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Dominance, pair bonds and boldness determine social-foraging tactics in rooks, *Corvus frugilegus*

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Socially foraging animals can search for resources themselves (produce) or exploit the discoveries made by others (scrounge). The extensive literature on producer–scrounger dynamics has mainly focused on scramble competition over readily accessible resources, thereby largely neglecting the variety of scrounging techniques individuals may use as well as the role of investment in food handling. Furthermore, although individual differences in boldness and social factors such as dominance have been described to influence foraging tactics, their potential interplay and effect in foraging contexts beyond the conventional producer–scrounger game remains unclear. We investigated the relationship between social-foraging tactic use and dominance, pair bonds and boldness in a foraging experiment focused on food handling and alternative scrounging tactics. We conducted a producer–scrounger experiment in a captive group of rooks in which individuals could produce by pulling up baited strings, or scrounge by retrieving fallen food items or joining a producer. There were three key findings: (1) dominant rooks adopted the producer tactic more often and more successfully than subordinates; (2) producing and scrounging by tolerance led to mixed benefits to paired birds; (3) bold birds scrounged by retrieving more often than shy birds. Importantly, individuals were highly consistent in their tactic use across conditions differing in food availability. Our study highlights the importance of taking both social factors and boldness (heterogeneity) into account when studying social-foraging dynamics and offers empirical data on food handling and alternative scrounging tactics that can be used to extend current models and experiments on social foraging.

Socially foraging animals can either search for resources themselves (produce) or exploit the discoveries made by others (scrounge; Giraldeau & Beauchamp 1999; Giraldeau & Caraco 2000; Giraldeau 2008). An extensive literature describes theoretical models and experiments investigating the dynamics behind these foraging behaviours and the conditions that influence this producer–scrounger (PS) game (Barnard & Sibly 1981; Giraldeau et al. 1994; Giraldeau & Caraco 2000; Giraldeau 2008; Broom et al. 2008). Surprisingly, most PS studies have focused only on the search for food and ignored the time needed to handle food. The latter is ecologically relevant as many food items are not immediately available for consumption and require preparation (Giraldeau & Caraco 2000; Bugnyar & Kotrschal 2002; Broom & Ruxton 2003; Ha & Ha 2003; Morand-Ferron et al. 2007a; Broom et al. 2008), such as the breaking of the protective shell of bivalves by many wading bird species (Norton-Griffiths 1967; Hockey et al. 1989; Stillman et al. 1997). Furthermore, whereas most PS research has focused on the exploitation of food patches through scramble competition (Giraldeau & Beauchamp 1999), individuals may use a variety of other techniques to obtain food from others, such as stealthy sequestering and food sharing (Brockmann & Barnard 1979; Giraldeau & Caraco 2000; Bugnyar & Kotrschal 2002). Investigating the social-foraging dynamics related to food handling and alternative scrounging tactics may therefore provide valuable insight into social foraging and the diversity of tactics that is frequently observed (Giraldeau 2008).

Recent studies on the conventional PS game, which focuses on the exploitation of patches through scramble competition, have shown that phenotypic differences may play a major role in determining the use of PS tactics (Barta & Giraldeau 1998; Beauchamp 2000, 2006; Liker & Barta 2002; Lendvai et al. 2006; Giraldeau 2008; Kurvers et al. 2009). For example, the payoffs of searching for food (producing) and exploiting the discoveries made by others (scrounging) are often strongly related to an individual's competitive ability as well as its explorative and risk-taking tendencies, with bolder individuals mainly producing and dominants mainly scrounging (Ens & Goss-Custard 1984; Barta & Giraldeau

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1998; Stillman et al. 2000; Liker & Barta 2002; Lendvai et al. 2006; Kurvers et al. 2010a). However, in a social-foraging context where foraging requires extensive handling time and multiple scrounging tactics are available, different phenotypic effects may be expected (Brockmann & Barnard 1979; Bugnyar & Kotrschal 2002; Morand-Ferron et al. 2007b; David et al. 2011). Extensive handling time increases the investment of producing, making it especially costly for lower-ranked individuals to produce because of their lower competitive ability (e.g. Giraldeau 2008; Broom et al. 2008). Furthermore, paired individuals may defend resources together (Robichaud et al. 1996; Emery et al. 2007; Seed et al. 2008), tolerate one another at a food patch (Beauchamp 2000; King et al. 2009) and share food with each other (Emery et al. 2007; Seed et al. 2008). Therefore, paired and unpaired individuals are expected to make different decisions as to whether to produce or scrounge. In addition, consistent individual differences in boldness may be expected to affect tactic use differently in a context that involves a large investment in food handling and in which alternative scrounging tactics are available. Not only are bolder individuals more likely to enter a feeding area first (Dyer et al. 2009), they are often the first to discover food patches (Beauchamp 2001), and rely less heavily on social information in making foraging decisions (Kurvers et al. 2010a; Webster & Ward 2011; but see Marchetti & Drent 2000). Bold individuals may therefore be expected to use alternative and more risky scrounging tactics especially when producing involves a long handling time. Thus, although in the conventional PS context it has been shown that phenotypic differences may play a major role on PS tactics, these and additional phenotypic effects may be expected to play different roles in foraging contexts in which food requires considerable handling effort and/or in which alternative scrounging options are available. Furthermore, investigating social factors in conjunction with consistent individual differences in behaviour is very relevant as they may be crucially linked to one another (Réale et al. 2007; Scheid & Noë 2010; Webster & Ward 2011) and actually drive consistent individual differences in the use of different foraging strategies (Beauchamp 2001; Morand-Ferron et al. 2007a; Bergmüller & Taborsky 2010).

