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The effect of personality on social foraging: shy barnacle geese scrounge more

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Animals foraging in groups can either search for food themselves (producing) or search for the food discoveries of other individuals (scrounging). Tactic use in producer–scrounger games is partly flexible but individuals tend to show consistency in tactic use under different conditions suggesting that personality might play a role in tactic use in producer–scrounger games. Here we studied the use of producing and scrounging tactics by bold and shy barnacle geese (*Branta leucopsis*), where boldness is a personality trait known to be repeatable over time in this species. We defined individuals as bold, shy or intermediate based on two novel object tests. We scored the frequency of finding food patches (the outcome of investing in producing) and joining patches (the outcome of investing in scrounging) by bold and shy individuals and their feeding time. Shy individuals had a higher frequency of joining than bold individuals, demonstrating for the first time that personality is associated with tactic use in a producer–scrounger game. Bold individuals tended to spend more time feeding than shy individuals. Our results highlight the importance of including individual behavioural variation in models of producer–scrounger games.

Keywords: producer–scrounger game; boldness; personality; foraging strategy; barnacle goose; *Branta leucopsis*

1. INTRODUCTION

Animals may either collect personal information about their environment, or they may observe other individuals to collect social information (Danchin *et al.* 2004). One of the best studied systems related to information gathering is known as the producer–scrounger game, in which individuals either search for food themselves (producing = personal information) or make use of information about food made available by other group members (scrounging = social information). Individual tactic use in producer–scrounger games is partly flexible and it has been demonstrated that individual scrounging behaviour depends on hunger level (Lendvai *et al.* 2004), dominance (Liker & Barta 2002) and predation risk (Mathot & Giraldeau 2008). However, individuals tend to use the same tactic under different conditions (Beauchamp 2001, 2006), suggesting that personality might play a role in tactic use.

Personality in animal behaviour describes the phenomenon that differences between individuals in behavioural and physiological traits are consistent over time and context (Gosling & John 1999; Koolhaas *et al.* 1999; Carere & Eens 2005; Groothuis & Carere 2005). Different behavioural and physiological reactions have a genetic basis (van Oers *et al.* 2005) and are often correlated. This suggests that these differences are fundamental aspects of the behavioural organization of individuals and are the subject of natural

(Dingemanse & Réale 2005; Smith & Blumstein 2008) or sexual selection (van Oers *et al.* 2008). The concept of inter-individual differences is also known as temperament (Réale *et al.* 2007), coping styles (Koolhaas *et al.* 1999) and behavioural syndromes (Sih *et al.* 2004a,b).

One of the best studied personality traits in a wide range of taxa is boldness. Several studies have demonstrated that bolder individuals are more often found in the leading edge of moving groups (Beauchamp 2000; Harcourt *et al.* 2009; Kurvers *et al.* 2009; Schuett & Dall 2009). In foraging groups, animals located on the edges are more likely to play producer (Barta *et al.* 1997; Mónus & Barta 2008). Taken together, these observations suggest that boldness might also predict the use of tactic in a producer–scrounger context. However, to our knowledge, no study to date has tested for a relationship between personality and producer–scrounger foraging tactic use.

We studied the relationship between the personality trait boldness and foraging tactic use in barnacle geese, *Branta leucopsis*. Boldness has been shown to be repeatable over time and to correlate with movement order towards a food patch in this species (Kurvers *et al.* 2009). We scored the boldness status of individuals by performing two novel object tests. Based on the outcomes of these tests we defined individuals as either bold individuals, shy individuals or intermediate individuals. We formed groups of one bold, one shy and two intermediate individuals and scored the frequency of producing and scrounging and the feeding time of the bold and shy individuals in a producer–scrounger game. As bold

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individuals are more often found in the leading edge of a moving group, we expected that shy individuals would have a higher percentage of scrounging than bold individuals. We scored the dominance of individuals living in a stable group situation prior to the producer–scrounger experiment, to control for any confounding dominance effect. In some species a relationship between the outcome of a novel object test and dominance has been reported (e.g. Verbeek *et al.* 1996, 1999; Sundström *et al.* 2004), but not in others (e.g. Freeman *et al.* 2004; Fox *et al.* 2009). In barnacle geese there is no relationship between the novel object score and dominance (Kurvers *et al.* 2009).

