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The effect of dominance hierarchy on the use of alternative foraging tactics: a phenotype-limited producing-scrounging game

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Abstract Group living is thought to be advantageous for animals, though it also creates opportunities for exploitation. Using food discovered by others can be described as a producer-scrounger, frequency-dependent game. In the game, scroungers (parasitic individuals) do better than producers (food finders) when scroungers are rare in the group, but they do worse when scroungers are common. When the individuals' payoffs do not depend on their phenotype (i.e. a symmetric game), this strong negative frequency dependence leads to a mixed stable solution where both alternatives obtain equal payoffs. Here, we address the question of how differences in social status in a dominance hierarchy influence the individuals' decision to play producer or scrounger in small foraging groups. We model explicitly the food intake rate of each individual in a dominance-structured foraging group, then calculate the Nash equilibrium for them. Our model predicts that only strong differences in competitive ability will influence the use of producing or scrounging tactics in small foraging groups; dominants will mainly play scrounger and subordinates will mostly use producer. Since the differences in competitive ability of different-ranking individuals likely depend on the economic defendability of food, our model provides a step towards the integration of social foraging and resource defence theories.

Key words Dominance hierarchy · Game theory · Group foraging · Phenotype limitation · Producer-scrounger

Introduction

Two of the major benefits of living in groups are thought to be safety from predation and increased foraging efficiency (Hamilton 1971; Caraco and Pulliam 1984; Clark and Mangel 1986; Elgar 1989; Székely et al. 1989, 1991). Group living, however, also creates opportunities for social foraging interactions among animals, most commonly the exploitation of others' efforts to find food (Barnard 1984). In ground-feeding passerines, for instance, some individuals in foraging flocks actively search for food patches (producers) while others (scroungers) wait for the producers to find a patch and rush in to feed from it (Barnard and Sibly 1981; Giraldeau et al. 1994).

The occurrence of producing and scrounging can be modelled as an alternative-option, n -person evolutionary game (Barnard and Sibly 1981; Maynard Smith 1982; Parker 1984). In the model the individuals play exclusively either producer or scrounger at any time and it is assumed that scrounger does better than producer when scrounger is rare in the group because many exploitable food patches are made available by producers. However, scrounging does worse when scrounger is common because the number of available food patches decreases quickly as a result of the decreasing number of producers while the number of competing scroungers at the same patch becomes high (Barnard and Sibly 1981). In a game with symmetric players this strong negative frequency dependence leads to a mixed evolutionarily stable strategy (ESS) where both alternatives obtain equal pay-offs (Maynard Smith 1982). Using this theoretical framework Vickery et al. (1991) found that in a rate-maximizing game the equilibrium proportion of scroungers depends strongly on the fraction of each food

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patch available only to producers (finder's share): the more food that is available only to producers, the smaller the equilibrium proportion of scroungers. Similarly, strong effects of finder's share were predicted from a starvation-minimizing model (Caraco and Giraldeau 1991). Both of these models, however, assume symmetric individuals, that is, their payoffs from the different options are independent of their phenotype (Parker 1982). Hence, how phenotypic limitations influence the use of producer or scrounger in a foraging context remains unexplored.

In contrast to theoretical investigations, most of the empirical studies of producer-scrounger systems reveal that the strategy used usually differs for individuals with different phenotypes (i.e. different rank in social hierarchy) (Gross 1996). Rohwer and Ewald (1981) found that dominant Harris' sparrows (*Zonotrichia querula*) usurped patches discovered by subordinates. In an experimental study Baker et al. (1981) reported that dominant dark-eyed juncos (*Junco hyemalis*) increased their food intake by frequently supplanting subordinates from patches they discovered. Theimer (1987) found, however, that the differences between dominant and subordinate juncos disappeared when food was more evenly distributed and hence less defensible (Grant 1993). Caraco et al. (1989) have pointed out that the dominant individual of pairs of captive *J. hyemalis* actively join the subordinate, increasing the chance of supplanting it from the food patches discovered by the subordinate.

To date, only Ranta et al. (1996) have presented a producer-scrounger foraging model in which the individuals differ in their "ability to compete for the food". However, in their model an individual's competitive ability determines the animal's foraging option (producer or scrounger). Therefore, their model could not address how phenotypic limitation affects the animal's decision to use producer or scrounger alternatives.

