

Producer-scrourger roles and joining based on dominance in a free-living group of Mexican jays (*Aphelocoma ultramarina*)

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Summary

While foraging, animals often exploit group members to obtain food. One way to describe this behaviour is with the producer-scrourger (PS) model, where scrourgers use social interaction to obtain food discovered by producers. Mexican jays (*Aphelocoma ultramarina*) are a group-foraging species with a linear dominance hierarchy. We studied interactions in a free-living foraging group to determine (1) if foraging interactions can be explained with the PS model, (2) if these roles are consistent and (3) if dominance or relatedness affects joining frequency. We recorded board-flipping, eating, and joining events during sets of feeding trials. We show that Mexican jays use PS roles and that these roles were consistent through many trials, but might have changed between trial sets. Relatedness and frequency of joining were not correlated. Dominance influenced joining in that joining was more likely to occur between birds with a larger difference in their dominance rank. In contrast to other studies, our results suggest that this effect is mediated through joiner preference. Scrourgers preferentially joined birds of lower dominance rank and high search activity. Producers with these qualities had fewer eating events with full access to seeds, suggesting that scrourging exacts a cost on producers.

Keywords: producer-scrourger, Mexican jay, *Aphelocoma ultramarina*, group foraging.

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Introduction

Unlike solitary foragers, animals foraging in groups can obtain food by searching or by social interaction with other group members. This scenario has been examined with the producer-scrounger (PS) model, where producers actively search for food and scroungers profit from producers' efforts through joining or stealing (Barnard, 1984). The PS model has been explored theoretically (Giraldeau & Caraco, 2000) and experimentally (Barnard & Sibly, 1981; Mottley & Giraldeau, 2000; Liker & Barta, 2002), but only recently in natural settings (Ha & Ha, 2003), where its adaptive utility can be placed in the context of natural group composition, including dominance hierarchies and relatedness among group members.

Although PS roles have been described in a number of avian species, it has been difficult to generalize results. Barnard & Sibly (1981) observed that house sparrows showed high fidelity to their roles as producer or scrounger, leading them to speculate that PS roles could be individually fixed. However, later experiments showed that role consistency and flexibility vary greatly from species to species and also depend on experimental conditions (reviewed in Beauchamp, 2001).

While the factors governing foraging tactic use are not fully understood, dominance rank is known to affect an individual's decision to be a producer or scrounger (Baker et al., 1981; Rohwer & Ewald, 1981; Theimer, 1987; Caraco et al., 1989). Barta & Giraldeau (1998) developed a model which predicts that strong differences in competitive ability will lead dominant birds to become scroungers because they can usurp food from subordinate producers. Some predictions of the model have been validated by experimental feeding trials (Liker & Barta, 2002), but experiments on other species have shown little correlation between dominance rank and PS role (Giraldeau & Lefebvre, 1986; Giraldeau et al., 1990; Beauchamp, 2006).

We were initially interested in PS roles in Mexican jays (*Aphelocoma ultramarina*) because food stealing is common when jays cache food. Also, jays that discover large ephemeral food sources are frequently joined by conspecifics (Brown, 1983). We wanted to know if joining and stealing in Mexican jays could be incorporated into the PS framework, which was originally developed from observations of kleptoparasitism (i.e., food stealing) and joining behaviour (Barnard, 1984).

As conspicuous ground-feeders, Mexican jays are a good species for obtaining foraging observations in the wild, an aspect of the empirical work on

PS behaviour that is lacking (but see Ha & Ha, 2003). They are rapid learners, quickly adapt to novel situations, and live in groups with a linear dominance hierarchy and variable levels of relatedness among group members (Brown & Brown, 1981). This allowed us to simultaneously test if dominance and/or relatedness affect joining behaviour. If relatedness were a strong predictor of joining, this would provide an alternative explanation of joining behaviour in that allowing a bird to join could be seen as a form of altruism (*sensu* Hamilton, 1964) rather than parasitism. Testing dominance effects on wild populations also avoids the possibility that dominance hierarchies or pair bond influences may shift in recently created groups of birds that are not familiar with one another (Giraldeau et al., 1990; Beauchamp, 2000).