2. MATERIAL AND METHODS

(a) Study subjects

We used captive-born wing-clipped barnacle geese, each fitted with a uniquely coded leg ring for identification ($n = 28$). Birds were sexed by cloacal inspection (14 females, 14 males) and were all unpaired. Before the start of the experiment we measured tarsus and culmen length (to the nearest 0.1 mm) using callipers and wing length (1.0 mm) using a ruler. One observer carried out all measurements to minimize observer biases. Body mass was measured on a digital balance (1.0 g). We used a principal components (PC) analysis of tarsus, culmen and wing lengths to derive a measure of body size. PC1 explained 79.8 per cent of the variation. Body condition was calculated as the residual from a regression of body mass on PC1.

All geese were kept as one group in an outdoor aviary of 12×15 m at the Netherlands Institute of Ecology in Heteren, The Netherlands. Throughout the experiments geese were fed *ad libitum* with a mixture of grains, pellets and grass. A pond (6×1 m) was present in the aviary, with continuous flowing water for bathing and drinking.

(b) Dominance score

Prior to the foraging experiment we scored agonistic interactions in a flock of 28 individuals (20 December 2008–1 February 2009). An interaction was defined as a direct confrontation between two geese, ranging from threats with lowered head and neck to active chases with flapping wings (Stahl *et al.* 2001). We identified the participants of each interaction, and scored the behaviour each used. We considered an interaction as being won by an individual when the opponent turned and walked or ran away (Stahl *et al.* 2001). In total we scored 991 interactions (mean number per individual: 70.8; range: 33–123 interactions). Since the number of known relationships was high (79.9%) we were able to construct a dominance matrix, which is more precise and informative than a simple dominance score (Poisbleau *et al.* 2006). A dominance matrix takes into account the identity of each opponent and all the interactions and is built in such a way that inconsistencies are minimized (de Vries *et al.* 1993).

(c) Novel object test

The novel object test used the procedure described in Kurvers *et al.* (2009). In short, we habituated individuals to an experimental arena of 3×9 m by introducing each individual seven times for 10 min in the arena (1–12 December 2008). After habituation we placed a novel object (a green plastic mat) in the middle of the arena, introduced each goose once for 10 min, and scored the minimal

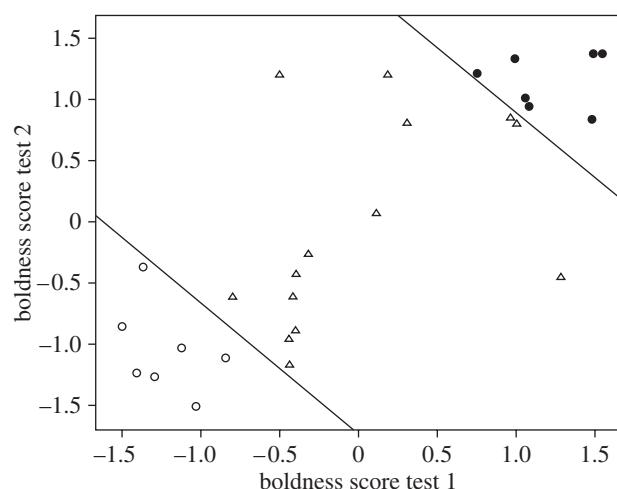


Figure 1. Relationship between the novel object score during two novel object tests for all individuals ($n = 28$). Open circles represent geese that were classified as shy ($n = 7$). Triangles represent geese that were classified as intermediate ($n = 14$). Filled circles represent geese that were classified as bold ($n = 7$). Parallel lines represent the borders between three boldness classes.

distance (cm) reached between the goose and the novel object, as well as the time elapsed (s) before the goose came within 50 cm of the novel object (15–16 December). If geese never approached within 50 cm of the novel object they were assigned an approach latency of 601 s. The test was repeated with another novel object (a brown deep-pile rug) on 17 and 18 December 2008. We calculated principal components (PCs) for each test as an independent measure of novel object score. PC1 explained 85.3 and 90.9 per cent of the variation for test one and test two, respectively. The correlations of both variables with PC1 were negative, implying that high values of PC1 correspond to bolder individuals. We used the average novel object score over the two tests as a measure of boldness.

