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Three-Player Social Parasitism Games: Implications for Resource Defense and Group Formation

Ian M. Hamilton* **and Lawrence M. Dill**†

Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada

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abstract: Individuals that produce resources are often exploited by several individuals; such exploitation may or may not be tolerated. We modeled the decision of a resource owner to accept one scrounger (the "satellite") and of both of these to accept being joined by another (the "floater"). In general, satellites tolerated floaters when competition between them was low, while owners tolerated satellites when facilitation between satellite and floater was high. When floaters were likely to find resources without joining, owners were more likely to resist satellites. In some cases, Nash equilibria were also mutually beneficial for two of the three individuals. Our model makes the counterintuitive prediction that mutually beneficial coalitions between satellites and floaters can only arise when the net benefits arising from the other's presence are low. When facilitation between satellites and floaters is high, satellites and owners may form mutually beneficial groups and groups with division of labor, or alternatively, owners may benefit from encouraging floaters to join. Finally, our model suggests there must be differences in competitive ability or some benefit of familiarity for owners to tolerate satellites but not floaters. We discuss empirical evidence for these and other predictions of the model.

Keywords: social exploitation, kleptoparasitism, mutualism, alternative tactics.

Many organisms obtain limited resources by exploiting the investment of others (Barnard 1984*b*). These include metabolic parasites, which directly obtain nutrition from their hosts (Kennedy 1984), and social parasites, which use the investment of others to circumvent costly behaviors. The costs of finding food and mates and of providing parental care are among those that can often be reduced by the use of social parasitism. Parasitic foraging is often referred to as "kleptoparasitism" and encompasses a diverse range of interactions between and within species (Barnard 1984*a*; Giraldeau and Caraco 2000). In many species, males parasitize mating opportunities by intercepting females attracted to the displays or territories of other males (Gross 1996). Males may also gain mating opportunities by "sneaking" fertilizations (Arak 1984; Gross 1996). Some animals reduce the costs of parental care by using nest sites constructed by others (e.g., digger wasps *Sphex ichneumoneus*; Brockmann et al. 1979) or by depositing their eggs in the clutches of others (brood parasitism; Andersson 1984; Rothstein and Robinson 1998), forgoing subsequent parental care.

Each of these resources may be obtained through a variety of mechanisms. In some cases, an individual usurps the entire resource controlled by another, often aggressively. For example, dominant birds in a flock may displace subordinates from resources they discover (e.g., Rohwer and Ewald 1981). In other cases, individuals join others that are successful at finding a resource and share it. For example, satellite male frogs may maintain proximity to calling males, intercepting females attracted to the calls (Howard 1978). When groups are more productive at producing food or offspring than solitary individuals, dominant members of the group may attempt to monopolize group production. This interaction has been extensively examined under the framework of optimal skew theory (Vehrencamp 1983; Keller and Reeve 1994; Hamilton 2000; Johnstone 2000). Finally, resources may be obtained without direct interaction with the host. For example, kleptoparasitic kangaroo rats (*Dipodomys merriami*) enter and remove seeds from the undefended caches of conspecifics (Daly et al. 1992).

Social parasitism may also occur within or between species. Parasitism of parental care and food often involve interspecific interactions. Several groups of birds are obligate interspecific brood parasites (Rothstein and Robinson 1998). Similarly, some birds (e.g., parasitic jaegers

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* Corresponding author. Present address: Department of Biology, Concordia University, Montreal, Quebec H3G 1M8, Canada; e-mail: ihamilt@vax2.concordia.ca.

† E-mail: ldill@sfu.ca.

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Stercorarius parasiticus; Arnason and Grant 1978) and spiders (*Argyrodes* spp.; Vollrath 1984) obtain food primarily by kleptoparasitizing other species. However, both brood parasitism and kleptoparasitism are also common within species. Parasitism of mating opportunities would be expected to occur primarily within species, in the absence of a benefit to heterospecific mating.

Within this diversity of interactions, intraspecific kleptoparasitism by joining feeding opportunities has been the main focus of theoretical models such as the producer-scrounger game (Barnard and Sibly 1981; Giraldeau and Caraco 2000). In the producer-scrounger game, foragers search for either prey (producers) or opportunities to kleptoparasitize (scroungers). These are assumed to be mutually exclusive. The fitness payoff to scrounging is higher than that of producing when scroungers are very rare but decreases with increasing frequency of scroungers. When scroungers are very common, they do poorly relative to producers. At equilibrium, producers and scroungers do equally well. This equilibrium is an evolutionarily stable strategy (ESS; Maynard Smith 1982) because no individual can increase its fitness by unilaterally switching to the other tactic.

Although the producer-scrounger game has been applied primarily in the context of intraspecific kleptoparasitism, its general framework is broadly applicable to other forms of parasitism that meet its assumptions. One key assumption of the basic producer-scrounger game is that producers tolerate scroungers and that scroungers also tolerate one another at a patch. However, in nature, producers may respond to scrounging attempts in a number of ways, including resisting, tolerating, or avoiding the scrounger (reviewed in Barnard 1984*a*). Scroungers may also resist being joined by others (Barnard 1984*a*). Understanding when producers and scroungers are likely to tolerate being joined is therefore a critical component of understanding how social parasitism influences behavioral decisions.

The decision to tolerate will be influenced by a number of factors, including the costs of resisting, any additional benefits that scroungers may bring, such as decreased predation risk, and the degree to which others compete with or facilitate current group members. Multiple scroungers will compete for the resources taken from the producer. Strong competition among scroungers may lead to them avoiding others (spiders; Vollrath 1984) or defending producers against competitors (glaucous gulls *Larus hyperboreas*, Ingolffson 1969; stallions *Equus caballus*, Feh 1999). However, just as many scroungers use successful foragers to gain information or access to a resource, searching for producers or usurping resources from producers may be facilitated by the presence of others (e.g., parasitic jaegers; Arnason and Grant 1978). In some cases, scroungers may mutually benefit from such facilitation and attempt to displace resource owners as a coalition (e.g., herbivorous reef fish, Robertson et al. 1976; Foster 1985; coatis *Nasua narica*, Gompper 1996) and may even recruit others into the group (e.g., ravens *Corvus corax*, Marzluff and Heinrich 1991; Heinrich and Marzluff 1991).

The responses of both producers and scroungers to further parasitism will be influenced by those of other potential members of the group. For example, satellite pied wagtails (*Motacilla alba*) feed on the territories held by dominant birds. Satellites help defend feeding territories from nonterritorial floaters and are tolerated by the territory owner only when rates of intrusion by floaters are high (Davies and Houston 1981). Thus, the decision by floaters to join or not influences the decision of territory owners to tolerate. In Caribbean striped parrotfish (*Scarus iserti*), dominance-structured groups defend territories, with subordinates producing most of the resources (Clifton 1989, 1990, 1991). Subordinates rarely defend against large intruders, which are often attacked by dominant members of the group, but will defend against smaller intruders, which are not attacked by dominants (Clifton 1989). A subordinate's decision to defend thus appears to be influenced by the decisions of dominants.

In this article, we investigate how the relationships between a resource owner and two potential scroungers—a satellite to the owner and a floater—influence the decisions of both the resource owner and satellite to resist or tolerate scroungers and of the floater to join. We examine how variation in competition and facilitation between the satellite and floater, the abilities of both owners and satellites to defend resources, and the opportunities for the floater to find resources elsewhere influence these decisions. We then discuss when various combinations of behaviors are stable and how these simple relationships can give rise to other social interactions, such as the formation of mutually beneficial coalitions or territorial groups, task specialization, and recruitment of floaters by either parasites or owners.

Model

For the purposes of the model, our primary interest is in the origin of these decisions rather than their subsequent elaboration. Therefore, we assume that there is initially no coordination of either defensive or parasitic effort or long-term association among individuals, although these may be secondarily selected in some cases. We begin with a pair composed of an individual that finds, attracts, or otherwise produces resources (the "owner") and an individual attempting to take a proportion of those resources from the owner (the "satellite"). The satellite may or may not be tolerated by the owner. This pair is encountered by another searching individual (the "floater") that may also attempt to scrounge resources from the owner. We use the term "owner" rather than "producer" because the floater may be able to find resources without depending on a producer were it to choose to not join the pair. This scenario and the terminology of the model are based upon territorial-satellite systems, such as the pied wagtails and striped parrotfish previously discussed. However, the general framework could also be applicable to other systems, such as a resource owner encountered by two independently searching floaters, if one has already made the decision to attempt to join. For example, in western buffalo bream (*Kyphosus cornelii*), nonterritorial fish kleptoparasitizing territories of conspecifics are often joined by others (I. M. Hamilton, personal observation). In either case, the owner may choose between three tactics: tolerating both the satellite and floater, resisting both (i.e., attempting to exclude or recover the resource from both the satellite and floater), or resisting only one scrounger. We assume that if the owner attempts to resist only one scrounger, it will be the floater. We refer to this tactic as "partial resistance." The consequences of relaxing the assumption that owners always resist floaters if they resist at all are discussed later. The satellite may choose between two tactics: tolerate or resist the floater. The floater also may choose between two tactics: joining the pair or searching for undefended resources. All parameters of the model are listed in table 1. The owner controls some amount of resources, V, that it will use over the time period of the model. There may be a trade-off between resisting and producing so that the total amount of usable resources produced by the owner is reduced somewhat if it must resist one or both of the scroungers. We incorporate this trade-off as follows:

$$V = V_{\max} - ZC(n);\ V \geq 0, \tag{1}$$

where $V_{\max}$ is the maximum possible amount of resources produced by the owner, $C(n)$ is a measure of the direct cost of resisting, in terms of units of resources, n is the number of scroungers resisted (i.e., $n = 0$ if the owner does not resist, $n = 1$ if only the satellite or floater is resisted, and $n = 2$ if both are resisted), and Z is a constant that translates the cost of resisting into the loss of producing ability. In addition to the loss in producing ability, the owner directly assumes a cost equivalent to $C(n)$ units of resources, depending on the number of scroungers being resisted.