We investigated the relationship between social-foraging tactic use and three phenotypic factors, namely dominance, pair bonding and boldness. Importantly, our foraging experiment extends the conventional PS game by focusing on two often neglected factors: time needed to handle food and alternative scrounging tactics, namely joining a tolerant producer or retrieving food items dropped on the ground by producers. To address these questions we used rooks, *Corvus frugilegus*, as a model species as they are highly social, form life-long pair bonds and establish a linear dominance hierarchy (Clayton & Emery 2007; Emery et al. 2007). We presented a captive group of 19 birds with bait attached to strings tied to branches in their aviary, a set-up that has been successfully used in avian cognitive research (Heinrich 1995; Heinrich & Bugnyar 2005). Individuals could ‘produce’ by successfully pulling up a baited string, ‘scrounge’ by joining or retrieving, or they could choose not to participate at all. In this particular set-up, producing required a considerable time investment and the ability to defend the resource, while scrounging by displacing a producer was not viable because of the high chance the string would drop. Rooks are rarely observed foraging alone on the ground in their natural environment because it entails a higher risk of predation. Therefore, scrounging by retrieving can be seen as naturally risky for rooks. Furthermore, this tactic contains an element of uncertainty. A scrounger’s success will depend not only on its own actions as there is variability when food items fall after they have been successfully pulled up by a producer. To determine the consistency of individual tactic use we presented the foraging experiment in a low (one baited string) and high (eight baited strings) food availability condition. In addition, we measured individual feeding rates on a maintenance diet to investigate the effect of hunger on foraging motivation and behaviour (Lendvai et al. 2004). Prior to the social-foraging experiment, we determined dominance ranks and affiliation scores for each individual and acquired boldness scores using a novel object test (Kurvers et al. 2010a).

We predicted that: (1) dominance would be positively related to the use and success of the producing tactic; (2) paired individuals would benefit from the high tolerance with their partner as it may increase their producing success and the ability to scrounge by joining; and (3) boldness would be positively related to scrounging by retrieving. We expected individuals to be consistent in their tactic use independent of food availability.

METHODS

Subjects and Housing

A group of five male and 14 female adult rooks served as subjects and were housed in an outdoor aviary (8 × 20 m and 3 m high) at the University of Cambridge Sub-Department of Animal Behaviour, Madingley, U.K. The birds were members of a group that was collected under English Nature Permit 20030108 from two colonies in Cambridge on 16 and 17 April 2003 and that were subsequently hand-raised. Aviaries were constructed of wood and mesh, had gravel floors and contained several perches of varying height, width and length throughout. All individuals could be identified by coloured leg rings. Birds had ad libitum access to water and a maintenance diet of soaked dog biscuits, egg, cheese, bread, cooked vegetables, seeds, nuts and fruit, except during the experimental procedures when the group was deprived of their diet for 4 h. The behavioural observations and boldness tests were conducted from May to August 2010 and the social-foraging experiment was conducted from August to October 2010. Birds were kept for future behavioural experiments after the conclusion of the study. All experiments were conducted in accordance with the university’s guidelines under the U.K. Home Office project licence PPL 80/1975.

Dominance

Prior to the social-foraging experiment we scored agonistic and affiliative interactions to determine the dominance rank and pair bonds in the group (Table A1 in the Appendix). Observations were made from 10 m outside the aviary between 1300 and 1430 hours for 16 days (May–July 2010). Data were collected ad libitum (Altmann 1974) and interactions were recorded as events with The Observer 5.0 software (Noldus Information Technology, Wageningen, The Netherlands) and analysed with MatMan 1.1 (idem). We scored 345 agonistic interactions, ranging from threats to active chases with feather pulling.

Pair Bonds

Pairs were identified using ‘dyadic affiliation scores’ (DAS) using the formula: DAS = (affiliation directed from x to y + affiliation directed from y to x)/(affiliation directed by x to all individuals in the group + affiliation directed from y towards all individuals in the group), with the calculations based on the ‘index of association’ (Martin & Bateson 2007). We separated affiliative behaviours into active and passive affiliations (Table A1 in the Appendix). Active affiliations are important for establishing and maintaining a pair bond, while passive affiliations are related to interindividual tolerance (Emery et al. 2007). Individuals were only considered

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paired if they had the highest DAS with each other in the active, passive and combined affiliation categories.

Boldness Test

We conducted a novel object test to determine individual boldness scores. We use the term 'boldness' for approaching a baited novel object (Wilson et al. 1993; Greenberg & Mettke-Hofmann 2001; Frost et al. 2007), although some authors have proposed using the term 'exploration' (Réale et al. 2007). For 40 trials each of 5 min (maximum five trials/day) we presented a novel object next to a cup baited with eight waxmoth larvae, *Achroia grisella*. We presented the novel object to the group rather than to each individual separately because it has higher ecological relevance (Webster et al. 2007), as in natural conditions it is likely that rooks would be confronted with such a situation while in the presence of conspecifics. The novel object was unique in each trial (varying in material, colour and size) and its position in the aviary was randomized across trials. For each trial we recorded which of the 19 individuals approached the novel object to within 1 m. Based on the average number of trials in which an individual approached (4.3 ± 1.45 trials) we classified individuals with approach scores higher than the average as bold ($N = 6$) and those with scores lower than the average as shy ($N = 13$). To exclude the possibility that feeding motivation influenced approach scores in the novel object test we ran an additional 40 control trials during which only the baited food cup was presented. The conditions were presented concurrently with randomized order for condition.