Based on the outcomes of the novel object tests we assigned individuals to different groups. Individuals with the highest average novel object score were defined as bold individuals ($n = 7$), individuals with the lowest average novel object score were defined as shy individuals ($n = 7$). All other individuals were defined as intermediates ($n = 14$) (see also figure 1). Bold and shy individuals were given an extra colour ring for identification. We formed seven pairs of focal individuals, consisting of one bold and one shy individual and seven pairs of companion individuals, consisting of two intermediate individuals.

(d) Foraging experiment

The experimental arena measured 5.5×11 m. We placed 99 flowerpots (height: 20 cm, diameter opening: 22 cm) at an equidistance of 55 cm at the end of the arena opposite the entrance (figure 2). Flowerpots were empty, or contained a 5×5 cm sod of the grass perennial ryegrass (*Lolium perenne*), cut to a height of 1 cm. This grass is an important food source of wild barnacle geese (Prins & Ydenberg 1985). We fastened the sod using a long nail stuck through the sod and pot, and into the ground.

To habituate the individuals to the experimental conditions we supplied half of the pots with grass and introduced all the geese as one group to the experimental arena. Thereafter, we gradually decreased the group size

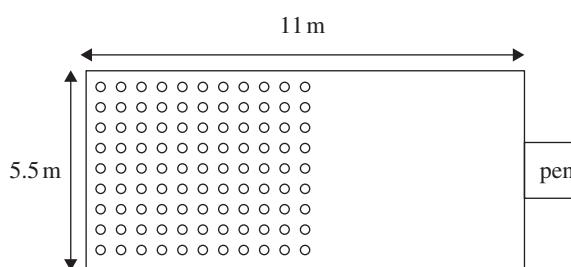


Figure 2. Overhead schematic view of the experimental arena used for the foraging experiment. The solid lines represent a fence covered with white plastic. The floor was covered with anti-root cloth. The circles represent 99 flowerpots that either contained a small patch of grass ($n = 10$) or were empty. Geese were introduced to the arena from the pen by opening a sliding door opposite to the flower pots.

and the number of pots filled. Prior to the start of the experiment all individuals had been introduced eight times to the experimental arena. During experimental trials we filled 10 randomly chosen pots with a sod of grass ('food'). Sods were replaced after each trial if grazed upon. We removed the food from the aviary at 17.00 h the day preceding each experiment.

During each trial we formed groups of four individuals, consisting of one pair of focal individuals (one bold and one shy) and one pair of companion individuals (two intermediates). The first day we randomly assigned one focal pair to one companion pair. Thereafter, we used a rotating system to pair the couples. The order of introducing the groups on each day was randomized. Geese were used once a day resulting in seven trials per day and each focal pair was tested twice against each companion pair, resulting in 98 trials over a period of 14 days (5–20 February 2009).

Each morning the geese were placed in groups of four in smaller holding enclosures to facilitate transport between the outdoor enclosure and the experimental arena. Prior to a trial the group of four geese was gently driven towards the wooden pen that served as the entrance of the experimental arena (figure 2). The group was held for 1 min in the wooden pen before being admitted to the arena for 10 min. All the experiments were performed between 09.00 and 13.00 h, local time.

All the trials were video-taped and we scored the behaviour of the two focal individuals from the recordings. Feeding events were identified either as 'finding' or 'joining'. We did not use the terms producing and scrounging because we observed the actual feeding events and not the tactic use directly, i.e. whether a bird was searching as a producer or scrounger (Mottley & Giraldeau 2000; Coolen *et al.* 2001; Liker & Barta 2002). In a 'finding event' an individual discovered a filled pot at which no other individual was present and fed from it. In a 'joining event' an individual attempted to start feeding at a filled pot where another individual was foraging at the arrival of the focal individual. We distinguished between 'successful joining' (individual actually fed from the pot) and 'unsuccessful joining' (individual was not successful in feeding from the pot). We calculated the joining proportion for each individual for each trial as the total number of joining events divided by the sum of the total number of finding events plus the total number of joining events. We calculated the proportion of successful joining events as the number of successful joining events divided by