If the owner resists, the satellite and floater succeed at gaining some proportion of resources from the owner with probabilities $P_S(1)$ for one and $P_S(2)$ for both. Generally, $P_S(2) \geq P_S(1)$. This is because owners may have difficulty simultaneously defending against multiple scroungers. If the owner does not resist, both $P_S(1)$ and $P_S(2)$ equal 1. We refer to the ratio of $P_S(2) : P_S(1)$ as "facilitation" because it is a measure of how much more likely the satellite and floater are to access the owner's resources if the owner is attempting to resist both. There are other ways that the presence of the satellite or floater could facilitate one another. For example, two scroungers could remain at a patch for longer than one, although their probabilities of entering the patch do not change. However, this possibility is not considered in our model.

If a satellite or floater is successful, it takes $K(1)$ units of resources from the V units produced by the owner. If they are both successful, they take $K(2)$ units of resources, which are divided equally. Neither $K(1)$ nor $K(2)$ can exceed V. We assume that $K(1)$ is the maximum amount that one scrounger could take. Thus, assuming that the satellite and floater have equal resource needs, the ratio of $K(1) : K(2)$ is a measure of competition between them. When $K(1) = K(2)/2$, there is no competition. If there is pure scramble competition, $K(1) = K(2)$.

The satellite can successfully resist the floater, if it chooses to do so, with probability P_R. If the satellite attempts to resist the floater, it assumes a cost D. For both the owner and satellite, the costs associated with resisting the floater are not realized if the floater does not choose to join.

If the floater does not join, it may be able to find resources elsewhere. We assume that there are Q units of resources in the environment that would be missed by the floater if it attempts to join. We further assume that there will be scramble competition among all the floaters that do not join pairs for these Q resources. For simplicity, Q is divided equally among those floaters that do not join. We define the opportunity cost for the floater, therefore, as

$$\frac{Q}{N_F(1 - p_{FJ})}. \tag{2}$$

N_F is the total density of floaters, and p_{FJ} is the proportion of floaters that attempt to join. We refer to Q/N_F as the minimum opportunity cost of joining. This value is the minimum opportunity cost because if more floaters join, the realized opportunity cost of joining increases.

Tables 2 and 3 formally present the fitness payoffs for each role and tactic, given the tactics played by the other two roles. Assuming that owners, satellites, and floaters encounter one another randomly, the fitness payoff to playing a particular tactic is the sum of the payoffs for playing that tactic against each combination of tactics played by the other two roles multiplied by the probability of that combination appearing in a large population. For example, the fitness payoff to an owner resisting, w_{OR}, is

Table 1: List of symbols used

Symbol	Definition
$C(n)$	Cost, in units of resources, to the owner if it resists n scroungers
D	Cost, in units of resources, to the satellite if it resists the floater
I	Tactic played by owners of resisting satellites and tolerating floaters (app. B)
$K(n)$	Value of resources used by n scroungers if they gain access to the owner's resources
n	Number of scroungers ($n = 1$ for satellite or floater alone; $n = 2$ for satellite and floater together)
N_F	Population size for floaters
P	Tactic played by owners of resisting floaters and tolerating satellites
p_{FJ}	Proportion of floaters that attempt to join owners and satellites
p_{OR}	Proportion of owners that resist both satellites and floaters
p_{OP}	Proportion of owners that resist only floaters
p_{OT}	Proportion of owners that tolerate both satellites and floaters
P_R	Probability that the satellite can successfully resist the floater
p_{SR}	Proportion of satellites that resist floaters
$P_S(1)$	Probability that one scrounger can gain access to the owner's resources, if it is resisted by the owner
$P_S(2)$	Probability that the satellite and floater together can gain access to the owner's resources, if they are both resisted by the owner
Q	Value of resources that can be accessed by all floaters that do not join
R	Tactic of resisting all scroungers; owners playing R resist both satellites and floaters; satellites playing R resist floaters
T	Tactic of tolerating all scroungers; owners playing T tolerate both satellites and floaters; satellites playing T tolerate floaters
V	Value of the resources controlled by the owner if it successfully resists all scroungers
V_{max}	Maximum value of resources the owner can control
w_{FJ}	Fitness payoff to floater if it attempts to join; payoff if owner plays tactic X and satellite plays tactic Y is w_{FXYJ}
w_{FL}	Fitness payoff to floater that leaves (does not attempt to join)
w_{OI}	Fitness payoff to owner that resists only satellites (app. B); payoff if satellite plays tactic X and floater plays tactic Y is w_{OIXY}
w_{OP}	Fitness payoff to owner that resists only floaters; payoff if satellite plays tactic X and floater plays tactic Y is w_{OPXY}
w_{OR}	Fitness payoff to owner that resists both satellites and floaters; payoff if satellite plays tactic X and floater plays tactic Y is w_{ORXY}
w_{OT}	Fitness payoff to owner that tolerates both satellites and floaters; payoff if satellite plays tactic X and floater plays tactic Y is w_{ORXY}
w_{SR}	Fitness payoff to satellite that resists floaters; payoff if owner plays tactic X and floater plays tactic Y is w_{SXRY}
w_{ST}	Fitness payoff to satellite that tolerates floaters; payoff if owner plays tactic X and floater plays tactic Y is w_{SXTY}
Z	Constant translating the cost of resisting satellite and floater into a loss of the value of the owner's resources
ε	Mutation rate; proportion of individuals changing tactics each generation

$$w_{OR} = p_{FJ}[p_{SR}w_{ORRJ} + (1 - p_{SR})w_{ORTJ}] + (1 - p_{FJ})p_{SR}w_{ORRL}. \tag{3}$$

The probability that a floater will join is p_{FJ}, and the probability that a satellite will resist that floater is given by p_{SR}. The payoffs to partially resisting or tolerating follow the same format, using the appropriate terms for each combination of resisting and joining by the satellite and floater.

The fitness payoff to a satellite that resists, w_{SR}, is

$$w_{SR} = p_{FJ}(p_{OR}w_{SRRJ} + p_{OP}w_{SPRJ} + p_{OT}w_{STRJ}) + (1 - p_{FJ})(p_{OR}w_{SRRL} + p_{OP}w_{SPRL} + p_{OT}w_{STRL}). \tag{4}$$

The probabilities that an owner will resist, partially resist, or tolerate are given by p_{OR}, p_{OP}, and p_{OT}, respectively. These three must add up to 1. The fitness payoff to the satellite for tolerating again follows the same format, using the appropriate terms for each combination of owner's and floater's tactics.

The fitness payoff to a floater that joins, w_{FJ}, is

$$w_{FJ} = p_{SR}(p_{OR}w_{FRRJ} + p_{OP}w_{FPRJ} + p_{OT}w_{FTRJ}) + (1 - p_{SR})(p_{OR}w_{FRTJ} + p_{OP}w_{FPTJ} + p_{OT}w_{FTTJ}). \tag{5}$$

The fitness payoff to a floater that leaves (w_{FL}) is given by equation (2).

A set of tactics is evolutionarily stable when it is at a Nash equilibrium, that is, when no individual can improve its payoff by unilaterally switching to another tactic. Because of the complexity of analytical solutions to this

Table 2: Reward matrix for the various combinations of tactics

	If the floater joins			If the floater leaves		
	R	P	T	R	P	T
R	RRJ	PRJ	TRJ	RRL	PRL	TRL
T	RTJ	PTJ	TTJ	RTJ	PTJ	TTJ

Note: R = resist; T = tolerate; L = leaves; J = joins; For owners, P = resist floater. Each element of each matrix refers to the set of expected intake rates for the owner, satellite, and floater, if the owner plays the corresponding column tactic against a satellite playing the corresponding row tactic.

model, we present the results of simulations. For those situations for which simple analytic solutions could be obtained (e.g., $p_{FJ} = 1$), the analytical solutions confirmed the results of simulations. In our simulations, a random proportion of each role (owners, satellites, and floaters) was initially assigned to each of the possible tactics. We determined the relative fitness of each tactic as described above. We then allowed the population of each role to reproduce, with the contribution of a particular tactic to the next generation being its relative fitness multiplied by its current representation in the population. Note that fitnesses were not compared to those of other roles since, in this model, we are interested in the decisions of each role rather than in the stable distribution of individuals among roles. This simulation technique assumes that fdensity-dependent processes that are random with respect to role and tactic keep population sizes constant. Each generation, a small proportion ($e = 1 \times 10^{-7}$) of individuals switched tactics. This tested the stability of equilibria to small perturbations. At a stable equilibrium, the proportions of each tactic will return to the equilibrium if disturbed. We considered stability to have been reached when the fitness of each role playing each tactic that was represented in the population did not increase or decrease by more than 5×10^{-7} between generations for four consecutive generations.

Results and Discussion

All possible combinations of pure strategies, along with their biological interpretations, are outlined in table 4. In figures 1–3, we show the owner's and satellite's tactics that are stable over a range of values of competition and facilitation between satellite and floater. In figure 1, there is no trade-off between producing and defending (i.e., $Z = 0$), and there are no opportunities for floaters to find resources elsewhere (i.e., $Q = 0$). The panels of figure 1 refer to differences in the absolute and relative costs of resisting for satellites and owners (discussed below). Figure 2 shows the influence of changes in opportunity costs of joining on the stable combination of tactics used by owners and satellites. Figure 3 shows the influence of changing Z, the trade-off between producing and defending on these combinations of tactics.