We designed feeding trials to determine (1) if certain individuals prefer producer or scrounger roles within a foraging group, (2) if the roles are consistent over consecutive trials and (3) if dominance rank or relatedness affect joining behaviour. By examining patterns of joining behaviour, we were also able to explore how certain characteristics of a producer might affect a scrounger's decision to join and if this had negative consequences for the producer (e.g., smaller 'finder's share').

Methods

Study area and subjects

The study was conducted on the property of the American Museum of Natural History's Southwestern Research Station, located in the Chiricahua Mountains of southeastern Arizona, USA. The habitat is open woodland of pine (*Pinus*), oak (*Quercus*), and juniper (*Juniperus*) near a riparian corridor. The experimental flock is part of an individually colour-banded population that has been under continuous study since 1969 (Brown, 1994).

The flock is not visited regularly by the public and does not receive supplemental feeding. Though the birds can be summoned to a feeding area with a whistle (Brown, 1997), they are relatively naïve and wary of humans. Jays visited the feeding station singly or in small groups. After they arrived at the feeding station, we were able to redirect their attention to a nearby clearing, in which we placed a feeding grid (see below). After several practice trials, the jays learned to come directly to the feeding grid upon hearing the whistle.

Trials were conducted in winter of 1993 (12 trials over a period of one month), and fall and winter of 1997 and 1998 (nine trials over a period of three months). During the trials in 1993, the flock consisted of eight individuals (seven colour-banded and one unbanded). During 1997, there were 11 birds (10 colour-banded and one unbanded). Four birds were present in both years. Within each set of trials, group composition remained stable.

Trial procedure

In 1993, the feeding grid contained 42 small, square boards (arranged 7×6) made of wood. In 1997, the feeding grid contained 25 wooden boards (arranged 5×5). The boards used in 1993 were slightly smaller (5×5 cm as opposed to 8×8 cm). In both years the boards were evenly-spaced with approximately 1 m between each board. Each covered a small handful (10-30) of sunflower seeds. The flock was summoned to the feeding area for several introductory trials during which flock members descended to the grid and learned to uncover sunflower seeds hidden beneath the boards. We ended the test trial phase when all members of the flock had descended to the grid to retrieve seeds. The fact that all birds flipped at least one board in the initial experimental trials indicates that differential learning was most likely not an important factor in observed foraging differences. Also, Mexican jays commonly forage on the ground where they turn over leaves, bark, and rocks in search of food (Brown, 1994). Thus, board-flipping is probably not a radical departure from normal foraging behavior for this species.

To observe feeding trials, a 10 power spotting scope was positioned in a hidden location 20 m away from the grid. After the birds descended, we recorded flipping, eating and joining events, and the focal bird's colour band combination. Each trial lasted approximately 10 min, until all seeds had been uncovered or until several consecutive flips failed to uncover new seeds.

A flipping event was recorded when a bird moved a board (whether lifted or tossed) such that seeds were exposed to other birds. This included events where a board was partially lifted, seeds taken, and the board dropped because this activity often exposed seeds along the edges of the board. An eating event was recorded when a bird took seeds, regardless of whether it had uncovered those seeds. A joining event was recorded when a bird joined another bird at a food source. When a bird joined two birds in the act of feeding, this was recorded as two joining events.

Though terminology has varied from study to study (summarized in Giraldeau & Beauchamp, 1999), throughout this paper we try to refer to individuals and their general tactics as 'scrounger' and 'producer', while we describe their associated behaviours in the context of the feeding trials as, respectively, 'joining' and 'flipping' (also called 'searching').

Dominance ranking

Interactions at a feeding station have been used to determine a linear dominance hierarchy within flocks of Mexican jays (Barkan et al., 1986). To formulate our dominance hierarchy, we compared simple percent of winning encounters between jays interacting at a food source. Prior to each set of feeding trials in their respective years, jays were summoned to a partially buried can filled with sunflower seeds, which was surrounded by a circle of rocks. Winning interactions and losing interactions at the feeder were recorded. Dominance was calculated as a percentage equal to winning interactions divided by total interactions (Table 1).

Data analysis

Our study pools results from 1993 and 1997. Four birds were present in the flock for both trial sets. We treat these birds as independent data points because of the relatively long time separating the two sets of trials and the different flock composition and dominance hierarchies in those years. Results were standardized to correct for variation between years by calculating the mean for each variable in each year and using deviations from the mean in our analyses, resulting in some negative numbers.