the total number of joining events. We included the unsuccessful joining attempts in our calculation of proportion joined since the number of unsuccessful joining attempts contains important information on the foraging tactic an individual is following (regardless whether this tactic is successful or not). Excluding the cases of unsuccessful joining attempts would result in a less accurate estimation of the actual foraging tactic use. In addition we scored the total feeding time (s). Feeding time was defined as the total time a focal individual had its head in a filled pot. We could not measure the bite rate from our recordings. In addition, we scored the order of arrival on the food patch and the number of different sods visited. Based on the linear dominance hierarchy each focal individual was rated a dominance score unique for each trial ranging from 1 (most dominant in the group of four) to 4 (most subordinate in the group of four) (see details below).

In a few trials ($n = 12$) not all four individuals foraged, which clearly affected the behaviour of other group members. Since we know that the foraging success of barnacle geese depends on the behaviour of other group members (Kurvers *et al.* 2009) and the reluctance to forage might affect the joining opportunities of other group members, we excluded these trials from our analyses, leaving a total of 86 trials in which all individuals foraged.

(e) Statistics

We organized all observed dominance interactions between individuals in a sociometric matrix. 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, Wageningen; and see de Vries *et al.* 1993). Statistical significance of K is calculated using a χ^2 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).

We determined the repeatability of the novel object test by calculating the mean squares from a one-way analysis of variance (ANOVA) with individual as the main effect. Repeatability was calculated following Lessells & Boag (1987) and its s.e. following Becker (1984).

We compared differences between bold and shy individuals in dominance, body size and body condition using a *t*-test.

To test the effect of personality type and dominance on the use of tactic, we used linear mixed effect models. To analyse the effect on proportion joined and on the proportion of successful joining events, we used generalized linear mixed models with binomial errors and a logit-link function. To analyse the effect on feeding time, order of arrival and number of sods visited, we used general linear mixed models. Feeding time was log-transformed to meet the assumption of normality. As fixed effects in all models we fitted boldness, dominance, body condition, body size and sex. To avoid pseudoreplication we fitted focal individual nested within focal pair and companion pair as random effects. We started with full models containing all terms. Minimal adequate models were obtained by stepwise deletion of non-significant terms ($p > 0.1$), starting with

the least significant term. To compare the explanatory power of two subsequent models we used a log-likelihood ratio test, which follows a χ^2 distribution, with degrees of freedom equal to the difference in the number of parameters between the two models. We used the package *lme4* for generalized mixed model procedures and *nlme* for general mixed model procedures in R (v. 2.7.2). For all other calculations we used SPSS (v. 15.0).

3. RESULTS

(a) Dominance

The value of Kendall's linearity index ($K = 0.66$, $p < 0.001$), Landau's index and the corrected index of the sociometric matrix were high ($h = 0.66$, $h' = 0.68$, $p < 0.001$), allowing the use of a linear order to rank individuals. Dominance rank was significantly and positively correlated with both body size ($r = 0.70$, $p < 0.001$) and body condition ($r = 0.62$, $p < 0.001$). Males were on average higher in dominance rank than females ($t_{26} = 5.51$, $p < 0.001$), in better body condition ($t_{26} = 3.70$, $p = 0.001$) and larger ($t_{26} = 4.35$, $p < 0.001$).

(b) Novel object test

In agreement with earlier findings in this species, novel object score was highly repeatable (mean \pm s.e., 0.81 ± 0.07 ; see also figure 1) and there was no sex difference in novel object score ($t_{26} = 0.35$, $p = 0.73$). There were no differences between bold ($n = 7$) and shy individuals ($n = 7$) in dominance rank ($t_{12} = 0.46$, $p = 0.65$), body size ($t_{12} = 0.09$, $p = 0.93$) and body condition ($t_{12} = 0.17$, $p = 0.87$).