The model of phenotype limited strategies (Parker 1982, 1984; Repka and Gross 1995; Gross 1996) is an effective tool to investigate dominance-driven producer-scrounger systems theoretically, because it assumes that the individual's payoff from a given tactic (i.e. producer or scrounger) depends on both the individual's phenotype and the frequency of the use of that tactic in the population. In this paper we use tactic *sensu* Gross (1996): a behavioural option chosen by an individual according to a strategy. When the phenotype variation is continuous (e.g. social status in a dominance hierarchy) and only two tactics are available, the model predicts that an individual will use the tactic that gives the higher payoff for its phenotype and that there is a threshold phenotype in the population. All of the individuals with a phenotype above the threshold will play one tactic and all others below the threshold will play the other tactic. Individuals at the threshold could play both. Moreover, in contrast to Ranta et al. (1996), the individuals' payoffs usually differ at the Nash equilibrium, the point where no individual could achieve a higher payoff by

changing its foraging tactic unilaterally (Parker 1982). Based on this model, it is widely accepted that dominants play mainly scrounger in foraging groups because of their competitive superiority i.e. their ability to get the larger part of a shared patch. However it is not clear how the amount of food available solely to the producer (finder's share) or the strength of the ability to prevent others from using a patch (competitive ability) influence the decision to use alternative foraging tactics by different-ranking individuals. Moreover, the model of phenotype-limited strategies assumes that a "large number" of individuals play the game (Repka and Gross 1995), a condition that is rarely fulfilled in situations of group foraging.

Here, assuming that the individuals' competitive abilities depend on their social ranks (i.e. high-ranking individuals are competitively superior), we address the question of how the magnitude of differences in social status in a dominance hierarchy influence the individuals' decision of playing producer or scrounger in small foraging groups. We model explicitly the food intake rate of each individual in a dominance structured foraging group, and numerically calculate the Nash equilibrium for them. We then investigate how changes in the parameters of the model (i.e. finder's share, differences in competitive ability of different-ranking individuals and group size) affect the decisions of individuals of different social status. The model was developed with flocks of small seed-eating birds in mind but applies to any situation where groups of foragers exploit patchy, shareable resources.

The model

We consider a small group of G individuals ($G \leq 20$) foraging on patchily distributed food during T time units. The patches contain F indivisible food items. We assume that the group is maintained *a priori* by some mechanism other than foraging, e.g. anti-predation advantages, and so we do not consider the individuals' decision to join or leave the group. We also assume patch exploitation time is negligible compared to search time.

We use the "priority of access to resources" definition of dominance which does not necessarily involve aggressive interactions (Drews 1993) and assume scramble competition (Milinski and Parker 1991). We presume that all individuals differ in their ranks and that a linear social hierarchy exists within the group (i.e. if individual A dominates B and B dominates C then A also dominates C). Therefore, we assigned a unique rank i ($i = 1, 2, \dots, G$) to each individual (most dominant: $i = 1$; most subordinate: $i = G$). The rank i of a given individual determines its competitive weight: $CW_i = (G + 1 - i)^C$, where C is a measure of the difference in competitive ability of different-ranking individuals (Ranta 1993). The proportion of food consumed by individual i from a

shared patch is then given by: $CW_i/\Sigma CW_j$, where ΣCW_j is the total competitive weight of foragers eating from the same patch (Ranta 1993). With this representation, when C is equal to zero there are no competitive differences among the individuals (i.e. they get equal shares from patches), while higher C depicts situations where the first-ranking (dominant) individuals have a competitive advantage over the last-ranking (subordinate) individuals; they consume a larger portion of the patch (Fig. 1) (Alonso et al. 1997). On the other hand, individuals with different competitive ranks are assumed not to differ in their ability to search for food, i.e. they find food patches at the same rate (Wiley 1991; Tiebout 1996).