We used linear regression to determine relationships between variables. Before analyzing the raw data, we calculated a producer and scrounger index for each individual to standardize for varying activity rates. The producer index reflects how much an individual actively searched for food. Therefore, we defined the producer index as the number of flipping events per trial, regardless of whether the individual was joined (Table 1).

The scrounger index reflects the proportion of eating achieved through joining (Table 1). It standardizes for different individual foraging rates by calculating the number of eating events that resulted from the scrounger joining another bird divided by the total eating events for the scrounger.

Table 1. Variables used in the analysis and formulas for their calculations based on the field-collected data.

Variable	Formula
Indices for each bird:	
Dominance index	$w/(w + l)$
Producer index	f (average per trial)
Eating frequency	e (average per trial)
Scrounger index	j_g/e
Index of attractiveness to scroungers	j_d/e
Index of full access to food	$e - j_d$
Indices for each dyad (A-B):	
Joining frequency1 (A joins B)	$j_g (A \rightarrow B)/e$ (by B)
Joining frequency2 (B joins A)	$j_g (B \rightarrow A) /e$ (by A)

Field-collected data from the experiment: f = number of flipping events; e = number of eating events; j_g = number of joining events (followed by eating) by a bird; j_d = number of eating events when a bird was joined by at least one other bird. Data collected at single feeders: w = number of winning interactions by a bird; l = number of losing interactions by a bird.

Thus, higher eating rates did not necessarily result in a higher scrounger index.

We used dyads — pairings of two birds — to investigate the effect of dominance and relatedness on joining frequency. For both dominance and relatedness analyses, joining frequency was calculated as the number of joining events by the scrounger divided by the total opportunities for joining, i.e., the total number of eating events by the bird being joined (Table 1). This obviated the conclusion that a bird was joined more often simply because it ate more often. Each pairing produced two reciprocal dyads (e.g., Bird A joined Bird B and Bird B joined Bird A). We used these data in a linear regression analysis of joining frequency and dominance difference in each dyad, excluding dyads in which no joining occurred. However, because each pairing occurs more than once, and each bird appears several times in the regression, we used robust variances for cluster-correlated data (Williams, 2000) as implemented in the statistics package Stata Intercooled 8.2 (StataCorp, 2003). This allowed us to control for correlations within clusters of data at the hierarchical level of our choosing (e.g., dyad or bird) when calculating p -values. For relatedness analysis, one dyad was produced for each pairing by taking an average of the joining frequency for each pair and then comparing these

frequencies between dyads with and without relatedness. Relatedness data (provided by J.L. Brown) came from a long-term study of the population and was determined by pedigree. We considered two birds to be related if they were cousins or more closely related ($r \geq 0.125$).

To determine if certain characteristics of producers were particularly attractive to scroungers, we calculated an index of attractiveness for each producer, which was a proportion equal to the number of eating events where the producer was joined over all eating events associated with producing for that bird. We calculated correlation (and regression) between the index of attractiveness and the number of eating events/trial as a proxy for food intake. We also calculated the contributions of the scrounger index, producer index and dominance percentage to the index of attractiveness with a multiple regression analysis (all variables were standardized to correct for variation between years as mentioned above). This allowed us to determine the unique effects that producing, scrounging, and dominance had on attractiveness irrespective of interactions between these characters.

Finally, to assess whether being preferentially joined was costly, we calculated an index of full access to the resource (Table 1), which represents the number of eating events in which the bird was not joined and, therefore, could take as many seeds as it liked. This index was then correlated to the index of attractiveness. If each bird had the same total number of eating events, or if the number of eating events was randomly distributed among birds and if eating did not affect the attractiveness (as appeared to be the case in our data), then a negative correlation is expected where more attractive birds have fewer eating events with full access to food. We compared linear and non-linear binomial regressions to determine which relationship explained a higher proportion of the variance.