(c) Foraging experiment

Shy individuals joined significantly more than bold individuals, with the proportion being twice as large (shy: 47.8%, bold: 22.5%; $\chi^2_1 = 5.60$, $p = 0.018$; figure 3a). Dominance (just as body condition, body size and sex) did not affect the proportion of joining events (body condition: $\chi^2_1 = 2.94$, $p = 0.09$; all other $p > 0.1$; figure 4a). However, the proportion of being successful in a joining event increased with increasing dominance ($\chi^2_1 = 7.03$, $p = 0.008$; figure 4b). Boldness (just as body size, body condition and sex) did not affect the proportion of successful joining (all $p > 0.1$; figure 3b).

There was no significant difference in feeding time between bold and shy individuals ($\chi^2_1 = 3.74$, $p = 0.053$; figure 3c) and neither dominance ($\chi^2_1 = 3.14$, $p = 0.077$; figure 4c) nor sex ($\chi^2_1 = 3.71$, $p = 0.054$) significantly affected feeding time. There was also no effect of body size or body condition on the time spent feeding (all $p > 0.1$). Boldness, dominance, body condition and sex did not affect the order of arrival at the food patch (all $p > 0.1$), while larger individuals arrived earlier than smaller individuals ($\chi^2_1 = 4.02$, $p = 0.045$). Boldness, dominance, body condition and body size did not affect the number of different sods visited (all $p > 0.1$), while males visited more sods than females ($\chi^2_1 = 8.36$, $p = 0.004$).

To test for individual consistency in foraging tactic use throughout the experiment we calculated the average joining proportion for each individual for the first half of the experiment (day 1–7) and for the second half of the experiment (day 8–14). There was a strong positive

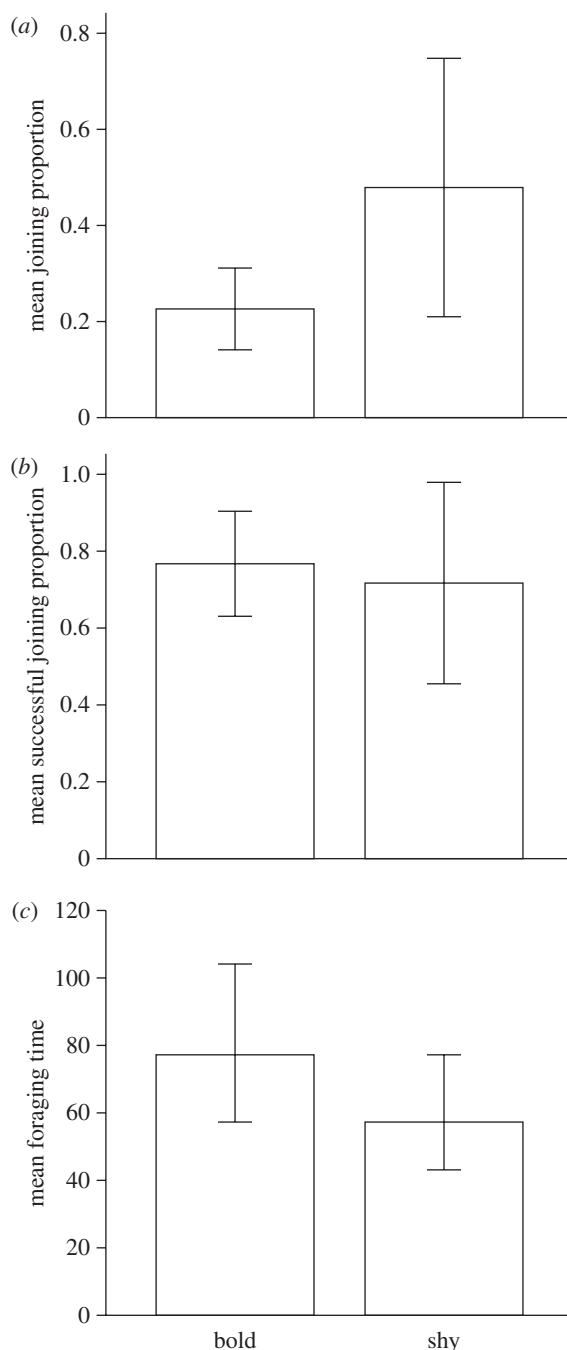


Figure 3. The effect of difference in boldness on (a) proportion of joining; (b) proportion of successful joining events; and (c) feeding time. Shown are means (a,b) and backtransformed means (c) \pm 95% confidence intervals. Bold individuals: $n = 7$; shy individuals: $n = 7$.

correlation between the results from the first and second half of the experiment ($r = 0.93$, $p < 0.001$) indicating that individuals were consistent in their foraging tactic use.