For most combinations of parameters, we found a single stable solution to the game, although there were some simulations in which no stable solution was found after 10,000 generations. These are denoted as "unstable" in the figures. When the opportunity cost of joining was 0, the stable solution, if there was one, always included pure strategies for both the owner and satellite (fig. 1; table 4). When this cost was higher, owners sometimes played a mixed strategy (fig. 2*a*, 2*b*). In such cases, owners played a stable mixture of resisting and partially resisting. At sufficiently high cost of joining so that floaters never joined, tolerance and resistance were neutrally stable for satellites because the payoffs to each were identical.

In general, satellites tolerated floaters when competition was low (fig. 1). Interestingly, the owner tolerated at least one scrounger only when facilitation among scroungers was high (fig. 1). This is because an owner that has difficulty defending against two simultaneous scroungers can devote all of its defensive efforts to one if it tolerates the other.

The stable combinations of owner's and satellite's tactics were influenced by the absolute and relative costs of resisting (fig. 1). Not surprisingly, when the costs of resisting were low for both owners and satellites, both were more likely to resist than when the costs of resisting were high (fig. 1*a* vs. 1*b*; fig. 1*c* vs. 1*d*). Similar results were obtained if costs were kept the same but $K(1)$ was changed. In figures 1*a* and 1*b*, owners are better able to resist floaters than satellites and can do so at a lower cost (i.e., $[1 - P_S(1)] > P_R$ and $C[1] < D$). In figures 1*c* and 1*d*, we reversed the relative abilities of owners and satellites to resist floaters. When satellites were better able to resist satellites and lower cost than owners, satellites tended to resist at lower levels of competition, and owners tended to resist at higher levels of facilitation (fig. 1*a* vs. 1*c*; fig. 1*b* vs. 1*d*).

The minimum opportunity cost of joining had strong effects on the decisions of the owner and satellite. In figure 2, we show the stable combinations of owner's and satellite's tactics at increasing opportunity costs of joining for the floater. In all other respects, figure 2*a* corresponds to figure 1*a*, and figure 2*b* corresponds to figure 1*b*. As Q increased, the owner resisted the satellite at higher levels of facilitation (fig. 2). This change in the owner's tactic was most apparent when competition between satellite and floater was sufficiently high that the satellite resisted the floater. As we show in figure 2, the shift in the boundary between the owner resisting and partially resisting or tolerating was relatively slight when the ESS tactic for satellites was tolerance. In addition, the unstable region apparent at high costs of resisting (fig. 1*b*) was invaded by

Table 3: Payoffs for the various combinations of tactics

Combination/payoff	Equation
RRJ:	
Owner's payoff (w_{ORRJ})	$P_R\{[1-P_S(2)]V+P_S(2)[V-K(1)]\}+(1-P_R)\{[1-P_S(2)]V+P_S(2)[V-K(2)]\}-C(2)$
Satellite's payoff (w_{SRRJ})	$P_S(2)\{P_RK(1)+(1-P_R)[K(2)/2]\}-D$
Floater's payoff (w_{FRRJ})	$(1-P_R)P_S(2)[K(2)/2]$
PRJ:	
Owner's payoff (w_{OPRJ})	$P_R[V-K(1)]+(1-P_R)\{[1-P_S(1)][V-K(1)]+P_S(1)[V-K(2)]\}-C(1)$
Satellite's payoff (w_{SPRJ})	$[1-P_S(1)]K(1)+P_S(1)\{P_RK(1)+(1-P_R)[K(2)/2]\}-D$
Floater's payoff (w_{FPRJ})	$(1-P_R)P_S(1)[K(2)/2]$
TRJ:	
Owner's payoff (w_{OTRJ})	$\mathrm{P}_R[V-K(1)]+(1-\mathrm{P}_R)[V-K(2)]$
Satellite's payoff (w_{STRJ})	$P_RK(1)+(1-P_R)[K(2)/2]-D$
Floater's payoff (w_{FTRJ})	$(1-P_R)[K(2)/2]$
RTJ:	
Owner's payoff (w_{ORTJ})	$[1-P_S(2)]V+P_S(2)[V-K(2)]-C(2)$
Satellite's payoff (w_{SRTJ})	$P_S(2)[K(2)/2]$
Floater's payoff (w_{FRTJ})	$P_S(2)[K(2)/2]$
PTJ:	
Owner's payoff (w_{OPTJ})	$[1-P_S(1)][V-K(1)]+P_S(1)[V-K(2)]-C(1)$
Satellite's payoff (w_{SPTJ})	$[1-P_S(1)]K(1)+P_S(1)[K(2)/2]$
Floater's payoff (w_{FPTJ})	$P_S(1)[K(2)/2]$
TTJ:	
Owner's payoff (w_{OTTJ})	$V-K(2)$
Satellite's payoff (w_{STTJ})	$K(2)/2$
Floater's payoff (w_{FTTJ})	$K(2)/2$
RRL, RTL:	
Owner's payoff (w_{ORRL})	$[1-P_S(1)]V+P_S(1)[V-K(1)]-C(1)$
Satellite's payoff (w_{SRRL})	$P_S(1)K(1)$
Floater's payoff (w_{FRRL})	$Q/[N_F(1-p_{\mathrm{FJ}})]$
PRL, PTL, TRL, TTL:	
Owner's payoff (w_{OTRL})	$V-K(1)$
Satellite's payoff (w_{STRL})	$K(1)$
Floater's payoff (w_{FTRL})	$Q/[N_F(1-p_{\mathrm{FJ}})]$

Note: R = resist; T = tolerate; L = leaves; J = joins. For owners, P = resist floater.

both owners and satellites resisting as the opportunity cost of joining increased (fig. 2*b*).

Figures 3*a* and 3*b* again correspond to the same set of parameters as figures 1*a* and 1*b* (with the exception that *Z*, the trade-off between producing and resisting, was changed). Increasing *Z* resulted in tolerance by the owner being stable at lower facilitation (fig. 3 vs. fig. 1). The boundary between both the owner and satellite resisting (resist : resist) and the owner tolerating while the satellite resisted (tolerate : resist) was most sensitive to changes in *Z*. This was particularly apparent when the costs of resisting were high (fig. 3*b*).

Not surprisingly, floaters were less likely to attempt to join when the opportunity cost of joining was high. In figure 4, we show the proportion of floaters joining when the minimum opportunity cost of joining was >0, at various levels of competition between floater and scrounger. Again, figures 4*a* and 4*b* correspond to figures 2*a* and 2*b* when $Q/N_F = 0.0075$. In general, a floater was less likely to join if either the owner or satellite resisted it (fig. 4). For example, in figure 4*a*, the proportion of floaters joining when $K(1)/K(2) = 0.7$ decreases at $P_S(2)/P_S(1) \approx 1.25$, when the stable tactic for satellites shifts from tolerance to resistance. For a given combination of owner's and satellite's tactics, a floater was also more likely to join when competition between it and the satellite was low (fig. 4).

The effects of facilitation on the likelihood of joining depended upon the owner's tactic. If the owner resisted the satellite, the floater was also more likely to join when facilitation was high. If the owner tolerated the satellite (i.e., it partially resisted or tolerated), there was no effect of facilitation on the likelihood of the floater joining (fig. 4). Thus, as we show in both panels of figure 4, the proportion of floaters joining increased with increasing facilitation at low levels of facilitation (when both scroungers

Table 4: All possible combinations of owner's and satellite's tactics and their descriptions, along with the conditions when each is likely to be stable, should floaters join

Owner's tactic : satellite's tactic	Description	Conditions
Partial : resist	Owner tolerates satellite but resists floater, satellite resists floater	Competition intermediate, facilitation high, costs of resisting low
Tolerate : resist	Owner tolerates both satellite and floater, satellite resists floater	Competition high, facilitation high
Partial : tolerate	Owner tolerates satellite but resists floater, satellite tolerates floater	Competition low, facilitation high
Tolerate : tolerate	Owner tolerates satellite and floater, satellite tolerates floater	Competition intermediate, facilitation high, costs of resisting high
Resist : resist	Owner resists both satellite and floater, satellite resists floater	Competition high, facilitation low
Resist : tolerate	Owner resists both satellite and floater, satellite tolerates floater	Competition low, facilitation low

were resisted) but did not change with facilitation at higher levels (when only floaters were resisted).

An interesting result of this model is that the Nash equilibrium found by simulation may also be a mutually beneficial solution for at least two of the three roles (see app. A). That is, if an individual changed tactics, not only would it do worse, but one of the other individuals would also do worse (i.e., the Nash equilibrium is also a Pareto equilibrium for two of the roles). For example, for some combinations of parameters, resistance by the owner, tolerance by the satellite, and joining by the floater is a Nash equilibrium. Because of facilitation between satellite and floater, the satellite does better if the floater joins than if it leaves. Similarly, the floater does better if the satellite tolerates than if it resists. Thus, this solution is also a Pareto equilibrium for satellite and floater, given that the owner resists. The significance of the Nash equilibrium being a Pareto equilibrium is twofold. First, whereas in other situations reaching a cooperative optimum that maximizes the fitness of both roles may involve some "negotiation" between players (e.g., tit-for-tat), when the Pareto equilibrium is also a Nash equilibrium, no such negotiation is required (Giraldeau and Caraco 2000). Second, starting at the Pareto equilibrium, derived mutualisms may evolve because each role is selected to increase its investment in the other (Connor 1995).

We now discuss the various stable solutions to the game in more detail. We describe examples of each solution from the literature and discuss when mutually beneficial interactions might arise. We refer to each combination in the following format: owner's tactic : satellite's tactic.

Partial : Resist

When facilitation is high, the owner will tolerate the satellite. When this is so, the costs of resisting floaters are low, competition is intermediate, and the ESS is partial : resist (e.g., fig. 1*a*). Partial : resist may describe some examples of group territoriality, in which both owner and satellite defend themselves (and, as a consequence, each other) against intruding floaters. In territorial systems, satellite or subordinate individuals often contribute to the defense of a resource and are tolerated by an owner that also contributes to defense. For example, satellite pied wagtails are equally aggressive as territory holders toward intruders (Davies and Houston 1981).