The individuals can choose between two foraging tactics: producer and scrounger (Barnard and Sibly 1981). An individual playing producer actively searches for food, and finds patches at rate λ . After finding, it consumes a food items alone and shares the remainder $A = F - a$ items with the scroungers. The finder's share is defined as $FS = a/F$. The producers, in contrast to Ranta et al. (1996), never eat from patches found by others. On the other hand, scroungers never search actively for food; they forage only from patches found by producers (Vickery et al. 1991). This does not mean that there are individuals in the group who never search for food, as implied by Ranta et al. (1996); it only means that when an individual uses the scrounger tactic it does not look for food itself, though it could change to the producer tactic and then actively search for food (Caraco and Giraldeau 1991; Vickery et al. 1991). The group consists of N_P producers and N_S scroungers ($G = N_P + N_S$).

Under the above assumptions the rate of food intake of the i th-ranking individual playing producer is:

$$W_i^P = \lambda T \left(a + A \frac{CW_i}{CW_i + \Sigma CW_j} \right),$$

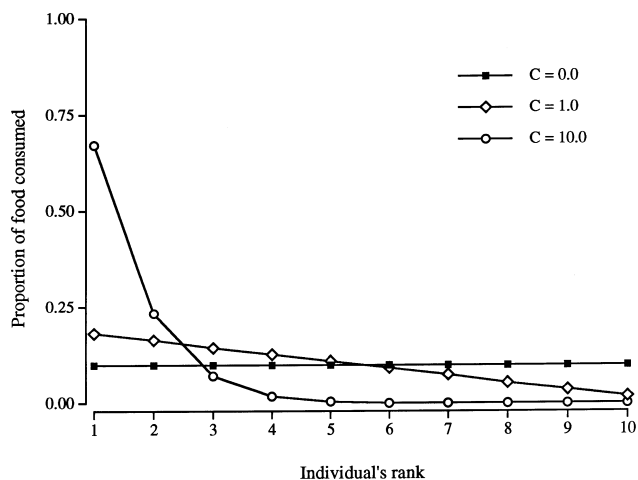


Fig. 1 The proportion of food obtained by a given ranking individual from a shared resource (i.e. from a patch after its producer has consumed the finder's share) under different values of differences in competitive ability (C)

where $\Sigma CW_j = \sum_{j=1}^{N_S} CW_j$ is the total competitive weight of scroungers. The rate of intake for the i th-ranking scrounger is given by:

$$W_i^S = \lambda TA \sum_{k=1}^{N_P} \frac{CW_i}{CW_k + \Sigma CW_j}$$

where CW_k is the k th producer's competitive weight while ΣCW_j is, as above, the total competitive weight of scroungers.

In order to determine the ESS we need to define states of groups of G individuals. Each state is characterized by an array of zeros and ones of length G . The zero value at position i in the array means that the i th-ranking individual plays producer, while value of one in the same place means that individual plays scrounger. The number of scroungers is simply the sum of the G values in the array. A state was considered to be stable if no individual could achieve a higher payoff by deviating its foraging alternative unilaterally (Nash equilibrium, Parker and Sutherland 1986). Since it is an individual's fitness relative to the population's average that is important for the spread of a strategy, we defined the payoff (P) as the rate of food intake relative to the average rate in the group: $P_i = W_i^X / [(\sum_{j=1}^G W_j^X) / G]$, where $X = \{P, S\}$, depending on the tactic used by the given individual (Maynard Smith 1982). In order to determine whether a state is stable, first we calculated the payoff for each individual then changed the tactic used by a given individual and recalculated the payoffs. If the payoff for the given individual following the change was increased, we considered the state unstable. We tested each individual in this way and the state was deemed stable when the change of tactic did not result in higher payoffs for any individual. This procedure implies the assumption that only one individual changes tactic at the same time, which is reasonable assuming that patches are often discovered. As another consequence of this assumption we have considered all locally stable states as equally stable on a wider scale, whereas in fact this may not necessarily be true. On the other hand, this assumption was used because of computational ease and because minor violations are unlikely to yield serious errors in our predictions. To describe the individuals' behaviour we generated all of the possible states for a group of a given size and checked each of them for stability. The state of only 1s (i.e. all individuals in the group play scrounger) was unstable by definition (Barnard and Sibly 1981). Once we had determined the stable states, we calculated the following variables for each individual in the group: the proportion of stable states in which the given individual plays scrounger and its mean food intake averaged across the stable states. We also recorded the equilibrium number of scroungers. To investigate the model we systematically changed the finder's share, the difference in competitive ability (competitive difference) and the group's size.

