other kleptoparasites has long been hypothesized to explain group foraging by these individuals (e.g., Arnason and Grant [1978], reviewed in Barnard [1984]). However, this explanation has rarely been tested against multiple alternative explanations, and, when it has, has not been supported (Bélisle 1998). To our knowledge, our results are the first to support within-group exploitation as an explanation for group foraging by kleptoparasites.

The producer–scrounger models assume that producing and scrounging are mutually exclusive alternatives. If not, opportunists (which can use both simultaneously) can occur in the population either as a pure strategy or in a stable equilibrium with producers or scroungers, so long as the efficiency of using both producing and scrounging is not severely compromised by attempting to use both tactics (Vickery et al. 1991). Group size in a population consisting of pure opportunists should not change with opportunity quality or the proportion of good and poor opportunities because all opportunists are assumed to join all opportunities discovered (Vickery et al. 1991). Our results do not support these predictions, but is our assumption that producing (initiating invasions) and scrounging (following) are mutually exclusive met in this system? We are unable to test with our data whether fish can efficiently search for both opportunities to invade and opportunities to follow other fish. However, fish that attempt to initiate invasions must focus attention on territories that are several meters away, while fish that attempt to follow invaders must focus attention on other roving fish, which are found in deeper, undefended areas when not invading. Because of this spatial separation, it may be difficult for a fish to monitor both at the same time. Understanding whether these fish can simultaneously and efficiently produce and scrounge warrants further investigation.

The producer–scrounger models require a finder's share, a, so that individuals initiating invasions gain more from doing so than followers (but cannot invade as often). Without this (i.e., if $a = 0$), all foragers should join all opportunities (as in the opportunist model described above; Beauchamp and Giraldeau [1996]). The models presented here also assume a cost of producing, in that the fish initiating invasions is likely to be chased. There must therefore be some benefit to initiating an invasion. There are at least two ways that initiators of invasions could gain such a benefit. First,

the first fish to invade may be more likely to feed on the invaded territory. We have insufficient data to test if this is so. A second, perhaps more plausible, finder's share is that the first fish gains something after the invasion, in addition to the food kleptoparasitized from the invaded territory. For example, the first fish to move through a defended territory may gain priority of access to an undefended patch, its own territory, or a refuge. This would provide the first fish with the requisite high fitness payoff to initiating an invasion.

Although we used the reaction of the territory holder to the previous group to exclude the possibility that our results reflected changes in defense with current group size rather than an adjustment of group size to the likelihood of being attacked, it is possible that the observed correlation between opportunity quality and group size resulted from more vigorous defense of territories at times when larger groups were likely, such as when densities of nonterritorial WBB were high. However, territorial defense generally decreases with intruder density or group size in fish (Grant 1997), because of the high cost of attempting to evict multiple individuals. As well, our results from occupied and unoccupied territories indicate that territorial defense does influence group size.

We did not find a significant decrease in group size during good opportunities as the proportion of good opportunities increased. Such a decrease was predicted by producer–scrounger models. However, because groups invading during good opportunities were generally small and because group size cannot be less than 1, it may have been difficult to detect such a decrease. There was a decrease in group size during poor opportunities as they became less common, as predicted by these models.

Several other kleptoparasitic fish and birds receive higher intake rates when foraging as a group than when solitary, because they are able to overwhelm territory holders. In other reef fish, kleptoparasitic groups are often much larger than those observed in this study (Robertson et al. 1976, Foster 1985). Foster (1985) found that group-foraging surgeonfish did not differ in intake rate from solitary fish when groups were small, like those observed in this study. The benefits of overwhelming territory holders may be restricted to large groups. In our study, intake rate increased with group size for groups larger than ~5 (although this was based on a small number of data points). Fish that tended to forage in the largest groups experienced intake rates similar to those of solitary fish. These groups were still no better at gaining access to resources than were solitary fish (Fig. 3a). We found that the proportion of individuals feeding in groups of 6–15 did not differ significantly from that of solitary fish (Fig. 3b). However, this conclusion was based on a conservative critical value for statistical significance, and solitary fish tended to be more likely to feed than did individuals in these groups. However, at least at one site (Kitson

Point), members of large groups attempted to invade territories more frequently than did those that typically foraged in small groups. In addition, on two occasions, during times other than territory watches, we observed very large groups (of more than 40 fish) invading territories. Although territory holders attempted to evict these groups, invading fish were able to feed on the territory for extended periods of time (>5 min, compared with <5 s for smaller groups). Therefore, the formation of larger groups may fit the aggregation model with foraging benefits. It is important to note, however, that these larger groups were very rare (Fig. 1).

This pattern is in contrast to that generally observed in groups of animals hunting single, divisible prey, a foraging system to which group-foraging kleptoparasites are sometimes compared. Among group hunters, small groups are more likely to show aggregative benefits than are large groups, which are vulnerable to exploitation by individuals that do not contribute to capturing prey (Packer and Ruttan 1988). Prey can only be captured once, and the marginal contribution of additional group members decreases with group size, whereas competition for the resource continues to increase. We suggest that, in some kleptoparasitic groups, the benefits to overwhelming continue to increase in larger groups, because kleptoparasites can remain at the resource for a longer period of time before being evicted. Therefore, an individual's contribution to increasing access to the resource is more likely to exceed the cost of increasing competition in larger groups than in smaller ones.

A consequence of this pattern is that there could be two stable equilibrium group sizes for WBB and other kleptoparasites of divisible resources. Small groups should tend to remain small, because there is little payoff to joining an intermediate-sized group. Larger groups may form during periods of low solitary success, generally poor opportunities, and high densities or if the finder's share of those initiating invasions is low. If these groups become large enough to experience aggregative benefits, they could become very large, as members of smaller groups and even solitary fish join.

Our study provides support for a novel social foraging model, at least in small groups of WBB, and suggests that a diversity of group sizes and reasons for grouping are likely in kleptoparasitic systems. Although we have assumed that opportunity quality is not under the influence of kleptoparasites, the behavioral tactics of territory holders and kleptoparasites are undoubtedly interrelated (e.g., Hamilton and Dill 2002). For example, the decision to defend a territory at all may be influenced by the rate of intrusion and the costs of evicting intruders (Grant 1997). Understanding the complex patterns of social foraging behavior in western buffalo bream and other animals with similar social systems will entail understanding the simultaneous decisions of kleptoparasites and territory holders and the decision to use either of these foraging tactics.

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