A key component of partial : resist is that both resist the floater equally. Because of this, partial : resist, when stable, is always mutually beneficial for the owner and satellite (app. A). If the owner switched to resisting both or tolerating both, the satellite would do worse because the satellite either would be less likely to get resources from the owner or would be more likely to have to share them with the floater. The owner would do better if neither the satellite nor the floater joined. However, given that they will attempt to join, the owner does better if the satellite resists. If the satellite switched to tolerating, the owner would be more likely to lose resources to the floater.

Partial : resist is only stable when the minimum opportunity cost of joining is very low (fig. 2), that is, when most or all floaters attempt to invade territories. When this cost is high, partial : resist is replaced by the owner either resisting or playing a mixed strategy of resisting and partially resisting. Davies and Houston (1981) observed that satellite wagtails were tolerated on feeding territories on days when intruder pressure was high. On days when intruder pressure was low, satellites were evicted. Intruder pressure was correlated with abundance of food on the territory (Davies and Houston 1981). When food was abundant, the opportunity cost of joining, relative to the value of the territory, would have been low. Under these conditions, intrusions were frequent and satellites tolerated.

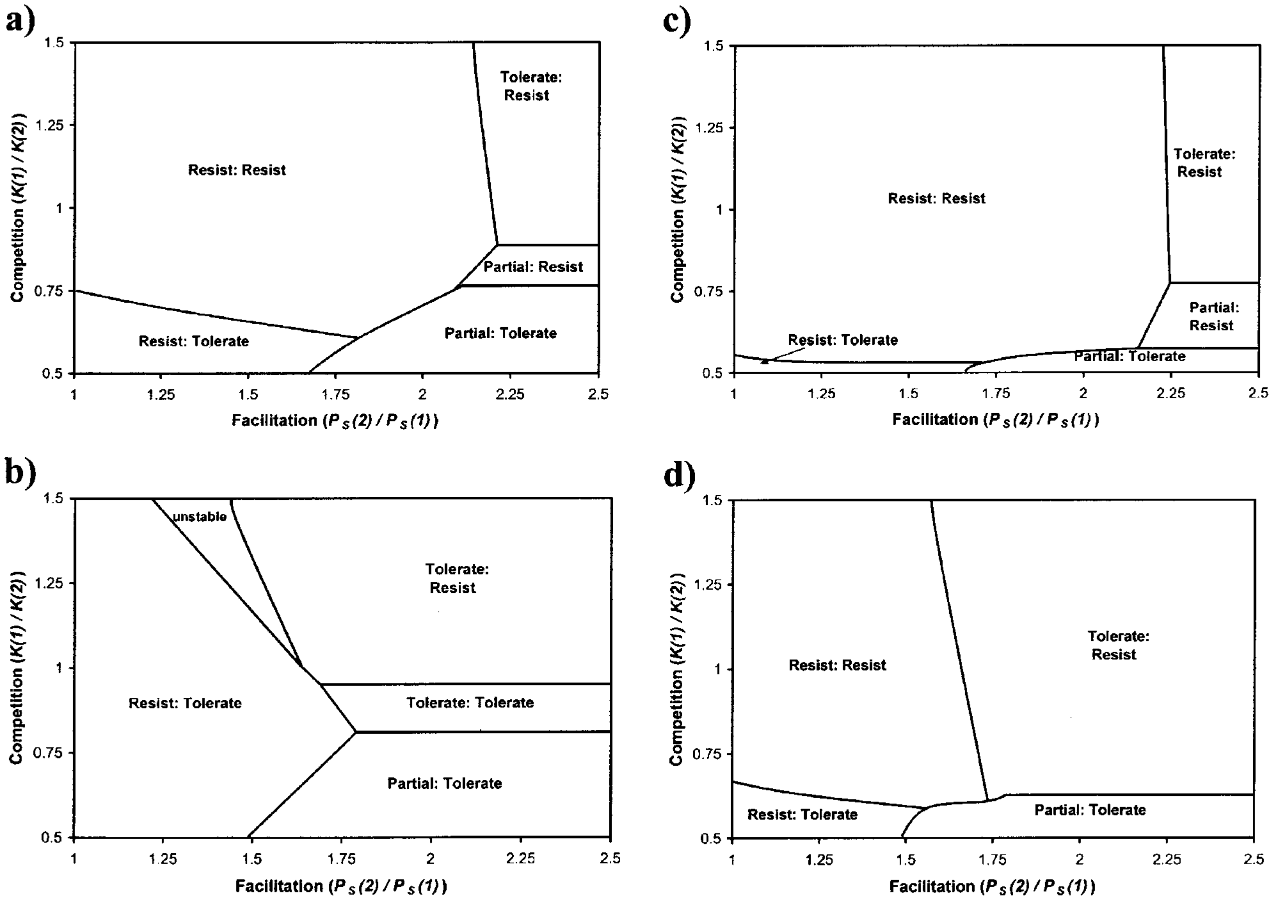

Figure 1: The influence of the costs of resisting scroungers on the evolutionarily stable combinations of owner's and satellite's tactics when all floaters attempt to join. *a*, The cost of resisting scroungers is low overall and lower for the owner than the satellite ($C[1] = 0.015$ units of resources; $C[2] = 0.0375$ units of resources; $D = 0.0225$ units of resources; $P_R = 0.4$). *b*, The cost of resisting scroungers is high overall but lower for the owner than the satellite ($C[1] = 0.05$ units; $C[2] = 0.125$ units; $D = 0.075$ units; $P_R = 0.4$). *c*, The cost of resisting scroungers is low but higher for the owner than the satellite (as in 1*a*, but $D = 0.01$ units and $P_R = 0.8$). *d*, The cost of resisting scroungers is high and higher for the owner than the satellite (as in 1*b*, but $D = 0.0333$ and $P_R = 0.8$). Results are shown over a range of competition between satellite and floater from no change in the maximum resources used by the satellite if joined (0.5) to competition that is sufficiently high that the satellite and floater together use fewer resources than the satellite alone (>1). The change in the satellite's access to resources when joined by a floater (facilitation) ranges from no change (1) to 2.5 times more likely to gain access. Other parameters in this example (see table 1): $V = 1$ unit; $K(1) = 0.4$ units; $P_S(1) = 0.4$; $Z = 0.1$.

Tolerate : Resist

In tolerate : resist, the owner tolerates both the satellite and floater, while the satellite resists. Tolerate : resist is likely when competition and facilitation between satellites and floaters are high (fig. 1). When competition is high, satellites tend to resist floaters, which allows owners to avoid paying the costs of resisting. Tolerate : resist is particularly likely when there is a strong trade-off between the owner's abilities to produce and defend resources (fig. 3). In this case, tolerate : resist may be a mutually beneficial solution for owner and satellite (app. A). If owners switched to resisting, they would produce fewer resources, which would then not be available to satellites. If satellites switched to tolerating, owners would lose resources to the floater. However, it need not be a mutually beneficial solution. If there is sufficiently little trade-off between producing and resisting that the amount a scrounger could take is always less than the amount produced, even if the owner resists, then the satellite will always benefit more from the owner resisting the floater than from tolerating (app. A).

Tolerate : resist can be mutually beneficial for owner and floater if the ratio of $K(1) : K(2)$ is >1 (app. A). This may effectively be the case if V_{max} increases with group size. For example, groups may be more effective at finding food