Results

The evolutionarily stable frequency of scroungers decreased as the finder's share of each patch increased for all values of competitive difference (Fig. 2). In the absence of competitive differences our model's predictions match those of Vickery et al. (1991) but they differ increasingly as competitive abilities differ more and more (Fig. 2). The effect of competition on the stable frequency of scroungers depends on the finder's share. When the finder's share is low competitive difference reduces the stable frequency of scroungers, but at large finder's share it has the opposite effect (Fig. 3). Hence, differences in competitive abilities actually increase the range of finder's shares under which scrounging is considered evolutionarily stable by symmetric games (Vickery et al. 1991) (Fig. 3).

The effect of differences in competitive abilities on the stable scrounger frequency also depends on group size. In small groups ($G < 10$), increasing competitive differences more commonly increases the stable scrounger frequency when finder's share is high but has no effects when finder's share is low (Fig. 4). The opposite trend is true for larger groups: increased competitive differences more commonly reduce scrounger frequency when finder's share is low and has no effects when finder's share is high (Fig. 4).

An individual's competitive rank influences its use of the scrounger tactic. Assuming that each stable state is equiprobable, the proportion of stable states for which a forager of a given rank uses scrounger can be used to estimate that individual's long-term use of the scrounger tactic. Our calculations show that there are several distinct ways in which an individual's rank influences its use of the scrounger tactic depending on the extent of competitive differences (Fig. 5). The most common (i.e. found at most studied parameter combinations) pattern

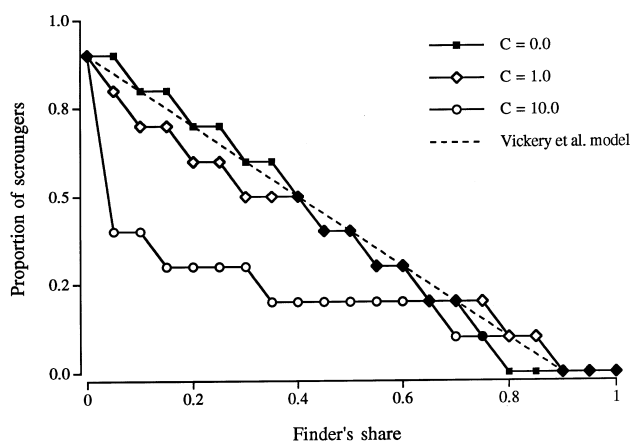


Fig. 2 The evolutionarily stable proportion of scroungers decreases with increasing finder's share in groups of ten individuals experiencing altered competitive differences (C). The dashed line denoted as Vickery et al. model was calculated using the model of Vickery et al. (1991)

we observed at low competitive differences involved constant use of scrounger independent of rank (Fig. 5a). Intermediate competitive differences led to a number of patterns depending on the values of the finder's share and group size (Fig. 5b). Interestingly, one pattern involved intermediate-ranked individuals playing scrounger more than either extreme of the competitive hierarchy (Fig. 5b, solid square). This pattern was increasingly common as group size increased. Strong dif-

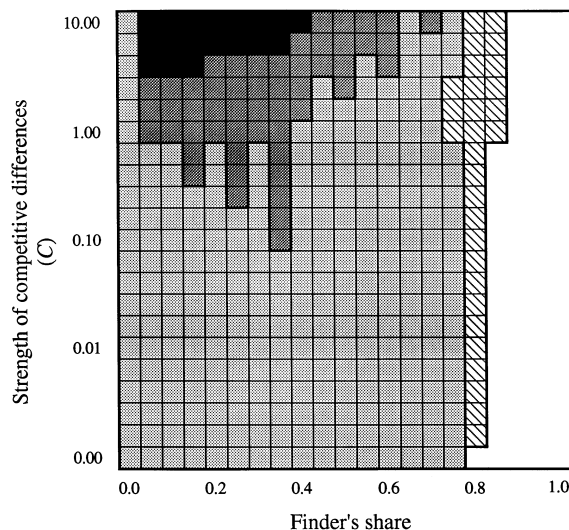


Fig. 3 The difference (D) in the stable proportion of scroungers when competitive differences among individuals are present ($C > 0$) and absent ($C = 0$) for different combinations of the finder's share and competitive differences. Negative values of D (stippled areas) mean that there are fewer scroungers in the group for the given combinations of values than there would have been in the absence of competitive differences; competitive differences reduce scrounging. Positive values (shaded areas) mean the opposite: competitive differences increase scrounging. Open areas represent value combinations where scrounging is unstable ($G = 10$). ■ $D < -0.25$; ■ $-0.25 \leq D < 0.0$; □ $D = 0.0$; ▨ $0.0 < D < 0.25$