Social-foraging Experiment

In the social-foraging experiment individuals could scrounge, either by retrieving food items dropped on the ground by producing individuals or by joining a tolerant producing individual, produce, by pulling up baited strings in the aviary (see Heinrich & Bugnyar 2005; photo sequence Fig. A1 in the Appendix), or decide not to participate at all. A week before the start of testing, the experimenter habituated the birds to the strings and the procedure of baiting the strings (Heinrich & Bugnyar 2005) by daily entering the aviary, clearly showing the bait (a peanut or piece of cheese), and randomly attaching it to the end of one of 10 already present 50 cm long strings (jute twine) hanging off branches in the aviary. All strings were positioned at ±2 m height and minimally 1 m apart to make each string approachable by multiple birds simultaneously. We minimized the effect of possible interindividual differences in string-pulling proficiency by starting the experiment only after all individuals had been observed to pull up a baited string successfully. In the test, we presented the rooks with either a single baited string in 42 trials (one-string condition) or eight baited strings in 35 trials (eight-string condition). The order of conditions was pseudorandomized across trials such that the same number of trials was run for each condition. Trials lasted for a maximum of 5 min. Time between the experimenter entering and leaving the aviary when baiting the strings was kept constant across conditions. For each trial, we recorded which individuals approached the string to within 1 m ('producing attempt'), successfully pulled up the string and obtained the bait ('producing success'), joined a producer and thereby obtained food ('scrounge by tolerance') or landed directly under the string to retrieve dropped food ('scrounge by retrieving'). The measure of approaching the string provides information about the extent to which individuals would decide to bear the cost of approaching the string. Scrounging by displacing a successful producer was not a viable tactic because of the high probability that the string would drop and thus food would again be out of reach. We used an approach distance of 1 m from the string to indicate attempts to produce as birds were always observed to land within this distance when approaching the string to produce.

Feeding Rate

As a proxy of feeding motivation we measured individual feeding rates at two adjacent feeding tables (50 × 50 cm and 140 cm high, approximately 150 cm apart) that are normally used for the provisioning of the maintenance diet. After the string-pulling experiment, for 10 consecutive days, we removed the maintenance diet from the aviary for 4 h and recorded activity at the tables for 20 min after providing the food again. We determined the average percentage of time that an individual was on either feeding table across the 10 trials ('feeding rate'). The size of the tables and the distance between them allowed multiple birds to feed simultaneously. Together with the relatively long time frame used for recording feeding rates, this set-up ensured that variation in dominance ranks would not influence the measure of interest.

Statistics

Dominance

We organized all observed dominance interactions between individuals in a sociometric matrix, which takes into account the identity of each opponent and all the interactions and minimizes inconsistencies (de Vries et al. 1993). To test for linearity we calculated Kendall's coefficient of linearity K, Landau's index h and the index of linearity h' using MatMan 1.1 (Noldus Information Technology). Statistical significance of K was calculated using a chi-square test. Both indices vary from 0 (complete absence of linearity) to 1 (complete linearity). The index h' is based on h and takes into account the existence of unknown relationships. Statistical significance of h' is provided by a resampling procedure using 10 000 randomizations (de Vries 1995). If the dominance is linear, MatMan calculates a rank order most consistent with a linear hierarchy by minimizing the number of inconsistencies and then minimizing the total strength of inconsistencies (de Vries 1998).

Boldness

Repeatability is a measure of the within-individual variance compared with the between-individual variance and describes the phenotypic variance explained by the individual (Kurvers et al. 2009). We determined the repeatability of individuals' performance across the novel object trials by calculating the mean squares from a one-way analysis of variance (ANOVA) with individual as the main effect following the method of Lessells & Boag (1987). We compared the number of birds that approached the cup between the novel object trials and the control trials using a Mann–Whitney U test. Spearman correlation tests were run to determine whether approach scores in the novel object and control condition were correlated.

Social-foraging experiment

We used generalized linear models (GLMs) to test which variables explained producing attempts, absolute and relative producing success, and scrounging by retrieving for each condition. Data were fitted to a binomial distribution with logit-link function and separate models were run with the number of trials in which an individual attempted to produce, had producing success and scrounged by retrieving as the numerator and the total number of trials as denominator. For the GLMs on the data of the relative producing success the number of trials in which an individual attempted producing was used as the denominator. As fixed effects, we fitted dominance (rank), if an individual was paired or not (yes/

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no), boldness (bold/shy) and feeding rate (continuous). Models did not include sex because dominance was strongly related to sex and additional models including sex revealed it had no significant influence on any of the other numerators. We started with full models with all explanatory variables. Interactions were not included in the models as based on our sample size they may be driven by one or two data points or, conversely, a real interaction may not be apparent owing to lack of data. Minimal adequate models were obtained by comparing models with dropped terms using Akaike's information criterion (AIC), with the lowest AIC_c value indicating the best model fit, which is considered the preferable method for observational data (Burnham et al. 2011). The results of the GLMs are presented in Table 1. Because of this model selection procedure, discussion of the GLMs' results are based on the effect sizes and not on significance of P values. For completeness, both effect sizes and P values are presented in Table 1. Correlations of producing attempts and scrounging by retrieving between the low food and high food availability conditions were analysed using the Spearman rank coefficient (r_S). Results of all statistics other than the GLMs were interpreted based on the significance of P values, with $P < 0.10$ reported as a trend and $P < 0.05$ as significant; means are stated ±SE throughout. All data were analysed in R 2.15.2 (R Development Core Team 2012).

RESULTS

Dominance

Rooks had a linear dominance hierarchy (Kendall's coefficient $K = 0.53$, $P < 0.001$; Landau's linearity index $h = 0.53$, $h' = 0.56$, $P < 0.001$), such that all birds could be assigned a rank from 1 (most subordinate) to 19 (most dominant; de Vries 1995). All males were dominant over all females.