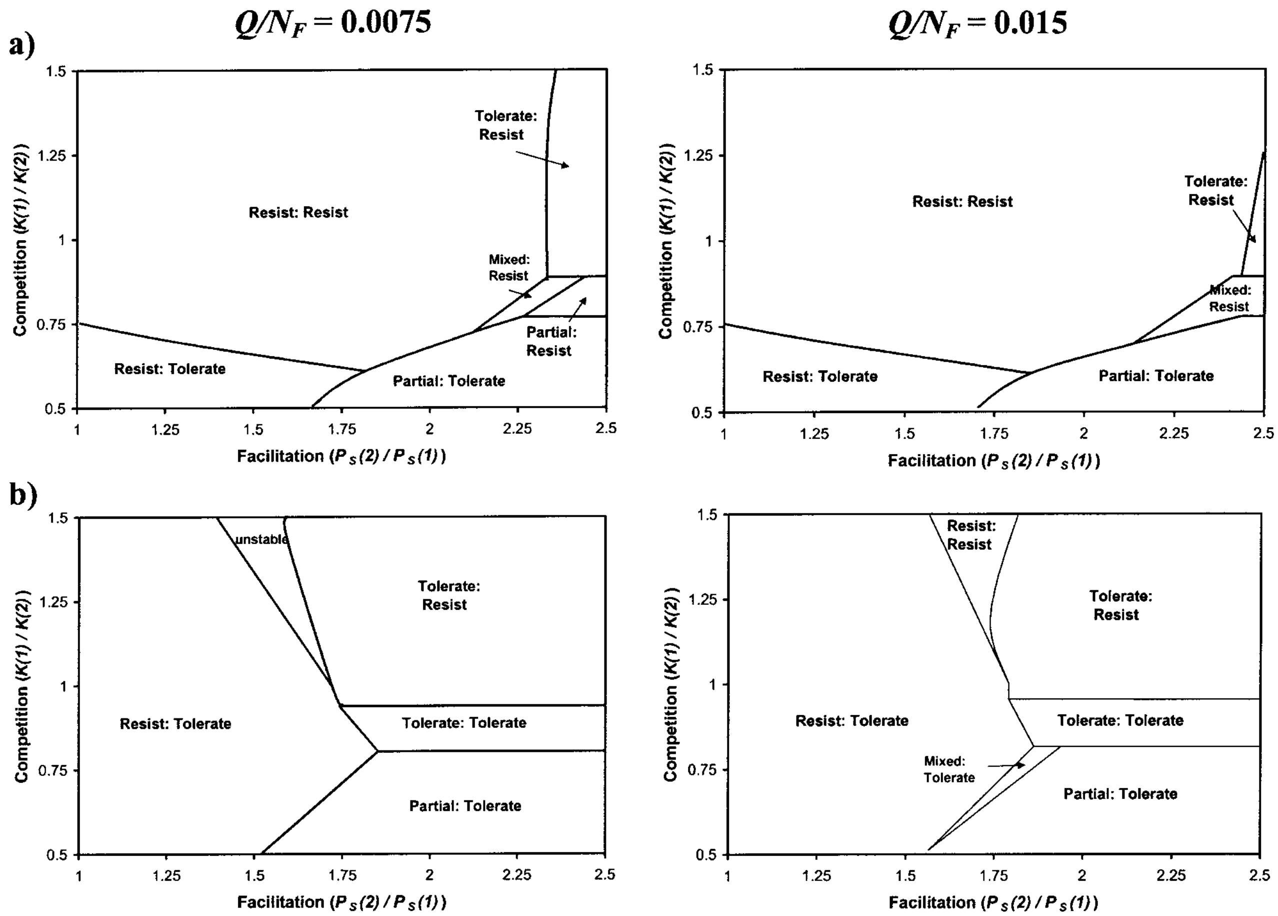

Figure 2: Evolutionarily stable combinations of owner's and satellite's tactics for the same combinations of parameters as in figure 1, when floaters do not all attempt to join. The left two panels show the evolutionarily stable strategy tactics when $Q/N_F = 0.0075$ units of resources. The right two panels show these tactics for $Q/N_F = 0.015$ units of resources. *a*, Low costs of resisting floaters ($C[1] = 0.015$ units of resources; $C[2] = 0.0375$ units of resources; $D = 0.0225$ units of resources). *b*, High costs of resisting floaters ($C[1] = 0.05$ units of resources; $C[2] = 0.125$ units of resources; $D = 0.075$ units of resources). Other parameters in this example are the same as in figures 1*a* and 1*b*.

than are solitary individuals. In this case, owners could benefit from encouraging floaters to join, particularly if the owner can control the proportion of resources taken by the floater (Vehrencamp 1983; Keller and Reeve 1994; Hamilton 2000). Interestingly, the ratio of $K(1):K(2)$ could also exceed one for the same $V_{\max}$ if there is some form of resource-wasting interference in which items that could be taken by the parasites are lost to them while they compete. If such competition is likely, owners could benefit from encouraging floaters to join. We know of no such cases among kleptoparasites or intrasexual parasites, but the possibility is intriguing.

Tolerate : resist is also interesting because pairs of owners and satellites are characterized by an apparent division of labor. The owner specializes by focusing on one task, finding resources, while the satellite focuses on another, defending itself (and, as a consequence, the owner as well). Our model predicts that division of labor does not arise as a secondary modification of mutually beneficial groups (reviewed in Connor 1995) but can be an emergent property in some groups. Furthermore, this task specialization arises even when owners are better at defending against floaters than are satellites. Fewell and Page (1999) found that pairs of normally solitary ant foundresses of the species *Pogonomyrmex barbatus* that were forced into foundress associations specialized into a nest-digging specialist and a reproductive specialist. If two nest-digging specialists were paired together, this specialization in two different tasks still arose. Although this system differs somewhat from that outlined in our model because both ants are capable of both tasks (whereas only owners are able to produce resources in our model), it is nonetheless evidence

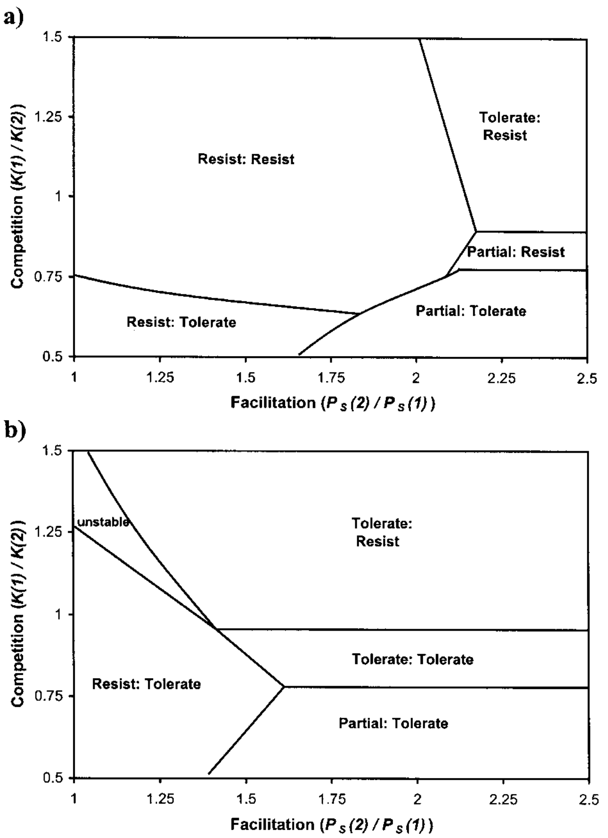

Figure 3: Influence of changing the strength of the owner's trade-off between producing and resisting (Z). All parameters except Z are the same as for figure 1. $Z = 0.5$. *a*, Low cost of resisting floaters (as in fig. 1*a*). *b*, High cost of resisting floaters (as in fig. 1*b*). Other parameters in this example (see app. A): $V = 1$ unit; $K(1) = 0.4$ units; $P_S(1) = 0.4$; $P_R = 0.4$; $Q = 0$.

that division of labor can emerge at the origin of group living rather than later.

Both tolerate : resist and partial : resist are characterized by defense of the resource by satellites. This suggests that some instances of "helping" by satellites or subordinates may have originated in selfish defense of territorial individuals by scroungers. Some cooperatively breeding societies include unrelated nonbreeding floaters that intrude upon territories (e.g., red-cockaded woodpeckers *Picoides borealis*, Walters 1990; Galápagos hawks *Buteo galapagoensis*, Faaborg and Bednarz 1990). We suggest that in such societies, satellites may have initially been tolerated because they were able to assist in defense of the territory against floaters. Similarly, in leks, satellite male waterbuck (*Kobus ellipsiprymnus*) are tolerated by resident males and conduct most of the defense against incoming individuals (Wirtz 1981), and subordinate stallions defend themselves and dominants against outside competitors more often than do dominants (Feh 1999). Because both owner and satellite resist floaters, albeit unequally, these latter situations are intermediate between those described by partial : resist and tolerate : resist. Both partial : resist and tolerate : resist are stable over a smaller range of parameters as the minimum opportunity cost of joining increases (fig. 2). Thus, strong ecological constraints on independent breeding, which should favor both floaters attempting to join and satellites remaining on or joining a dominant's territory in the first place (Vehrencamp 1983), would also lead to those satellites helping to defend the territory.

Partial : Tolerate

Partial : tolerate describes an equilibrium solution in which

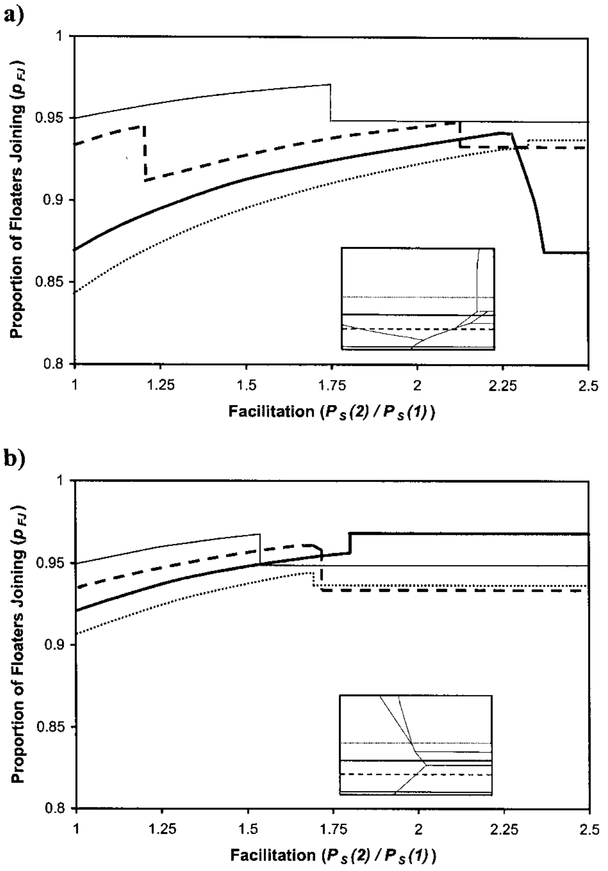

Figure 4: Evolutionarily stable proportions of floaters attempting to join (p_{FJ}) when the costs of resisting floaters for owners and satellites are low (*a*) and high (*b*). Line style denotes competition ($K[1] : K[2]$) between satellite and floater (*thin black line* = 0.54; *dashed line* = 0.7; *thick black line* = 0.86; *dotted line* = 1). $Q/N_F = 0.0075$. The inset panels are the first panels from figures 2*a* and 2*b*. See that figure for labels. The horizontal lines on the inset panels correspond to the values of competition shown on the main panels of this figure (i.e., *thin black line*: $K[1] : K[2] = 0.54$ in all cases).

the owner both produces resources and defends them. The satellite does neither but is tolerated by the owner nonetheless. Partial : tolerate is only stable when facilitation is high, and the owner must accept the satellite rather than defend against both it and the floater (fig. 1). Competition between satellite and floater must also be low. Higher competition would favor tolerance by the owner (because the satellite and floater together do not take much more than the satellite alone) and resistance by the satellite. The minimum opportunity cost of joining influences the stability of partial : tolerate. Partial : tolerate is most sensitive to the relative costs of resisting for owner and satellite (fig. 1*c*, 1*d*). When owners are more successful at resisting floaters than are satellites, partial : tolerate is stable at higher levels of competition between satellite and floater.