Results

Producer and scrounger roles

Most birds used both tactics and the frequency of tactic use varied continuously (Figure 1). There was a negative relationship between the producer and scrounger index within an individual's behaviour (regression: $F_{1,18} = 21.16$, $p < 0.001$, $R^2 = 0.56$). Frequency of eating and the producer index were marginally positively correlated ($F_{1,18} = 3.58$, $p = 0.076$,

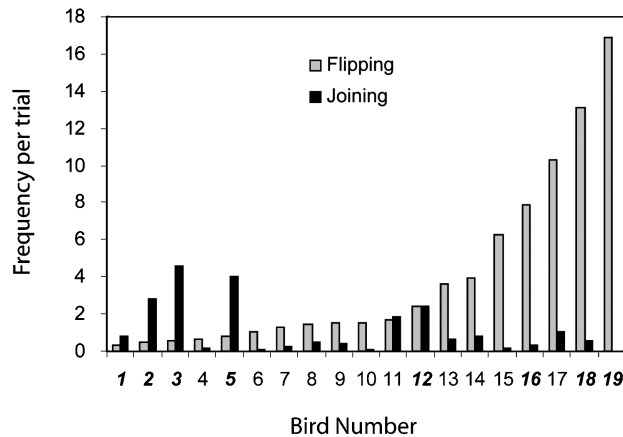


Figure 1. Frequency per trial of flipping and joining for individual birds. Birds from trial set in 1997 are indicated in bold italic.

$R^2 = 0.17$), while there was no relationship between frequency of eating and the scrounger index ($F_{1,18} = 0.63$, $p = 0.44$, $R^2 = 0.04$). Joining events were frequent, involving two and, more rarely, three birds. They almost never involved aggressive interaction or supplantation.

Consistency in tactic use

To evaluate individual consistency in tactic use, we compared results for early and late trials. Early trials were defined as the first third of total trials and late trials as the last third of total trials. There was a strong positive relationship between results from early and late trials for both the producer index ($F_{1,18} = 26.53$, $p < 0.001$, $R^2 = 0.61$; Figure 2A) and scrounger index ($F_{1,18} = 14.17$, $p = 0.002$, $R^2 = 0.46$; Figure 2B).

Effect of dominance and relatedness

Joining data were left-skewed and were normalized with transformation by taking the reciprocal of the square root of the number. There was no significant relationship between dominance percentage and producer index ($F_{1,18} = 0.02$, $p = 0.90$, $R^2 = 0.001$) or scrounger index ($F_{1,18} = 0.08$, $p = 0.79$, $R^2 = 0.004$). However, there was a significant correlation between the difference in dominance between two birds in a dyad and joining in the same dyad ($F_{1,67} = 16.50$, $p < 0.001$, $R^2 = 0.20$), with greater

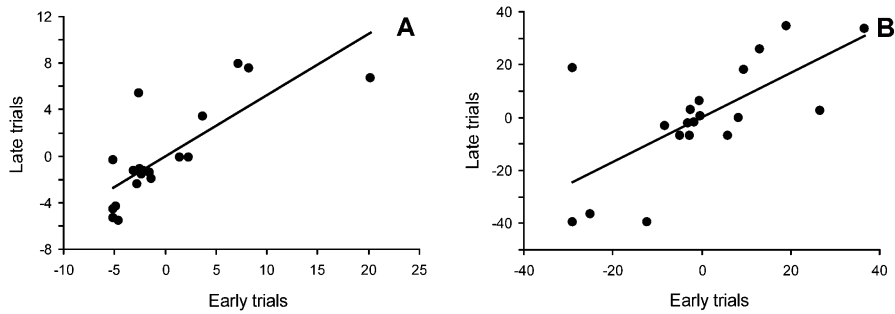


Figure 2. The relationship between early and late trials for the (A) producer index ($F_{1,18} = 26.53$, $p < 0.001$, $R^2 = 0.61$) and (B) scrounger index ($F_{1,18} = 14.17$, $p = 0.002$, $R^2 = 0.46$). Dots represent individuals. Numbered axes show deviations from the mean, which are used in order to standardize for between-year variation.