In both the one-string and eight-string conditions, dominance was positively related to the total number of attempts to produce and the total number of producing successes (Fig. 1) as well as to the proportion of successful trials out of all producing attempts (Table 1). Dominance did not play a role in scrounging by retrieving.

Pair Bonds

Based on our observation of 340 active and 516 passive affiliations six pairs were identified, one of which consisted of two females. Four of these pairs had built nests in the previous breeding season. Paired individuals performed fewer producing attempts than unpaired individuals (one string: paired: 24.0 ± 6.0%; unpaired: 31.9 ± 5.5%; eight strings: paired: 38.9 ± 5.7%; unpaired: 57.1 ± 12%). Although in the one-string condition the pair bond did not affect absolute producing success, paired birds had a higher proportion of successful producing attempts (relative producing success) than unpaired birds (paired: 33.3 ± 7%; unpaired: 6.6 ± 4%; Table 1). In 33 of the 42 trials, producing success was achieved by a paired individual, 21 of which when together with its partner. For 18 of these 21 trials the male was the first to arrive and pull the string; in 17 of these 21 cases the joining partner received some of the food, and in seven of 15 trials this occurred after both birds had pulled the string together. Furthermore, in 17 of 21 cases the primary producer was successful only after its partner had arrived at the string. In contrast to the one-string condition, in the eight-string condition not only the absolute success but also the relative success of paired birds was lower than that of unpaired birds (Table 1). Scrounging by retrieving was negatively related to the pair bond, in both the one-string and eight-string conditions (Table 1, Fig. 2a).

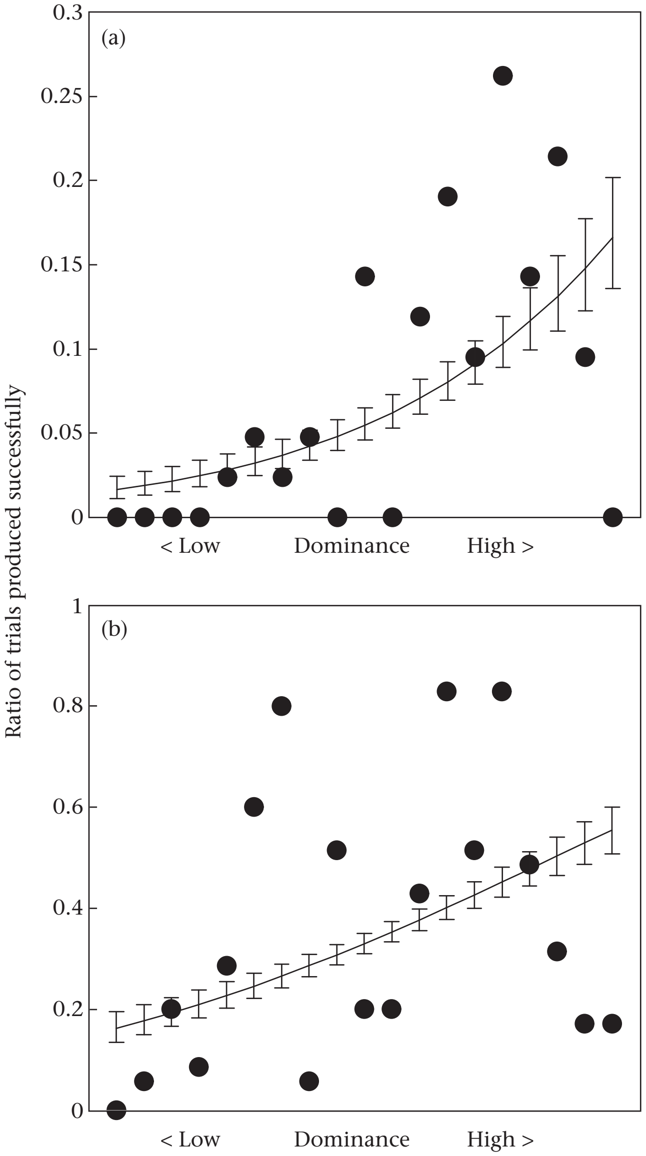

Figure 1. Influence of dominance rank on producing success in the (a) one-string ($N = 42$ trials) and (b) eight-string ($N = 35$ trials) condition. Points are mean values from raw data with ratio of trials based on the total number of trials per condition. Line shows predicted means ± SE from the minimal model, thus controlling for other significant terms in the model.

Boldness

Individuals were highly consistent in their approaching behaviour in the novel object condition; the repeatability of individuals' approaches during the first and second half of trials was high (0.93). Although more birds approached in each trial during the control than the novel object condition ($U = 240.50$, $N_1 = N_2 = 40$, $P < 0.001$), there was no significant correlation between the number of trials in which an individual approached in the novel object test and a control condition (40 trials; $r_S = -0.038$, $N = 19$, $P = 0.876$), nor did the number of approaches of shy individuals across the two conditions counterbalance those of bold individuals, suggesting foraging motivation did not affect approach scores in the novel object test.