Because the owner does not resist the satellite, the satellite gains no benefit from the floater joining (app. A). In addition, the owner would always do better if the satellite resisted (app. A). Therefore, partial : tolerate cannot be a Pareto equilibrium.

Overall, in the region where tolerance by the owner toward the satellite is stable (i.e., high facilitation), there is a shift from the owner defending the resource to the satellite defending the resource as competition between satellite and floater increases. There is evidence for such a shift from a herbivorous marine fish. As discussed above, large, dominant striped parrotfish use subordinates to locate patches of food on a territory (Clifton 1991). Territories are also invaded by floaters, and these are resisted by one or more fish on the territory. Our model predicts that when there is high competition between floaters and satellites (dominants), satellites should resist. When competition is lower, owners (subordinates) should resist. Large subordinates and dominants typically defend territories (Clifton 1989, 1990). However, dominants rarely defend against small intruders, while smaller subordinates do not contribute to defense unless intruders are also very small (Clifton 1989). Thus, as intruder size increases, there is a shift from partial : tolerate, in which only owners (subordinates) defend, through partial : resist, in which both owners and satellites (dominants) defend, to tolerate : resist, in which only dominants defend.

The shift from partial : tolerate to tolerate : resist with increasing relative size of the intruder qualitatively supports the prediction of our model that as competition between scroungers increases, satellites are more likely to resist, and this allows owners to avoid the costs of resisting. Alternatively, large fish may simply not compete with smaller subordinates. However, given that striped parrotfish are herbivores and that large fish on the territories feed on patches of algae discovered by smaller fish, smaller fish likely also face competition from large floaters.

Tolerate : Tolerate

Tolerate : tolerate is the solution assumed in the classical producer-scrounger game. The resource owner does not defend against intruders, who themselves equally share resources. We found tolerate : tolerate was never stable when the costs of resisting were low. When these costs were higher, tolerate : tolerate was stable at high facilitation and intermediate competition (fig. 1*b*). Thus, tolerate : tolerate should be expected when scroungers are difficult to effectively resist.

In the classical producer-scrounger game, the owner (producer) discovers a patch, takes some proportion of it (the "finder's share"), and shares the rest equally with joining, mutually tolerant kleptoparasites (Barnard and Sibly 1981; Giraldeau and Beauchamp 1999). Under the conditions of producer priority, the ratio of $K(1) : K(2)$ would be 3 : 4 (i.e., two-thirds of the food remaining after the finder's share is taken by the producer if two kleptoparasites join versus one-half of the food remaining if only one kleptoparasite joins). At this ratio, tolerate : tolerate can be stable if resisting kleptoparasites is costly or rarely successful. For situations to which the producer-scrounger game has been applied, such as flocks of birds (e.g., Giraldeau et al. 1994) or groups of sea slugs (*Placida dendritica*, Trowbridge 1991), this is probably a reasonable assumption.

Tolerate : tolerate can never be a Pareto equilibrium. Because the owner does not resist, the satellite gains no benefit from the floater joining, while the owner would always do better if the satellite resisted (app. A).

Resist : Tolerate

Resist : tolerate describes an equilibrium solution in which the satellite tolerates a floater and the owner resists both. Resist : tolerate is the ESS when there is both low competition and low facilitation between satellite and floater (fig. 1). When facilitation is relatively low, owners are able to defend against both satellite and floater almost as successfully as they can defend against the floater alone. When competition between satellite and floater is low, satellites gain little by to trying to exclude floaters. For resource "bonanzas," in which owners discover or defend very large patches relative to the amount that any individual can take, competition can be low, and these could therefore allow tolerance among kleptoparasites (see also Mesterton-Gibbons and Dugatkin 1999).

The best examples of both resist : tolerate and resist : resist (see "Resist : Resist") do not come from owner-satellite systems but from systems in which owners are parasitized by groups of mutually tolerant scroungers. In several species, individuals that do not have access to resources form coalitions, which apparently aid in overwhelming the defences of those controlling resources. Male blue-headed wrasse (*Thalassoma bifasciatum*) form groups, which do not interact aggressively, that intercept females attracted to displaying males (Warner and Hoffman 1980), and sneaker male sunfish (*Lepomis macrochirus*) intrude upon mating pairs in groups or in rapid succession, confusing the parental male (Gross 1982). Such coalitions are also found in foraging societies. Female coatis band together to displace dominant males from resources (Gompper 1996), many herbivorous fish form groups that invade the feeding territories of territorial herbivores (Robertson et al. 1976; Foster 1985), and juvenile ravens band together to gain access to carcasses defended by adults (Marzluff and Heinrich 1991). In at least the latter two cases, resource bonanzas are involved. A carcass can support many juvenile ravens (Marzluff et al. 1996), and the standing stock of algae on a herbivorous fish's territory is often much greater than the amount taken by any single invader (I. M. Hamilton, personal observation). Whether these interactions, which usually involve more than two floaters, are best classified as resist : tolerate or resist : resist will depend upon whether resources are shared equally among coalition members.

Resist : tolerate may be mutually beneficial for satellite and floater (app. A). Indeed, if a satellite (that is, a scrounger that has decided to take resources from an owner) is more likely to succeed if it were joined than it would on its own, it may encourage joining. For example, juvenile ravens recruit others to carcasses defended by adults by emitting food-associated calls (Heinrich and Marzluff 1991). Our model makes two counterintuitive predictions regarding such mutually beneficial coalitions of scroungers. First, these coalitions are expected when facilitation between scroungers is relatively low and not expected when facilitation is high. This is because floaters can only benefit from the presence of satellites when satellites are resisted. When facilitation is high, satellites are not resisted (fig. 1) and cannot facilitate floaters' access to resources. Second, coalitions can form at slightly higher levels of facilitation as the opportunity cost of joining increases (fig. 2). This is because satellites are more likely to be resisted with a higher opportunity cost of joining. In other words, when fewer floaters join, owners are more likely to resist satellites, which then allows those floaters that do join to benefit from satellites. In summary, as the potential net benefits to coalition formation for either the satellite or the floater increase, mutualistic coalitions become less likely. It should be noted, however, that when there is very low or no facilitation, it is no longer in the satellite's interest that the floater join (app. A). Even though the floater is tolerated, the interaction would not be mutually beneficial.

Not surprisingly, resistance by the owner is also more likely when its costs of resisting are low and its success at resisting both scroungers is high. Tolerance by the satellite is more likely when its costs of resisting are high and its success of resisting the floater is low. Thus, resist : tolerate is expected to be more likely when the owner is relatively good at resisting intruders and the satellite relatively poor.

Resist : Resist

Resist : resist is similar to resist : tolerate in that pairs of scroungers are resisted by the owner. Because of this, satellites may gain from the presence of floaters (app. A). However, the critical difference from resist : tolerate is that satellites also attempt to displace floaters from the scrounged resource once access has been gained. This is a consequence of the model's assumption that satellites are facilitated by the floater regardless of whether they tolerate the floater. This leads to the satellite being able to exploit both the resources produced by the owner and the increased access to those resources gained from the floater. Resist : resist is the ESS when competition is high and facilitation is low (fig. 1). As the cost of joining increases, resist : resist becomes stable at higher facilitation (fig. 2). Interestingly, the opportunity cost of joining has no influence on the boundary between resist : resist and resist : tolerate.

As we discussed earlier, some of the examples outlined in the previous section have characteristics of both resist : tolerate and resist : resist because coalition members do not have equal access to resources (e.g., ravens; Marzluff and Heinrich 1991). When a single prey item is involved, there may be complete exclusion of most floaters from resources that they helped acquire. For example, groups of parasitic jaegers often attempt to parasitize gulls (Arnason and Grant 1978). The success of the entire group of jaegers increases with the number of birds chasing, but only one bird eventually gets the fish.

Because floaters would always do better if resources were divided equally, resist : resist can never be a Pareto equilibrium in this model (app. A). The model assumes that the satellite either shares the resource equally or tries to exclude the floater altogether and that the probability that the satellite can exclude the floater is fixed. However, given that the satellite benefits from the presence of the floater, it may be able to encourage joining by conceding some of the resources it controls. If this is the case, the size of the concession given may be predicted from transactional skew models (Keller and Reeve 1994; Hamilton 2000; Johnstone 2000). The size of the concession should increase as facilitation and competition decrease and the opportunity cost of joining increases. However, the floater may be able to increase its likelihood of gaining access to the resource by increasing its investment in competition with the satellite. In this event, tug-of-war skew models predict the evolutionarily stable amount of investment in competitive effort by both individuals (Reeve et al. 1998; Johnstone 2000). These models predict that inequality in resource division in pairs of unrelated individuals should only be a function of their relative abilities to translate competitive effort into fitness.

There are other ways in which owners may resist scroungers that are not explicitly considered in the model. These include moving (Parker and Sutherland 1986; Holmgren 1995; Ruxton and Moody 1997; Hamilton, in press), hiding, or aggregating. Aggregating may favor resistance by the satellite if the satellite is able to profitably defend multiple owners (Ingolfsson 1969). Aggregating may also favor the floater leaving a particular producer and searching elsewhere in the group because the search costs of finding another, possibly unparasitized, owner in the group would be small. Movement or hiding by owners would increase search costs for floaters and may therefore increase the likelihood that a floater attempts to join.