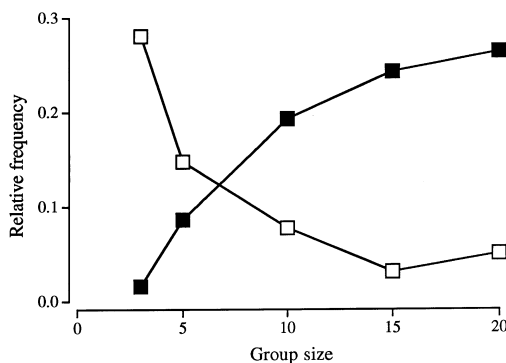
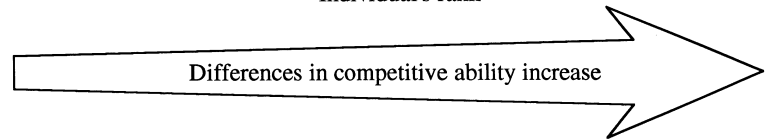
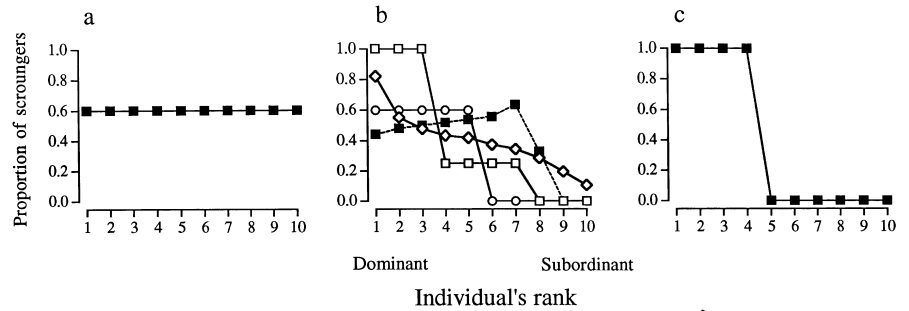


Fig. 4 Relative frequency of value combinations where competitive differences reduce (solid square) or increase (open square) the stable frequency of scroungers as a function of group size. The relative frequencies were calculated as the number of studied value combinations of finder's share and competitive differences where there was either positive or negative deviations in the stable proportion of scrounger divided by the total number of value combinations where scrounging was stable

Fig. 5a–c Representatives of different types of scrounging profiles, i.e. proportion of scrounging drawn against individuals' rank (**a** $FS = 0.3$, $C = 0.0251$; **b** *open diamond*: $FS = 0.45$, $C = 0.0398$; *open square*: $FS = 0.45$, $C = 0.1584$; *open circle*: $FS = 0.6$, $C = 0.6309$; **b** *solid square*: $FS = 0.5$, $C = 0.2511$; **c** $FS = 0.3$, $C = 3.9811$; $G = 10$ for all cases)



ferences in competitive abilities resulted in a step change from all scrounger (dominants) to all producer (subordinates) at some critical rank (Fig. 5c).

Food intake rates averaged across individuals in the group were affected by all changed parameters. Scroungers tended to have higher intake rates than producers, especially under strong competitive differences. Increasing the finder's share increased the average rate of intake for all values of competitive differences (Fig. 6). This effect can be traced to a reduction in the stable frequency of scroungers as the finder's share increases (Fig. 2). When competitive differences were strong, average intake rates were higher for lower finder's share and lower for higher finder's share compared to situations without competitive difference (Fig. 6). Once again these patterns are the result of changes in the stable frequency of scroungers (Fig. 3). Effects on an individual's intake rate depended on its competitive rank. As competitive differences increased, the best competitors (dominants) tended to enjoy increasing intake rates while the worse competitors (subordinates) actually suffered a reduction of intake rate (Fig. 7). As competitive differences increased, the number of best competitors enjoying an increased food intake actually declined (Fig. 7). In the presence of competition, individuals' food intake increased with competitive ability (i.e. with dominance status) in all cases. The difference in food intake rate between the best and worse competitors depended on how the use of scrounger was affected by competitive rank. Differences were lowest when scrounger use was independent of competitive rank and the greatest when tactic use was a step function from all scrounger to all producer at some critical rank. Increasing group size decreased the intake rate of both dominants and subordinates when differences in competitive ability were small. On the other hand, when competitive differences were strong, dominants' food intake rate increased with group size (within the studied range) while the subordinates' did not change.