Consistent individual differences in boldness were negatively related to both producing attempts and producing successes. Boldness did not affect relative producing success. These effects

Table 1
GLMs of approaching, absolute and relative success, and retrieving in the one-string and eight-string conditions of the social-foraging experiment

Fixed effect	One-string condition	z	P	Eight-string condition	z	P
	Estimate±SE			Estimate±SE		
Producing attempts						
(Intercept)	−1.41±0.29	−4.80	<0.001	−0.54±0.29	−1.88	0.06
Dominance	0.04±0.02	2.06	0.04	0.05±0.02	2.63	<0.01
Paired	−0.42±0.21	−2.05	0.04	−0.52±0.21	−2.50	0.01
Bold	−0.36±0.20	−1.79	0.07	−0.67±0.19	−3.42	<0.001
Feeding rate	0.07±0.03	2.75	<0.01	0.11±0.03	4.12	<0.001
Producing success (absolute)						
(Intercept)	−4.00±0.45	−8.96	<0.001	−1.70±0.32	−5.27	<0.001
Dominance	0.14±0.03	4.47	<0.001	0.10±0.02	5.03	<0.001
Paired				−0.87±0.22	−3.92	<0.001
Bold	−0.68±0.40	−1.72	0.09	−0.42±0.21	−1.95	0.05
Feeding rate				0.13±0.03	4.44	<0.001
Producing success (relative)						
(Intercept)	−3.29±0.68	−4.87	<0.001	−0.64±0.47	−1.35	0.176
Dominance	0.23±0.05	4.65	<0.001	0.14±0.03	4.86	<0.001
Paired	0.75±0.41	1.81	0.07	−0.78±0.33	−2.35	0.02
Bold						
Feeding rate	−0.15±0.08	−1.98	0.05	0.10±0.05	2.08	0.04
Scrounging by retrieving						
(Intercept)	−2.49±0.25	−10.09	<0.001	−1.13±0.30	−3.75	<0.001
Dominance						
Paired	−0.77±0.28	−2.89	<0.01	−0.70±0.24	−2.94	<0.01
Bold	0.99±0.27	3.62	<0.001	1.25±0.21	6.04	<0.001
Feeding rate				−0.07±0.03	−2.25	0.02

Minimal models were selected using an information theoretical model selection approach and results are discussed based on coefficient estimates. For completeness, *P* values are also presented. Coefficient estimates represent the change in the dependent variable relative to the baseline category and can therefore be interpreted as measures of effect size. Data were fitted to a binomial distribution with a logit-link function. The analyses were conducted on all 19 individuals.

were observed in both the one-string and eight-string conditions (Table 1). In contrast, scrounging by retrieving food items fallen on the ground was positively affected by boldness, with bold individuals scrounging considerably more than shy individuals, seen in both food availability conditions (Table 1, Fig. 2b).

Feeding Rate

In the one-string condition, individuals with higher feeding rates made more producing attempts. However, feeding rate did not affect the number of successful pulls and was negatively related to relative producing success (Table 1). In contrast, although in the eight-string condition feeding rate was also positively related to producing attempts, individuals with higher feeding rates had more producing success, both in terms of absolute numbers and in the proportion of pulls that were successful (Table 1). An individual's feeding rate did not influence scrounging by retrieving in the one-string condition and was negatively related to scrounging by retrieving in the eight-string condition (Table 1).

Individual Consistency in Tactic Use

In each trial, individuals could either engage in one of the foraging behaviours or not participate at all. On average, in the one-string condition, individuals participated in 31.3 ± 3.1% of the trials, with producing attempts accounting for 27.0 ± 3.9% and scrounging by retrieving for 7.8 ± 1.7% of trials. In less than 2% of trials did individuals attempt both to produce and to scrounge, which was not related to the frequency of producing attempts ($r_S = 0.123$, $P = 0.615$) or the relative producing success ($r_S = -0.09$, $P = 0.714$). The more individuals attempted to produce the less they scrounged by retrieving ($r_S = -0.455$, $P < 0.05$). In the eight-string condition, individuals participated on average in 69.0 ± 24.9% of the trials, with producing attempts accounting for 49.2 ± 24.3% and scrounging by retrieving for 19.9 ± 18.1% of trials; they did not attempt to produce in 50% of the trials in which they scrounged. Individuals were highly consistent in their tactic use across the two food availability conditions, both in terms of producing attempts ($r_S = 0.879$, $N = 19$, $P < 0.001$; Fig. 3a) and in scrounging by retrieving ($r_S = 0.755$, $N = 19$, $P < 0.001$; Fig. 3b).

DISCUSSION

In this study we investigated the use of various foraging tactics by rooks in a PS game that focused on investment in food handling and alternative scrounging tactics. In particular, we assessed how two social factors (namely dominance rank and whether a bird was paired or not) and individual differences in boldness influenced the use of producing and scrounging tactics. We tested a group of rooks in a string-pulling experiment and determined individual consistency in tactic use across conditions that differed in food availability. The experiment revealed three key findings. First, dominant rooks adopted the producer tactic more often, and more successfully, than subordinate rooks. Second, paired individuals often attempted to produce together, which increased the scrounging success of the joining partner, but resulted in mixed success for the producing partner. Third, bold individuals scrounged more often by retrieving than shy individuals. Individuals were highly consistent in tactic use across conditions with low and high food availability.

Dominance has increasingly been taken into account in studies on foraging dynamics (Barta & Giraldeau 1998; Stillman et al. 2000; Liker & Barta 2002; Beauchamp 2006; Lendvai et al. 2006). The majority of these studies have used the conventional PS game, in which individuals can either search for food or exploit the discoveries made by others, and found that higher-ranked individuals produce less and scrounge more than subordinates (but see Beauchamp 2006). These findings contrast with the result of our study. Here, dominants made more producing attempts and were