Our model also assumes that if the owner chooses to resist only one scrounger, it will resist the floater. However, when we relaxed this assumption (see app. B), we found that resisting only the satellite was stable over a wide range of conditions and that resisting only the floater could not be stable when the minimum opportunity cost of joining was >0 or when satellites also resisted floaters (fig. 5). This is because under these conditions, the floater may not successfully join, so that all else being equal, there is a lower cost to accepting the floater than the satellite, which will always join. In many of the examples we outlined previously, owners do tolerate satellites while resisting floaters. There are a number of possible reasons for this. First, satellites may generally be less costly to owners. This would suggest that in cases when satellites are indeed more costly than floaters, satellites should be evicted in favor of floaters. Second, if there is any long-term association between satellite and owner, the cost of accepting the satellite is better known than the cost of accepting the floater. Thus, the risk-averse decision would be to accept the satellite, even when the mean costs of satellites and floaters are the same. Third, the assumption that floaters may not always attempt to parasitize, while satellites always will, may not be valid. If floaters are as likely to join as satellites, resisting either may be stable. In this case, however, resisting only the satellite would be paradoxical because an evicted satellite would likely become a floater.

One drawback of our model is that it does not predict when an individual should play the role of owner, satellite, or floater or move among these roles. However, it does predict when resistance or tolerance toward joiners by either owners or satellites is expected. It is likely that these two sets of decisions are interrelated and that a greater understanding of social exploitation involves integrating decision making at these two levels. Nevertheless, our model emphasizes the importance of social exploitation and, specifically, competition over and facilitation of access to resources among scroungers in the evolution of group living. It also provides a general framework for predicting the conditions under which existing models of social exploitation, such as skew models and producer-scrounger models, are applicable. Furthermore, our model suggests how owners, satellites, and floaters responding to one another may give rise to a variety of more complex social behaviors, including satellites helping owners, coalitions of scroungers, and task specialization. We emphasize that, although there are many other possible origins for such behaviors (e.g., delayed dispersal, reduced predation risk, relatedness benefits), our model predicts the conditions that likely favor the evolution of these more complicated social systems from socially parasitic origins.

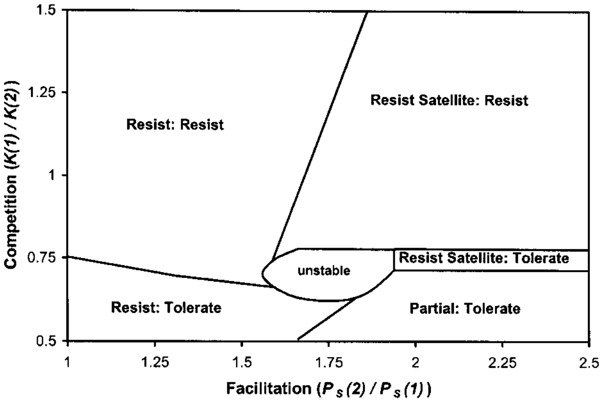

Figure 5: Evolutionarily stable combinations of tactics for the same parameters as figure 1*a*, when the resist-only-satellite tactic is included for the owner. Resist satellite is always able to invade tolerate : resist and partial : resist, as well as some areas where resist : resist was stable. If $Q > 0$, the resist-only-satellite tactic also always invades partial : tolerate.

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APPENDIX A

Influences of Changing Tactics on the Fitnesses of Other Roles

For owners, the partial differentials of the fitness equations, with respect to a change in the proportion of satellites resisting, are as follows:

$$\frac{\partial w_{\mathrm{OR}}}{\partial p_{\mathrm{SR}}} = p_{\mathrm{FJ}} P_{\mathrm{R}} P_{\mathrm{S}}(2)[K(2) - K(1)], \tag{A1}$$

$$\frac{\partial w_{\mathrm{OP}}}{\partial p_{\mathrm{SR}}} = p_{\mathrm{FJ}} P_{\mathrm{R}} P_{\mathrm{S}}(1)[K(2) - K(1)], \tag{A2}$$

$$\frac{\partial w_{\mathrm{OT}}}{\partial p_{\mathrm{SR}}} = p_{\mathrm{FJ}} P_{\mathrm{R}}[K(2) - K(1)]. \tag{A3}$$

From these, it is apparent that owners will benefit from satellites resisting whenever the satellite and floater together can take a larger amount of resources than the satellite alone. Note that this is not always the case; we have allowed for the possibility of resource-wasting competition between satellite and floater. In this case, owners would not benefit from satellites resisting.

The partial differentials of the fitness equations for owners, with respect to the proportion of floaters joining are as follows:

$$\frac{\partial w_{\mathrm{OR}}}{\partial p_{\mathrm{FJ}}} = [P_{\mathrm{S}}(1) - p_{\mathrm{SR}} P_{\mathrm{R}} P_{\mathrm{S}}(2)]K(1) - [P_{\mathrm{S}}(2) - p_{\mathrm{SR}} P_{\mathrm{R}} P_{\mathrm{S}}(2)]K(2) + C(1) - C(2), \tag{A4}$$

$$\frac{\partial w_{\mathrm{OP}}}{\partial p_{\mathrm{FJ}}} = P_{\mathrm{S}}(1)(1 - p_{\mathrm{SR}} P_{\mathrm{R}})[K(1) - K(2)] - C(1), \tag{A5}$$

$$\frac{\partial w_{\mathrm{OT}}}{\partial p_{\mathrm{FJ}}} = (1 - p_{\mathrm{SR}} P_{\mathrm{R}})[K(1) - K(2)]. \tag{A6}$$

Unless there is resource-wasting competition, these values are always negative ($P_{\mathrm{S}}[2] > P_{\mathrm{S}}[1]$ in eq. [A4]). When there is resource wasting competition, these values may be positive, if the costs of resisting scroungers are low. Owners may benefit, therefore, from being joined by floaters but only if competition between floaters and satellites is very high.

It is obvious that an increase in the proportion of owners resisting satellites will always have a negative effect on the fitness of satellites. The partial differentials of the fitness equations for satellites, with respect to the proportion of owners resisting floaters, are as follows. When $K(2) < V$,

$$\frac{\partial w_{\mathrm{SR}}}{\partial p_{\mathrm{OP}}} = p_{\mathrm{FJ}}[1 - P_{\mathrm{S}}(1)](1 - P_{\mathrm{R}})\left[K(1) - \frac{K(2)}{2}\right], \tag{A7}$$

$$\frac{\partial w_{\mathrm{ST}}}{\partial p_{\mathrm{OP}}} = p_{\mathrm{FJ}}[1 - P_{\mathrm{S}}(1)]\left[K(1) - \frac{K(2)}{2}\right]. \tag{A8}$$

Because $K(1)$ is always $\geq K(2)/2$, these values are always positive, and satellites always benefit from owners resisting satellites. When $K(2) = V$, which is likely if there is a substantial trade-off for the owner between producing resources and defending resources, these equations are as follows:

$$\frac{\partial w_{\mathrm{SR}}}{\partial p_{\mathrm{OP}}} = p_{\mathrm{FJ}}(1 - P_{\mathrm{R}})\left\{\frac{P_{\mathrm{S}}(1)V}{2} + [1 - P_{\mathrm{S}}(1)]K(1) - \frac{V}{2}\right\}, \tag{A9}$$

$$\frac{\partial w_{\mathrm{ST}}}{\partial p_{\mathrm{OP}}} = p_{\mathrm{FJ}}\left\{\frac{P_{\mathrm{S}}(1)V}{2} + [1 - P_{\mathrm{S}}(1)]K(1) - \frac{V}{2}\right\}. \tag{A10}$$

The changes in the fitness of a satellite, given a change in the proportion of floaters joining, are as follows:

$$\begin{aligned}\frac{\partial w_{\mathrm{SR}}}{\partial p_{\mathrm{FJ}}} = {} & \{p_{\mathrm{OP}}[1 - P_{\mathrm{S}}(1)] - 1\}\left[K(1) - \frac{K(2)}{2}\right](1 - P_{\mathrm{R}}) + p_{\mathrm{OR}}\left\{K(1)[1 - P_{\mathrm{S}}(1) - P_{\mathrm{R}} - P_{\mathrm{R}}P_{\mathrm{S}}(2)]\right. \\ & \left. - \frac{K(2)}{2}(1 - P_{\mathrm{R}})[1 - P_{\mathrm{S}}(2)]\right\} - D,\end{aligned} \tag{A11}$$

$$\frac{\partial w_{\mathrm{ST}}}{\partial p_{\mathrm{FJ}}} = \{p_{\mathrm{OP}}[1 - P_{\mathrm{S}}(1)] - 1\}\left[K(1) - \frac{K(2)}{2}\right] + p_{\mathrm{OR}}\left\{K(1)[1 - P_{\mathrm{S}}(1)] - \frac{K(2)}{2}[1 - P_{\mathrm{S}}(2)]\right. \tag{A12}$$

These equations can only be positive if $p_{\mathrm{OR}} > 0$ and the ratio of $P_{\mathrm{S}}(2) : P_{\mathrm{S}}(1)$ is greater than the ratio of $2K(1) : K(2)$, that is, if the gains from facilitation exceed the costs of additional competition.

Finally, the floaters will obviously do worse if they are resisted by either the owner or a satellite than if they were tolerated. The partial differential of the fitness of a joining floater, with respect to a change in the proportion of owners resisting satellites is as follows:

$$\frac{\partial w_{\mathrm{FJ}}}{\partial p_{\mathrm{OR}}} = -\frac{K(2)}{2}(1 - p_{\mathrm{SR}}P_{\mathrm{R}})[1 - P_{\mathrm{S}}(2)]. \tag{A13}$$

This value is always negative because an increase in resisting satellites necessarily means an increase in resisting floaters in this model.