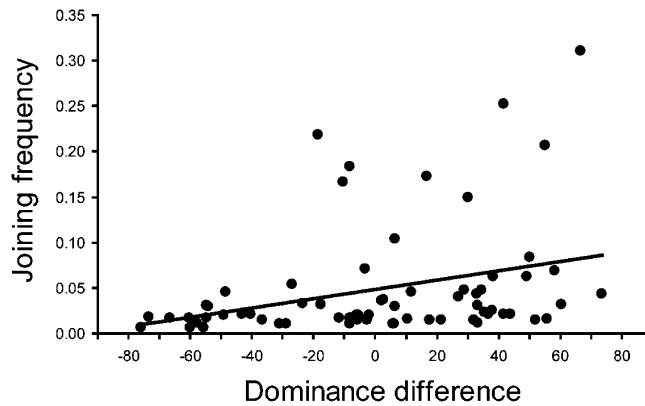


Figure 3. The relationship between joining frequency and dominance difference. Dots represent dyads ($N = 68$). Dyads with no joining have been excluded. The x-axis represents the difference in dominance percentages, with 0 indicating a dyad with birds of equal dominance. Robust variance estimation produced differing p -values for correlations depending on whether the hierarchical level of the clustering was on the dyad ($F_{1,51} = 6.57$, $p = 0.01$, $R^2 = 0.10$) or the individual bird (joining bird: $F_{1,17} = 3.92$, $p = 0.064$, $R^2 = 0.10$; joined bird: $F_{1,17} = 3.89$, $p = 0.065$, $R^2 = 0.10$).

difference in dominance indicating higher incidence of joining by the bird of higher dominance (Figure 3). The significant relationship remained when we controlled for correlations within dyads using robust variance estimation for cluster-correlated data ($F_{1,51} = 19.11$, $p < 0.001$, $R^2 = 0.20$) and in the most conservative test when controlling for correlations within individ-

ual birds, first using the joined bird ($F_{1,17} = 8.46$, $p = 0.01$, $R^2 = 0.20$) and then using the joining bird ($F_{1,17} = 11.52$, $p = 0.003$, $R^2 = 0.20$).

Of the 221 total observed joining events, only 12 were between related individuals. Dyads of related and unrelated individuals did not significantly differ with respect to joining frequency (Mann-Whitney test: $U = 375.5$, $p = 0.50$).

Attractiveness to scroungers

To assess what qualities might be attractive to scroungers, we used a multiple regression analysis with backward selection, starting with the scrounger index, producer index and dominance index as independent variables and index of attractiveness to scroungers as the dependent variable. The scrounger index ($t = -1.18$, $p = 0.26$) did not contribute to the model and was excluded. The dominance index ($t = -2.37$, $p = 0.03$) and producer index ($t = 3.53$, $p = 0.003$) both significantly contributed to the model and explained 46% of total variance (multiple regression: overall $F_{2,16} = 8.77$, $p = 0.003$, $R^2 = 0.46$). Individuals with high producer index and low dominance index were more attractive to scroungers (Figure 4), suggesting that lower ranking individuals that flipped more boards got proportionally more attention from scroungers. Although producer index was correlated with the eating frequency (Pearson's $R = 0.713$; regression: $F_{1,17} = 17.55$, $p < 0.001$, $r^2 = 0.508$, $y = 0.44x - 0.0005$) there was no significant relationship between the index of attractiveness and the eating frequency ($F_{1,17} = 0.11$, $p = 0.75$, $R^2 = 0.006$).

Consequences of scrounging

If the number of eating events was randomly distributed among birds of different attractiveness (as appeared to be the case in our data because there is no correlation between eating and attractiveness, see above) then a simple mathematical consequence would be a negative correlation between index of attractiveness (X) and the index of full access to food (Y). We found that full access to the resource declined ($F_{1,18} = 4.56$, $p = 0.048$, $R^2 = 0.21$) in birds with high attractiveness to scroungers (Figure 5). A curvilinear model was a better fit to the data ($R^2 = 0.27$) than a linear model ($R^2 = 0.21$).