Neither changes in foraging time (T), in food finding rate (λ) nor in amount of food (F) influenced the above results.

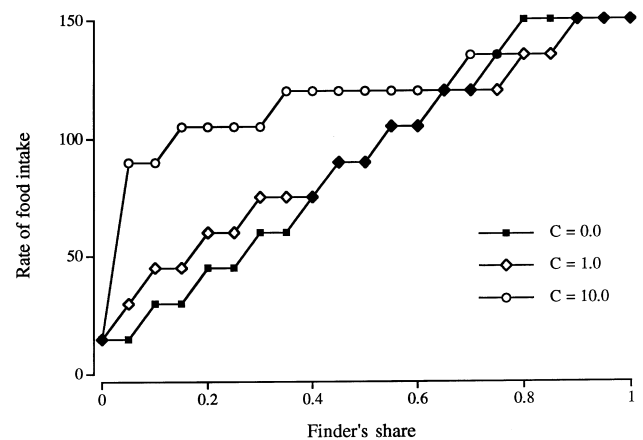


Fig. 6 An average individual's rate of food intake in a group of ten as the function of finder's share (FS) and competitive difference (C)

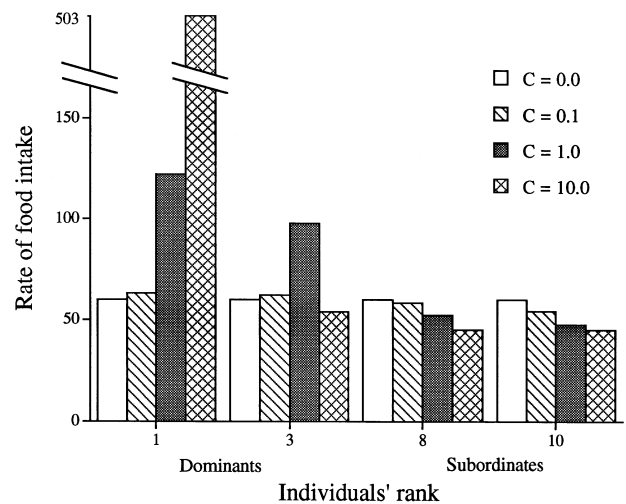


Fig. 7 Changes in rate of food intake of different-ranking individuals with competitive difference (C) ($FS = 0.3$, $G = 10$ for all cases)

Discussion

Our model addresses how the extent of phenotypic differences within small foraging groups influences the in-

dividuals' use of alternative foraging tactics. It predicts that phenotypic differences among group foragers do not always affect their use of producer or scrounger tactics. When the individuals are more or less similar they should all equally play scrounger independently of their competitive rank. Increasing the competitive asymmetries induces competitively superior individuals to use mostly scrounger, while competitively inferior ones play mainly producer. It is only when the competitive differences are further enlarged (i.e. superior individuals can monopolize the whole or at least a significant part of the food patches) that individuals are predicted to specialize exclusively on one role: dominants use scrounger and subordinates play producer only. Increasing the differences in competitive abilities among group foragers also leads to a decrease in the evolutionarily stable proportions of scrounger and hence a higher average rate of food intake for the group. Not all foragers in the group, however, benefit from this raised average intake rate: dominants (scroungers) gain while subordinates (producers) actually lose. This result suggests that group cohesion can only be maintained for some range of competitive asymmetry, beyond which subordinate producers may find it profitable to leave the group. This point, however, needs further modelling work. The effects of group size on food intake rate are also influenced by the degree of competitive differences. Small asymmetries lead to decreasing food intake rate with increasing group size for both dominants and subordinates. On the other hand, when competitive differences are strong dominants' intake rate increase and subordinates' do not change with increasing group size.