4. DISCUSSION

Consistent with our hypothesis, we found that individuals classified as 'shy' showed a higher proportion of joining than bold individuals suggesting that personality affects scrounging behaviour. We did not find an effect of boldness on the order of arrival at the food patch or the number of different sods visited indicating that shy

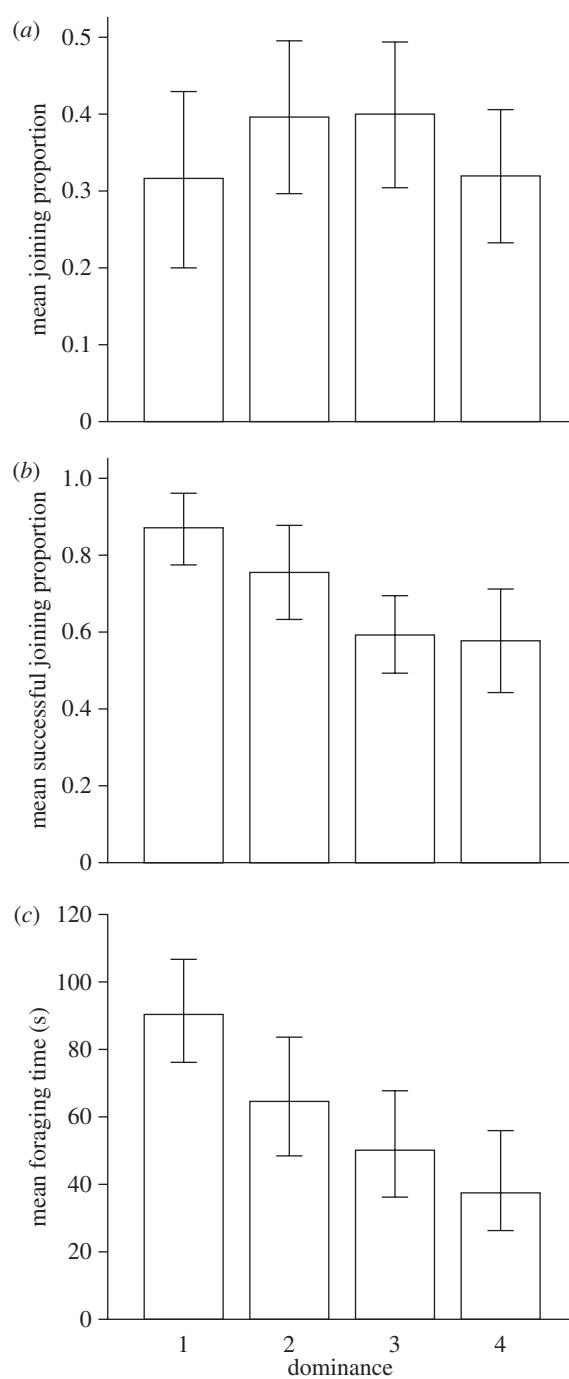


Figure 4. The effect of dominance on (a) proportion of joining; (b) proportion of successful joining events; and (c) feeding time. Shown are means (a,b) and backtransformed means (c) $\pm 95\%$ confidence intervals. 1 = most dominant; 4 = most subordinate.

individuals were not more reluctant than bold individuals to approach the feeding area or to move between patches. The positive correlation between an individual's joining proportion in the first and second half of the experiment indicates that individuals were consistent in their foraging tactic use. Additionally, we had already found a relationship between personality and social foraging tactic in two different contexts: in an experiment on movement order towards a food source we found that bold individuals led more often than shy individuals and that shy individuals followed more often (Kurvers *et al.* 2009). Another experiment on the use of social foraging cues revealed

that shy individuals made more use of social foraging cues (Kurvers *et al.* in preparation). These observations indicate that personality in barnacle geese is important in foraging tactic use under different conditions.