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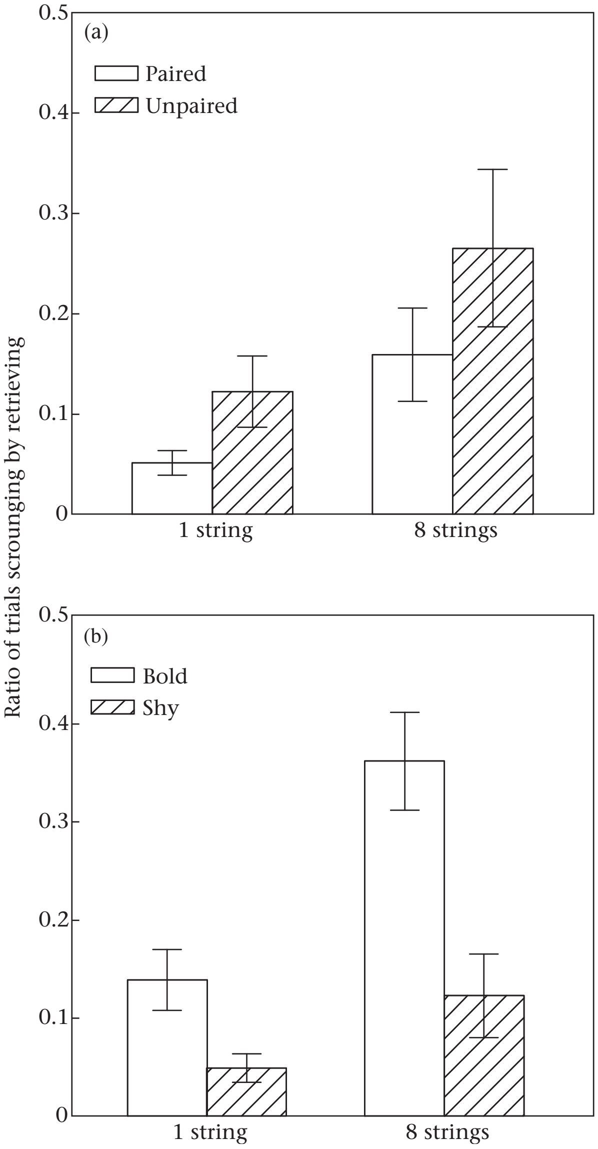

Figure 2. Influence of (a) the pair bond and (b) boldness on scrounging by retrieving in both the one-string and eight-string condition. Shown are mean ± SE ratio of trials out of the total number of trials per condition during which an individual used the scrounging by retrieving tactic. Paired individuals: $N = 12$; unpaired individuals: $N = 7$; bold individuals: $N = 6$; shy individuals $N = 13$.

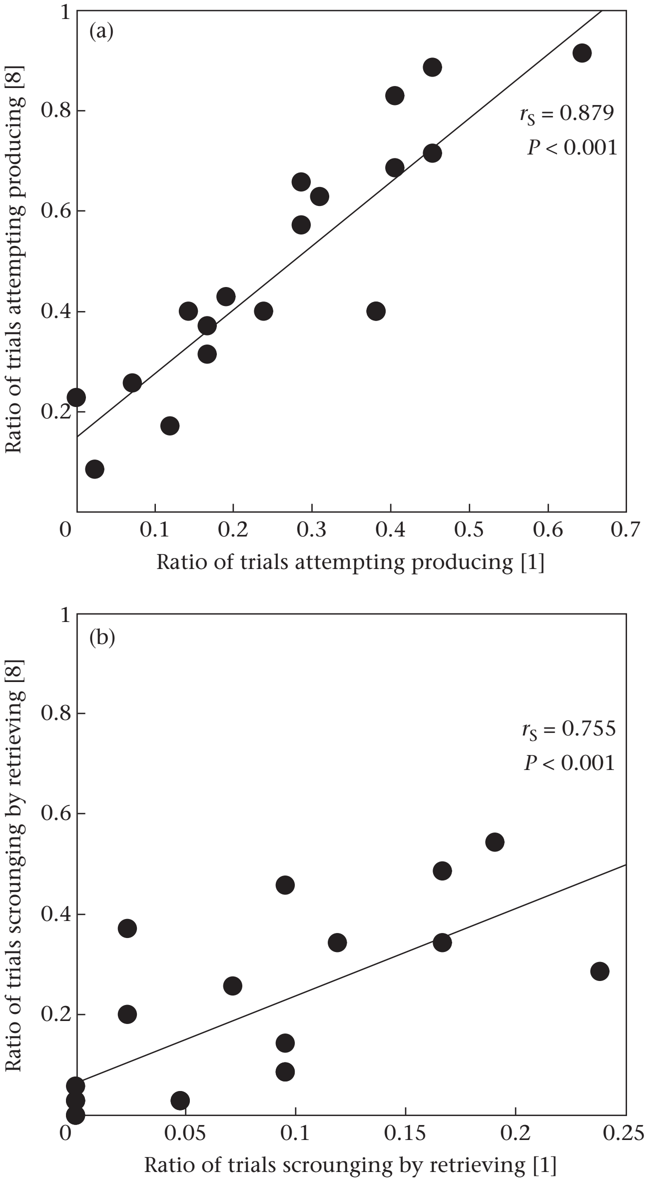

Figure 3. Consistency in tactic use across conditions differing in food availability for attempts of (a) producing and (b) scrounging by retrieving (one string [1]: $N = 42$; eight strings [8]: $N = 35$). Shown are mean ± SE ratio of trials out of the total number of trials per condition during which an individual (a) attempted to produce or (b) scrounged by retrieving.

more successful at doing so than subordinates. This contrasting effect is likely to be strongly influenced by the extensive handling time needed to pull up a string successfully. This may change the payoffs and the probability of producing success in such a way that, for subordinates, attempting to produce might become too costly. This effect might have been strengthened further by the ineffectiveness of scrounging by displacing an individual after it had successfully pulled up the string as this would result in it dropping the string, thereby putting the bait out of immediate reach. In a situation with a relatively high availability of food, the probability of being displaced while attempting to produce is expected to be low and producing success to be high. If this goes together with a reduction in clumping of the food, this may minimize the benefits of being high in dominance status for food intake (see Theimer 1987; Giraldeau 2008). However, when we presented the birds with eight baited strings (thus high food availability with a reduction in food clumping), dominance was again positively related to both the amount individuals attempted to produce and their success in producing. Although this result might to a certain extent have been influenced by the feedback related to the probability of producing success between the two conditions, the investment in food handling is expected to play the major role. Despite food being much more available and less clumped, the probability of producing success may still be low because of the probability of being displaced still being high owing to the extensive handling time. Overall, these findings thus seem to suggest that a large investment in food handling may have an important and consistent effect on the payoffs of producing related to dominance.