APPENDIX B

Incorporating the Resist-Only-Satellite Tactic

Incorporating a fourth tactic for the owner, that is, tolerating the floater and resisting the satellite (tactic I), yields the following rewards. For the owner:

$$w_{\mathrm{OIRJ}} = P_{\mathrm{R}}\{[1 - P_{\mathrm{S}}(1)]V + P_{\mathrm{S}}(1)[V - K(1)]\} + (1 - P_{\mathrm{R}})\{[1 - P_{\mathrm{S}}(1)][V - K(1)] + P_{\mathrm{S}}(1)[V - K(2)]\} - C(1), \tag{B1}$$

$$w_{\mathrm{OITJ}} = [1 - P_{\mathrm{S}}(1)][V - K(1)] + P_{\mathrm{S}}(1)[V - K(2)] - C(1), \tag{B2}$$

$$w_{\mathrm{OIRL}} = [1 - P_{\mathrm{S}}(1)]V + P_{\mathrm{S}}(1)[V - K(1)] - C(1). \tag{B3}$$

For the satellite:

$$w_{\mathrm{SIRJ}} = P_{\mathrm{S}}(1)\left[(1 - P_{\mathrm{R}})\frac{K(2)}{2} + P_{\mathrm{R}}K(1)\right] - D, \tag{B4}$$

$$w_{\mathrm{SITJ}} = P_{\mathrm{S}}(1)\frac{K(2)}{2}, \tag{B5}$$

$$w_{\mathrm{SITJ}} = P_{\mathrm{S}}(1)K(1). \tag{B6}$$

For the floater:

$$w_{\mathrm{FIRJ}} = (1 - P_{\mathrm{R}})\left\{P_{\mathrm{S}}(1)\frac{K(2)}{2} + [1 - P_{\mathrm{S}}(1)]K(1)\right\}, \tag{B7}$$

$$w_{\mathrm{FITJ}} = P_{\mathrm{S}}(1)\frac{K(2)}{2} + [1 - P_{\mathrm{S}}(1)]K(1). \tag{B8}$$

Literature Cited

Andersson, M. 1984. Brood parasitism within species. Pages 195–228 *in* C. J. Barnard, ed. Producers and scroungers: strategies of exploitation and parasitism. Croom Helm, London.

Arak, A. 1984. Sneaky breeders. Pages 154–194 *in* C. J. Barnard, ed. Producers and scroungers: strategies of exploitation and parasitism. Croom Helm, London.

Arnason, E., and P. R. Grant. 1978. The significance of kleptoparasitism during the breeding season in a colony of Arctic skuas *Stercorarius parasiticus* in Iceland. Ibis 120:38–54.

Barnard, C. J. 1984*a*. The evolution of food-scrounging strategies within and between species. Pages 95–126 *in* C. J. Barnard, ed. Producers and scroungers: strategies of exploitation and parasitism. Croom Helm, London.

———. 1984*b*. When cheats may prosper. Pages 6–33 *in* C. J. Barnard, ed. Producers and scroungers: strategies of exploitation and parasitism. Croom Helm, London.

Barnard, C. J., and R. M. Sibly. 1981. Producers and scroungers: a general model and its application to feeding flocks of house sparrows. Animal Behaviour 29: 543–550.

Brockmann, H. J., and C. J. Barnard. 1979. Kleptoparasitism in birds. Animal Behaviour 27:487–514.

Clifton, K. E. 1989. Territory sharing by the Caribbean striped parrotfish, *Scarus iserti*: patterns of resource abundance, group size and behaviour. Animal Behaviour 37:90–103.

———. 1990. The costs and benefits of territory sharing for the Caribbean coral reef fish, *Scarus iserti*. Behavioral Ecology and Sociobiology 26:139–147.

———. 1991. Subordinate group members act as food-finders within striped parrotfish territories. Journal of Experimental Marine Biology and Ecology 145:141–148.

Connor, R. C. 1995. The benefits of mutualism: a conceptual framework. Biological Reviews of the Cambridge Philosophical Society 70:427–457.

Daly, M., L. F. Jacobs, M. I. Wilson, and P. R. Behrends. 1992. Scatter hoarding by kangaroo rats (*Dipodomys merriami*) and pilferage from their caches. Behavioral Ecology 3:102–111.

Davies, N. B., and A. I. Houston. 1981. Owners and satellites: the economics of territory defense in the pied wagtail (*Motacilla alba*). Journal of Animal Ecology 50: 157–180.

Faaborg, J., and J. C. Bednarz. 1990. Galápagos and Harris' hawks: divergent causes of sociality in two raptors. Pages 357–384 *in* P. B. Stacey and W. D. Koenig, eds. Cooperative breeding in birds: long-term studies of ecology and behavior. Cambridge University Press, Cambridge.

Feh, C. 1999. Alliances and reproductive success in Camargue stallions. Animal Behaviour 57:705–713.

Fewell, J. H., and R. E. Page, Jr. 1999. The emergence of division of labour in forced associations of normally solitary ant queens. Evolutionary Ecology Research 1: 537–548.

Foster, S. A. 1985. Group foraging by a coral reef fish: a mechanism for gaining access to defended resources. Animal Behaviour 33:782–792.

Giraldeau, L.-A., and G. Beauchamp. 1999. Food exploitation: searching for the optimal joining policy. Trends in Ecology & Evolution 14:102–106.

Giraldeau, L.-A., and T. Caraco. 2000. Social foraging theory. Princeton University Press, Princeton, N.J.

Giraldeau, L.-A., C. Soos, and G. Beauchamp. 1994. A test of the producer-scrounger foraging game in captive flocks of spice finches, *Lonchura punctulata*. Behavioral Ecology and Sociobiology 34:251–256.

Gompper, M. E. 1996. Sociality and asociality in white-nosed coatis (*Nasua narica*): foraging costs and benefits. Behavioral Ecology 7:254–263.

Gross, M. R. 1982. Sneakers, satellites and parentals: polymorphic mating strategies in North American sunfishes. Zeitschrift für Tierpsychologie 60:1–26.

——— 1996. Alternative reproductive strategies and tactics: diversity within sexes. Trends in Ecology & Evolution 11:92–98.

Hamilton, I. M. 2000. Recruiters and joiners: using optimal skew theory to predict group size and division of resources within groups of social foragers. American Naturalist 155:684–695.

———. In press. Kleptoparasitism and the distribution of unequal competitors. Behavioral Ecology.

Heinrich, B., and Marzluff, J. M. 1991. Do common ravens yell because they want to attract others? Behavioral Ecology and Sociobiology 28:13–21.

Holmgren, N. 1995. The ideal free distribution of unequal competitors: predictions from a behaviour-based functional response. Journal of Animal Ecology 64:197–212.

Howard, R. D. 1978. The evolution of mating strategies in bullfrogs, *Rana catesbeiana*. Evolution 32: 850–871.

Ingolffson, A. 1969. Behavior of gulls robbing eiders. Bird Study 16:45–52.

Johnstone, R. A. 2000. Models of reproductive skew: a review and synthesis. Ethology 106:5–26.

Keller, L., and H. K. Reeve. 1994. Partitioning of reproduction in animal societies. Trends in Ecology & Evolution 9:98–102.

Kennedy, C. R. 1984. Host-parasite interrelationships: strategies of coexistence and coevolution. Pages 34–60 *in* C. J. Barnard, ed. Producers and scroungers: strategies of exploitation and parasitism. Croom Helm, London.

Marzluff, J. M., and B. Heinrich. 1991. Foraging by common ravens in the presence and absence of territory holders: an experimental analysis of social foraging. Animal Behaviour 42:755–770.

Marzluff, J. M., B. Heinrich, and C. Marzluff. 1996. Raven roosts are mobile information centres. Animal Behaviour 51:89–103.

Maynard Smith, J. 1982. Evolution and the theory of games. Cambridge University Press, Cambridge.

Mesterton-Gibbons, M., and L. A. Dugatkin. 1999. On the evolution of delayed recruitment to food bonanzas. Behavioral Ecology 10:377–390.

Parker, G. A., and W. J. Sutherland. 1986. Ideal free distributions when individuals differ in competitive ability: phenotype-limited ideal free models. Animal Behaviour 34:1222–1242.

Reeve, H. K., S. T. Emlen, and L. Keller. 1998. Reproductive sharing in animal societies: reproductive incentives or incomplete control by dominant breeders? Behavioral Ecology 9:267–278.

Robertson, D. R., H. P. A. Sweatman, E. A. Fletcher, and M. G. Clelland. 1976. Schooling as a mechanism for circumventing the territoriality of competitors. Ecology 57:1208–1220.

Rohwer, S., and P. W. Ewald. 1981. The cost of dominance and advantage of subordination in a badge signalling system. Evolution 35:441–454.

Rothstein, S. I., and S. K. Robinson. 1998. Parasitic birds and their hosts: studies in coevolution. Oxford University Press, New York.

Ruxton, G. D., and A. L. Moody. 1997. The ideal free distribution with kleptoparasitism. Journal of Theoretical Biology 186:449–458.

Trowbridge, C. D. 1991. Group membership facilitates feeding of the herbivorous sea slug *Placida dendritica*. Ecology 72:2193–2203.

Vehrencamp, S. L. 1983. A model for the evolution of despotic versus egalitarian societies. Animal Behaviour 31:667–682.

Vollrath, F. 1984. Kleptobiotic interactions in invertebrates. Pages 61–94 *in* C. J. Barnard, ed. Producers and scroungers: strategies of exploitation and parasitism. Croom Helm, London.

Walters, J. R. 1990. Red cockaded woodpeckers: a "primitive" cooperative breeder. Pages 67–102 *in* P. B. Stacey and W. D. Koenig, eds. Cooperative breeding in birds: long-term studies of ecology and behavior. Cambridge University Press, Cambridge.

Warner, R. R., and S. G. Hoffman. 1980. Population density and the economics of territorial defense in a coral reef fish. Ecology 61:772–780.

Wirtz, P. 1981. Territorial defense and territory take-over by satellite males in the waterbuck *Kobus ellipsiprymnus* (Bovidae). Behavioral Ecology and Sociobiology 8: 161–162.

Associate Editor: Joan M. Herbers