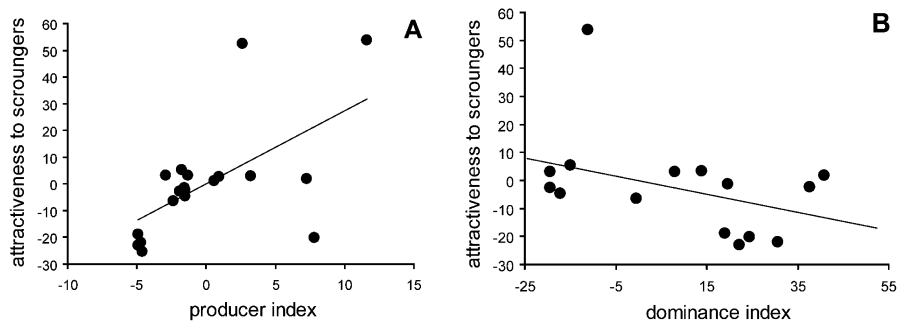


Figure 4. Simple regressions for the effect of the producer index (A; $y = 2.75x - 0.00005$; $R^2 = 0.36$, $F_{1,17} = 9.38$; $p < 0.007$) and dominance index (B: $y = -0.32x - 0.00002$; $R^2 = 0.16$, $F_{1,17} = 3.05$; $p < 0.10$) on the index of attractiveness to scroungers. Simple regression relationships are shown in the graphs A and B, but multiple regression analysis showed significant effects of these two independent variables on the index of attractiveness (results in text).

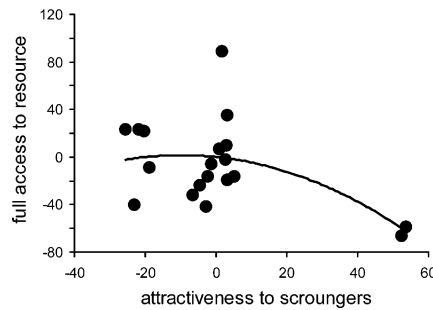


Figure 5. Relationship between the index of attractiveness to scroungers and the index of full access to the resource ($F_{1,18} = 4.56$, $p = 0.048$, $R^2 = 0.21$). A curvilinear model (27.7% variance explained) provided a better fit to the data than a linear model (16.5% variance explained).

Discussion

Consistency in producer-scrourer behaviours

Foraging tactics vary continuously among individuals: some birds specialize in one tactic while other birds use multiple tactics (Figure 1). Some birds rarely flipped boards, preferring instead to wait for more joining opportunities, while other birds flipped boards apparently without looking for joining opportunities. Still other birds used both tactics opportunistically and in roughly equal proportion. Increased use of one tactic led to decreased use

of the other tactic. These results confirm that PS roles exist in Mexican jays and that in contrast to studies of some other species (e.g., Barnard & Sibly, 1981), roles are flexible (i.e., most birds use a mix of both tactics).

Within the one to three month duration of each set of feeding trials, individuals showed consistency in tactic use (Figure 2). High consistency in use of foraging tactic has also been found in other species with dominance hierarchies (Caraco et al., 1989; Beauchamp, 2001). However, we found some evidence of long-term inconsistency when we looked at data for the four birds present in both years. Although the low number of joining events prevented calculation of producer and scrounger indices, a qualitative assessment of the raw data suggests that some individuals changed the proportion of their tactic use over the four year span between trial sets. One bird apparently switched roles (ratio of joining to being joined changed from 0/6 in 1993 to 7/2 in 1997), two birds kept somewhat similar roles (8/6 to 7/2; 3/8 to 0/48), and only one bird seemed to maintain its role (1/10 to 1/15). These data suggest that long-term change in the individual (e.g., age, competitive ability) or change in the group (e.g., dominance hierarchy, group size) might trigger a change in PS behaviour.

Relatedness does not affect joining

Mexican jays often live in flocks of closely related individuals, so we asked if related birds are more likely to join one another. Were this hypothesis supported, it would provide an alternate explanation to the PS model in that joining could be seen through the lens of altruism (*sensu* Hamilton, 1964) and not parasitism (Barnard, 1984). Our results do not support the hypothesis that relatedness affects joining behaviour. In 1993, the flock included a family unit consisting of a mated pair and their three offspring as well as more distant kin. In 1997, two pairs of birds were closely related. Nevertheless, only 12 out of 221 joining events were between related individuals. While we predicted that PS roles would have the largest effect on joining behaviour, we find our strong rejection of relatedness somewhat surprising in light of the fact that helper birds are willing to invest large quantities of time and effort into feeding other birds' young, and that this system is thought to have evolved through kin selection (Brown, 1987). Our results corroborate a study on northwestern crows (*Corvus caurinus*), which found no relationship between joining frequency and relatedness, though aggression level was decreased toward related scroungers (Ha et al., 2003).