Some empirical findings seem to support predictions of our asymmetric model. For instance, most studies of group foraging report that when food is patchily distributed dominants mainly use the scrounger tactic while subordinates mostly play producer (Baker et al. 1981; Rohwer and Ewald 1981; Czikeli 1983; Theimer 1987; Caraco et al. 1989; Clifton 1991). However, some studies could not find an effect of dominance on tactic use even if they clearly used clumped food resources and well-defined hierarchies existed. This is the case, for instance, in studies of captive feral pigeons (*Columba livia*), spice finches (*Lonchura punctulata*) and zebra finches (*Poephila guttata*) (Giraldeau and Lefebvre 1986, 1987; Giraldeau et al. 1990). Our model predicts that the extent of asymmetries must have been larger in the species where dominance affected role use than in those cases where it did not. Future studies should address this prediction. Moreover, in those studies where dominance affected tactic use, dominants obtained higher food intake rates than the subordinates did when food was patchily distributed (Baker et al. 1981; Theimer 1987; Caraco et al. 1989) No such difference was reported in one study where dominance had no effect on tactic use (Giraldeau et al. 1990).

A direct test of the model, however, requires a controlled manipulation of individual differences in com-

petitive ability. The individuals' competitive differences could be manipulated directly by hormone treatment and/or badge size modification in birds (e.g. Rohwer 1977; Rohwer and Rohwer 1978). Moreover, because body length is a measure of competitive ability in fish (Ranta and Lindström 1990), competitive differences could also be modified directly by altering body length composition of groups of fish. However, resource defence theory suggests that this can also be achieved indirectly by altering the size and quality of food patches, creating conditions that promote their economic defendability and hence the extent to which they can be effectively monopolized by dominant individuals (Grant 1993; Grant and Guha 1993; Grand and Grant 1994). Large differences in competitive ability may arise when the bigger, stronger individuals in the group decide to defend food patches aggressively, leading to the partial or full exclusion of smaller, weaker individuals. Resource defence theory predicts that aggressive defence will be promoted by spatial aggregation of food into small (i.e. easy to defend) and rich (i.e. high yield) patches (Grant 1993). Therefore, when individuals forage on highly aggregated and abundant food patches, one should expect to find strong effects of dominance hierarchy on the use of scrounger and producer tactics.

Richness of food patches, independently of its effect on extent of player asymmetry, may also affect the producer-scrounger game through its influence on the finder's share. When the patch is rich, the producer can only consume a small portion of the total patch before the arrival of scroungers (small finder's share) hence leading to a high, stable proportion of scrounging. On the other hand, low patch richness allows the producer to eat most of the patch before the scroungers arrive (high finder's share) and hence leads to low, stable proportions of scrounging.

The model's prediction that the stable frequency of scrounger decreases with increasing finder's share is in agreement with earlier models whether they assumed symmetric (Vickery et al. 1991; Caraco and Giraldeau 1991) or asymmetric (Ranta et al. 1996) players. In addition, both our model and that of Ranta et al. (1996) predict that scroungers should be the competitively superior individuals. But, only our model predicts that the extent of competitive asymmetry will affect the use of tactics. Finally, only our model allows the dominants' and subordinates' food intake to differ at equilibrium, as is expected in an asymmetric game (Parker 1982; Parker and Sutherland 1986; Gross 1996).

The model of phenotype-limited strategies (Parker 1982; Repka and Gross 1995; Gross 1996) predicts a step change from all scrounger to all producer in the use of tactics as competitive rank decreases for any dominance-structured foraging groups. We obtained this result with small groups only when the differences in competitive abilities were very strong. So, the step effect may not be general for all dominance-structured foraging groups. The differences between the model of phenotype-limited strategies and our model, however, could be tested by

manipulating the individuals' differences in competitive abilities (see above): our model predicts a change in tactic use with increasing competitive differences while the model of phenotype-limited strategies does not. Future studies should manipulate the extent to which dominants can effectively monopolize small food patches while foraging in groups. This can be done by manipulating the extent of a resource's economic defendability. Such tests are currently under way in our laboratories and suggest that both group foraging models and resource defence theory can be integrated to generate useful predictions about social foraging behaviour.

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