The pair bond (paired/unpaired) had a strong effect on how often birds attempted to produce and were successful as well as

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how often they scrounged by tolerance and by retrieving fallen food items. When food availability was low, paired individuals had a higher chance of producing successfully than unpaired birds. On average, in one out of two trials, paired individuals joined each other at a producing attempt and, in more than 80% of these attempts, success was achieved after the primary producer was joined by its mate. This seems to suggest that paired birds benefit from their ability to defend resources together (Robichaud et al. 1996; Emery et al. 2007; Seed et al. 2008) and, furthermore, that unpaired individuals may have to work harder to get their share of the food. This is indeed supported by the finding that unpaired individuals scrounged more by retrieving and performed more producing attempts than paired individuals. However, looking at the costs and benefits of the pair bond in more detail, we see that having a partner did not influence absolute producing success in the one-string condition. In addition, paired individuals might join their producing partners preferentially only at the moment when producing success seems likely, thus reducing the benefit of increased defensibility. Furthermore, in more than 80% of cases the joining partner received (some of) the food (either by food sharing or taking (some of) the bait); thus producing for paired birds may actually be costly. This is supported by the finding that when food availability was high, both absolute and relative producing success was lower for paired compared to unpaired birds. Thus, although for paired individuals scrounging by tolerance was a highly successful strategy (see also Bugnyar & Kotrschal 2002), producing when paired might actually be relatively costly in the short term, especially when food availability is high. This is interesting as scrounging by tolerance was performed by the female of a pair 85% of the time. However, a producing male may still benefit from tolerating its partner's scrounging, as this may strengthen their pair bond (Emery et al. 2007; von Bayern et al. 2007) and ultimately result in higher fitness benefits (e.g. increased mating opportunities). To our knowledge such a nuance has never been addressed in PS models. This might also explain the high levels of social tolerance between the individuals in a pair (Beauchamp 2000; Seed et al. 2008): during seven trials we observed paired birds to produce successfully by pulling the string together.

Consistent individual differences in boldness had a very strong effect on use of the scrounging tactic. As predicted, bold individuals scrounged more by retrieving fallen food items than shy individuals, with both low and high food availability. We predicted this effect because this particular scrounging technique entails both an element of risk of predation and uncertainty because of dependence on the producer's action. In the wild, single rooks are rarely seen foraging on the ground owing to a high risk of predation. Despite the absence of predators in the aviary setting, the captive-housed rooks spend most of their time away from the ground and in most cases will land on the ground with multiple individuals simultaneously (J. W. Jolles, unpublished data). Furthermore, retrieving fallen food items contains an element of uncertainty that is beyond the action of the scrounger, as food items will not fall during or after every successful producing action. Although Kurvers et al. (2010a) reported that boldness was positively related to producing in barnacle geese, *Branta leucopsis*, which seems to contradict our finding, both results may be explained by the commonality of risk and uncertainty in foraging tactics. In Kurvers et al.'s study, individuals could produce by discovering new food patches, which is a more risky and uncertain tactic than scrounging on these new discoveries. This would suggest that the relationship between boldness and the use of producing and scrounging tactics might depend on the risk and uncertainty involved in both tactics. This hypothesis is supported by the finding that bold individuals are often the first to enter a feeding area and discover food patches (Beauchamp 2001; Dyer et al. 2009) and are more flexible in their responsiveness (Marchetti & Drent 2000; Frost et al. 2007). Owing to the small size of dropped food items and the difficulty of discerning them from the ground substrate, we could not investigate the determinants of scrounging propensity and scrounging success in more detail. Further studies are needed to provide insights into the relative benefits and costs of this scrounging tactic and their effect on foraging choices.

In common with previous studies (Beauchamp 2001, 2006; Morand-Ferron et al. 2007a; Kurvers et al. 2010a), we found that individuals were highly consistent in their use of foraging tactics. Individuals chose the same tactics in both food availability conditions, even though high food availability could have enabled more individuals to choose successfully the more profitable producing strategy. Dominant individuals made more producing attempts and were more successful than subordinates, while, in contrast, scrounging by retrieving was positively related to boldness and the pair bond. This effect was observed irrespective of food availability. These findings may indicate that dominance, boldness and the pair bond lower the flexibility of individuals' tactic choices. Still, the current state of individuals may play a role in their tactic use, as is substantiated by the finding that individual differences in motivation to feed (feeding rates) had opposite effects on producing success under low and high food availability. Overall, these results suggest an interplay between social factors and individual differences in boldness that has an important effect on individual consistency in tactic use. This would support the idea of social niche specialization which suggests that individuals adopt different behavioural strategies to reduce competition with other group members (Bergmüller & Taborsky 2010).