Effect of dominance on scrounger preferences

In many theoretical (Barta & Giraldeau, 1999) and experimental treatments (Liker & Barta, 2002), dominant birds are more likely to play the role of scrounger because they can displace subordinate producers from discovered food sources. Our results likewise demonstrate the influence of dominance rank on PS roles, but in a different way. PS roles were not linked to dominance rank per se, but the greater the difference in dominance between two birds, the more likely it was that a joining event occurred between them, with the joiner usually being the bird of higher dominance (Figure 3). This resulted in the lower ranking birds attracting more scroungers (Figure 4). In other words, when a bird joins, it appears to take the joined bird's dominance rank into consideration, and preferentially chooses to join subordinate birds. This adds a new dimension to studies of dominance effects on PS roles, as joiner preference has thus far not been included in theoretical models or interpretations of experimental results.

Considering that joining behaviour appears to be mediated through joiner preference, we then asked what qualities existed in the joined birds that made them attractive to a scrounger and what consequences scrounging had on the joined bird. As expected, low dominance rank and high search activity (i.e., producing) were particularly attractive to a joiner, while scrounging activity was not. We did not record the exact number of seeds deposited under each board before the trials or how many seeds were removed upon each eating event, so we could not determine the 'finder's share', as it has been described in other studies (Vickery et al., 1991). However, our surrogate for the finder's share, the index of full access to the resource, shows a curvilinear decline for those birds that were most attractive to scroungers (Figure 5), as expected from the mathematical relationship between the formulas for index of attractiveness and the formula for index of full access to food. It illustrates the notion that scrounging is costly to the producer.

There are two logical predictions for groups in which there is preferential joining by individuals of higher dominance within the context of a linear dominance hierarchy. One prediction is that the proportion of producing and scrounging used by individuals varies continuously. This is because the individual of highest dominance rank can join all other individuals, and will benefit by being an extreme scrounger. The most subordinate individual, on the other hand, cannot obtain food, except by searching and, thus, will benefit from being an extreme producer (assuming it cannot leave the group). An

individual of middle dominance rank will most benefit from a mixed strategy of joining and searching. Adding more individuals to this theoretical hierarchy results in a group where the proportion of searching and joining — and thus producing and scrounging — varies continuously. Our observations support this prediction (Figure 1). The second prediction is that producers will be subordinates and scroungers will be dominants, a prediction not validated by our results. As mentioned earlier, we did not observe a direct relationship between the individual's dominance position and its joining behaviour. However, when joining occurred, it appeared to be mediated by the preference to join subordinate birds.

Mexican jay — a convenient model species

We suggest that PS behaviour might be influenced by other phenotypic traits and that this explains the more complex relationship between PS roles and dominance. For example, energy reserves, which might even be correlated to dominance rank, have been shown to be important in a bird's decision to use producer or scrounger foraging tactics (Lendvai et al., 2004). The shy-bold continuum (Wilson et al., 1994) offers a potential framework for investigating a phenotypic trait that could influence PS behaviour, as has been suggested in zebra finches (Beauchamp, 2006). Mexican jays demonstrate differing levels of boldness (for example, in their willingness to approach novel objects like traps), and this quality seems to be individually consistent (pers. observ.). Further work is needed to determine if shy-bold behaviour, energy reserves, or other phenotypic variables influence foraging behaviour and, in particular, PS roles in Mexican jays and other animals.

Because they live in stable flocks that can be studied relatively easily in natural settings, Mexican jays offer the potential for a wide range of descriptive and experimental studies seeking to clarify various aspects of PS behaviour. Changing such ecological variables as patchiness of the resource and its size (i.e., the finder's share) has been explored theoretically (Vickery et al., 1991), but little tested empirically (but see Di Bitetti & Janson, 2001). Experiments on multiple flocks of varying group size offer another route to testing predictions about PS equilibria (Mottley & Giraldeau, 2000). Using birds that live in free-living flocks with known relatedness and dominance hierarchies will allow the results to be integrated with foraging ecology (Ha & Ha, 2003) and interpreted in their full adaptive context.

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