We propose two possible mechanisms which can explain the correlation between boldness and scrounging. Firstly, bolder individuals can be more active in exploring the environment, which is confirmed by the observation that bolder individuals are more often in the leading edge of moving groups (Beauchamp 2000; Harcourt *et al.* 2009; Kurvers *et al.* 2009; Schuett & Dall 2009). Animals occupying the front positions in a foraging group are also the first to discover new food patches. A second mechanism may be that shy individuals have a higher tendency to stay close to conspecifics. The tendency to stay close to conspecifics is termed 'sociability', and although the relation between sociability and boldness is not well understood, Cote *et al.* (2008) showed that boldness and sociability were positively correlated in common lizards (*Lacerta vivipara*). In groups of foraging sheep it has been demonstrated that shy individuals show a lower tendency to split into smaller subgroups than bold individuals (Michelena *et al.* 2008) and in fish shy individuals have a higher shoaling tendency (Budaev 1997; Ward *et al.* 2004; Dyer *et al.* 2008). If it is true that shyer individuals stay closer to conspecifics, they may also be able to make more use of the scrounging tactic: by being closer to companions, the travel costs are reduced (Beauchamp 2008) and this might increase scrounging since patches are less likely to be empty when scroungers join.

We do not know yet if shy individuals invest more in acquiring social information than bold individuals or whether their higher frequency of joining is merely a by-product of their less reactive behaviour. It would be interesting to perform a test in which different personality types are given the opportunity to observe social information, without any prior information of the environment, and to see if in such a situation shy individuals indeed make more use of social information than bold individuals. An additional improvement to our design would be to score the actual time investments of individuals/tactic use, i.e. producing or scrounging. We only observed the outcomes of time investments (i.e. finding or joining). In spice finches, *Lonchura punctulata*, the head position is an indicator of the tactic an individual follows (Coolen *et al.* 2001). By directly observing the time investments of different personality types it would be possible to learn if shy individuals indeed spend more time in obtaining social information.

If individuals are all equal and entirely flexible in their tactic use one expects there to be no difference in foraging success between individuals, since individuals can change their tactic freely if its current tactic results in a sub-optimal foraging success. However, the foraging success for individuals that are not equal (e.g. in terms of searching efficiency or competitive ability) might differ. Ranta *et al.* (1996), in their model on producer-scrounger games, included two phenotypes differing in their ability to search for food patches and to compete for food. Their model predicted that in a situation where the patch-finder gets some of the discovered food before arrival of the other competitors, the intake rate of the two phenotypes would be unequal except in two cases;

that is, when producers do all or a disproportionately large share of the searching, and when the scroungers are the better competitors. Neither condition was met in our experiment. Shy individuals also frequently found their food (>50%) and most likely did not differ in competitive abilities since there was no difference between shy and bold individuals in dominance score. Food finders in our experiment clearly got some of the food before arrival of competitors since the consumption of grass requires only a short handling time (Durant *et al.* 2003). Bold and shy individuals consistently differed in their foraging strategies in our experiment suggesting that they were unequal. We found a borderline significant difference in feeding time between bold and shy individuals suggesting that the foraging success for both types indeed could be different although this result has to be treated with care. Most models of producer–scrounger games generally assume that individuals are equal and that foraging payoffs are independent of phenotype. Although individual tactic use in producer–scrounger games is indeed partly flexible and dependent on hunger level (Lendvai *et al.* 2004), dominance (Liker & Barta 2002) and predation risk (Mathot & Giraldeau 2008), it is more likely that the tactic followed is a combination between consistency and flexibility (Beauchamp 2001). Beauchamp (2006) have already shown that scrounging is related to individual foraging efficiency providing evidence for consistency in scrounging behaviour. Our observation that personality affects tactics use and the many recent examples of the presence of personality in a wide variety of species questions the general applicability of these models and stresses the need to take individual behavioural differences into account in modelling producer–scrounger games (see for example Ranta *et al.* 1996).