Our social-foraging experiment conforms to the first and main assumption of PS games, namely tactic incompatibility (Coolen et al. 2001), and enabled the study of food handling and alternative scrounging tactics in a social-foraging context. According to the second assumption of PS games, scrounger payoffs should be negatively frequency dependent (Mottley & Giraldeau 2000). Our results show that the investment in handling food may be an important driving factor for individual foraging tactic choices and that social factors and boldness may have strong and opposite effects relative to the conventional PS game. This may have implications for future studies on PS dynamics. Although foraging efficiency may play a large role in foraging tactic use under certain conditions (see e.g. Stillman et al. 2000), we do not expect this to be the case in our study. In our social-foraging experiment food-handling time was long and competitor density high, factors under which the influence of foraging efficiency is expected to be minor (Stillman et al. 2000). Furthermore, only after all individuals had already been observed to pull up a baited string successfully did we start with the social-foraging task. Given that persistent individual differences may often be related to dynamics that are peculiar to the group in which they occur (David et al. 2011; Morand-Ferron et al. 2011; but see Kurvers et al. 2010b), follow-up research on our social-foraging experiment should also study how a change in social composition may affect individual tactic use. Finally, more research is needed to investigate the payoffs of the various foraging tactics in relation to food-handling time, and how these payoffs may differ between different phenotypes.

To summarize, our study shows that individuals were highly consistent in the use of producing and scrounging tactics in a social-foraging context that focused on food handling and was strongly influenced by dominance, the pair bond and boldness. Our results add to a growing literature on heterogeneity in group behaviour stressing the importance of not treating group members as identical or interchangeable (Dyer et al. 2009; Nagy et al. 2010; Webster & Ward 2011; Jolles et al. 2013). Moreover, our study highlights the importance of considering social factors as well as consistent individual differences (often referred to as 'animal personality') for investigating social-foraging dynamics. The current

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study offers empirical data on food-handling time and alternative scrounging tactics that could be used to extend both current models and experiments on social foraging.

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Appendix

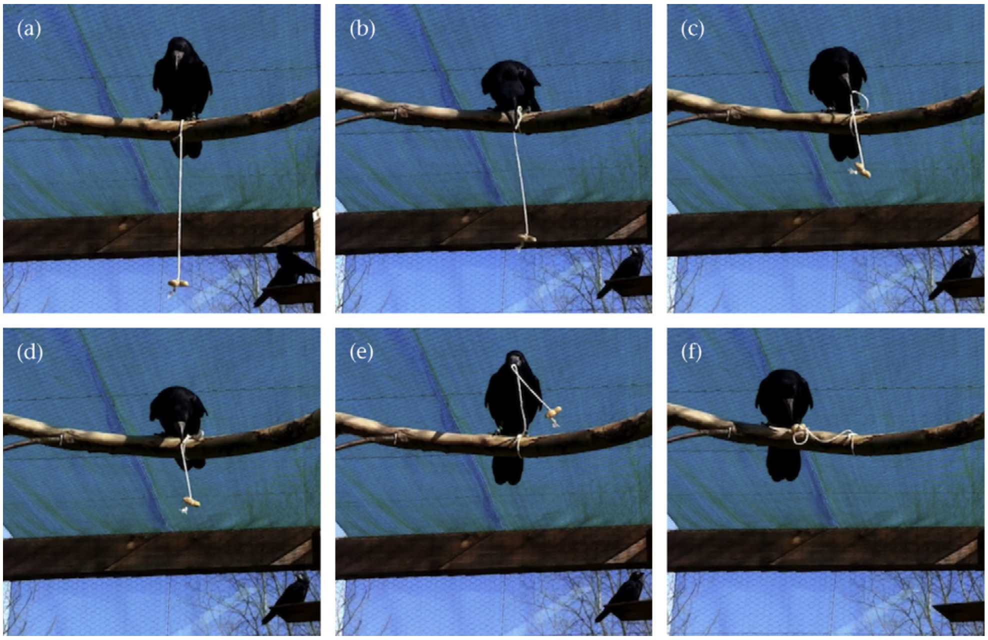

Figure A1. Sequence of photos that shows a successful producing attempt as seen in the social-foraging experiment. After arriving above the string (a), an individual had to grab the string with its beak (b), pull up the string (c) and stand on the string (d), and perform this sequence of behaviours up to three times (e) in order to get to the food item (f).

Table A1
Ethogram of agonistic and affiliative interactions used to determine the dominance rank and pair bonds in the group

Behaviour	Definition
Aggression	
Displacement	One individual retreats at the approach of another, which locates itself in the retreating individual's original position
Threaten	One individual makes a movement directly at, pecks at, flies at or lunges at another without making contact
Pecking	One individual uses its bill to peck at and make contact with another individual
Feather pulling	One individual grabs the feather(s) of another individual and makes a pulling motion
Chasing	A prolonged, continuous approach by one bird towards another bird that continuously moves away
Avoiding	One individual moves out of the way as another individual approaches
Active affiliation	
Bill twining	Two individuals interlock the mandibles of their bills, often accompanied by simultaneous displaying
Active food sharing	One individual places a food item into the bill of another individual, often after the recipient makes begging calls
Sitting in contact	Two individuals sit next to each other, maximum 5 cm apart
Allopreening	One individual nibbles or strokes the feathers of another
Dual object manipulation	Two birds manipulating the same object
Dual caching & cache recovery	Two individuals caching the same object or recovering and eating a previously cached food item
Passive affiliation	
Co-feeding	Two individuals foraging while in proximity to each other.
Sitting in proximity	Two individuals sit within one body length of each other, but more than 5 cm apart
Passive food sharing	One individual places a food item in front of another individual after which they eat from it together

Developed in collaboration with Corina Logan (Logan et al. 2012).

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