Recently, several studies have looked at various aspects of animal personality and their ecological consequences (e.g. Cote *et al.* 2008). However, the processes of the evolution of difference in personality traits and the maintenance of these traits in a population are largely unknown. Several mechanisms have been suggested such as frequency-dependent selection and spatio-temporal variation in environmental conditions (Dall *et al.* 2004; Dingemanse *et al.* 2004; Smith & Blumstein 2008). Recently, it has been suggested that the trade-offs between life-history traits could explain the evolution of personality traits (Wolf *et al.* 2007). Variation in boldness is believed to be a result of predation (Bell & Sih 2007) and it has been suggested that in the absence of predation, the costs of boldness are likely to disappear (Cote *et al.* 2008). In this scenario there is a trade-off between, for example, food intake rate and predation risk, with bold individuals enjoying a higher food intake rate but also a higher risk of being predated. A positive correlation between boldness and food intake rate has indeed been reported in several species (Biro & Stamps 2008). Our results seem to support this, since bold individuals spent more time feeding than shy individuals although this difference was at borderline significance. Similar foraging success is another possible mechanism for the maintenance of boldness differences. In a population of only bold individuals which all tend to act as producers, a shy individual would probably do better than a bold individual as they rely more on the scrounging tactic. As the number of shy individuals in the population

grows, the difference in success between the shy and bold individuals will probably decrease up to a certain point where both personality types perform equally. In such a scenario, the producer–scrounger context might maintain differences in boldness in a population with an underlying frequency-dependent selection process. In sparrow finches the intake rate of the scrounger tactic indeed decreased with increasing scrounging frequency, whereas there was little effect on the intake rate of the producer tactic, providing experimental evidence for a negative frequency-dependence of scrounger payoff on scrounger frequency (Mottley & Giraldeau 2000).

Our results have implications for producer–scrounger foraging dynamics since our results suggest that individuals form disassortative groups consisting of a mix of bold (producers) and shy (scroungers) individuals. Ranta *et al.* (1996) modelled the group-formation process of two phenotypes (producers and scroungers) and concluded that the foraging alliance of the two phenotypes was unstable. It is in the interest of producing animals to get rid of as many scroungers as possible because this increases their foraging gain. Interestingly, Dyer *et al.* (2008) showed that in guppies, *Poecilia reticulata*, more fish fed in mixed shoals (consisting of bold and shy individuals) in a novel foraging environment than shoals consisting of only bold individuals or shy individuals. This suggests that there might also be benefits for bold individuals to shoal with shy individuals. Possibly bold individuals profit from the presence of shy individuals because of their increased caution and vigilance (Dyer *et al.* 2008). There is a general lack of understanding of whether personality is an important factor in group-formation processes in wild populations and this is a field of research which deserves more attention.

We found no difference between bold and shy individuals in dominance rank, which agreed with our earlier finding that in barnacle geese there is no relationship between the novel object score (i.e. boldness) and dominance (Kurvers *et al.* 2009). We found no effect of dominance on the proportion of joining, though dominant individuals had a higher proportion of successful joining than subordinate individuals (figure 4b). A higher percentage of scrounging for dominant individuals is a well-described phenomenon (Liker & Barta 2002; McCormack *et al.* 2007; but see Lendvai *et al.* 2006). Studies on producer–scrounger games do not always differentiate between successful and unsuccessful joining events. Our study demonstrates that it can be important to distinguish between both, especially if one wants to understand differences in foraging success. We expected that dominant individuals, as a result of a higher proportion of successful joining events, also had a longer feeding time. However, we found only a tendency for more dominant individuals to have longer feeding times. Possibly subordinate individuals had ample opportunities to search for food at different pots. In barnacle geese in the field it has been demonstrated that subordinate individuals are the first to arrive at new food patches, and that dominant individuals use this information produced by subordinates (Stahl *et al.* 2001). Our results do not agree with this finding since dominance did not affect the proportion of joining, although dominant individuals had a higher proportion of successful joining indicating that they were better competitors.

To summarize, we have demonstrated that shy individuals exhibit a higher proportion of joining when compared with bold individuals. Bold individuals tend to have a longer feeding time than shy individuals. Although dominance did not predict the overall use of tactic, dominant individuals had a higher proportion of successful joining than subordinates. Our results highlight the importance of including individual behavioural variation in models of producer–scrounger games.

All animal experiments have been approved by the Animal Ethical Committee ('Dier Experimenten Commissie') of both the Royal Netherlands Academy of Arts and Sciences (KNAW) and the Wageningen University (protocol number 2008107.a).

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