

Original Article

# No evidence for negative frequency-dependent feeding performance in relation to personality

Ralf H.J.M. Kurvers,<sup>a</sup> Simone I. van Santen de Hoog,<sup>a</sup> Sipke E. van Wieren,<sup>a</sup> Ronald C. Ydenberg,<sup>a,b</sup> and Herbert H.T. Prins<sup>a</sup>

<sup>a</sup>Centre for Ecosystem Studies, Resource Ecology Group, Wageningen University, Droevendaalsesteeg 3a, 6708 PB Wageningen, The Netherlands and <sup>b</sup>Department of Biological Sciences, Evolutionary and Behavioural Ecology Research Group, Simon Fraser University, 8888 University Drive, Burnaby, Vancouver, V5A 1S6 Canada

An increasing number of studies report the presence of consistent individual differences in behavior and/or physiology over time and context, known as animal personality. A pivotal question in animal personality research concerns the mechanism(s) responsible for its evolution and maintenance. Negative frequency-dependent selection is considered to be one of these important mechanisms, although evidence for this is largely absent. Here, we studied whether the feeding performance of barnacle geese was negative frequency-dependent in a producer–scrounger game. We studied the feeding time of one bold or one shy individual in groups consisting of only bold or shy companions to study if the rare type in the group performs best. A previous study with this species showed that scrounging increased with shyness. Hence, we expected shy individuals to do better in the presence of bold companions due to the increased scrounging opportunity and bold individuals to do better in the presence of shy companions as there were ample opportunities to produce food. We found no evidence for negative frequency-dependent feeding success; rather, we found that, independent of their boldness score, all individuals enjoyed higher feeding success when foraging with bold than with shy companions. The higher foraging success of individuals foraging with bold companions is explained by a higher joining proportion in the presence of bold companions. Our results provide no evidence for negative frequency-dependent feeding success in barnacle geese but indicate that both bold and shy individuals can increase their foraging returns by associating with bold individuals. *Key words*: barnacle goose, boldness, foraging strategy, negative frequency-dependent selection, personality, producer–scrounger game. [*Behav Ecol* 23:51–57 (2012)]

## INTRODUCTION

Personality in animal behavior describes the phenomenon that differences between individuals in behavioral and physiological traits are consistent over time and context (Gosling and John 1999; Koolhaas et al. 1999; Carere and Eens 2005; Groothuis and Carere 2005). Different behavioral and physiological reactions have a genetic basis (van Oers, de Jong, et al. 2005) and are often correlated. This suggests that these differences are fundamental aspects of the behavioral organization of individuals. One of the pivotal questions in animal personality is the evolution and maintenance of animal personality. Several (non-mutually exclusive) mechanisms have been suggested, such as spatiotemporal variation in environmental conditions (Sih et al. 2003; Dall et al. 2004; Dingemanse et al. 2004; Smith and Blumstein 2008; Réale et al. 2010), differences in life-history trade-offs (Wolf et al. 2007; Gyuris et al. 2010; see also Biro and Stamps 2008; Réale et al. 2009), and sexual selection (Schuett et al. 2010). A fourth mechanism is negative frequency-dependent selection (Wolf et al. 2008). Negative frequency-dependent selection operates against common phenotypes, thereby favoring the rarer phenotype in a population. The rarer phenotype, for example, suffers less from predation. Negative frequency-dependent selection is used in

many areas of evolutionary biology (Maynard Smith 1982) and is predicted to be important in generating variation in personality (Sih et al. 2004; Réale et al. 2007; Wolf et al. 2008; Wolf and Weissing 2010).

Empirical evidence for a role of negative frequency-dependent selection in animal personality is, however, largely absent. In *Drosophila melanogaster*, there are 2 larval foraging types: rovers or sitters, depending on the allele frequency in the foraging gene. Although this is strictly speaking not a personality trait, Fitzpatrick et al. (2007) showed that under nutrient poor conditions, the rarer foraging type had a higher proportion of larvae that survived to pupation, providing evidence for negative frequency-dependent selection. Here, we studied the foraging success of individual barnacle geese, differing in boldness score, in groups of either all bold companions or all shy companions in a producer–scrounger game, to study if there is evidence for negative frequency-dependent feeding performance. Negative frequency-dependent feeding performance can open up the possibility for (but need not necessarily lead to) negative frequency-dependent selection. In a producer–scrounger game, individuals either search for food themselves (producing) or join food discoveries of other individuals (scrounging). The producer–scrounger game (Barnard and Sibly 1981) is characterized by negative frequency dependence of the scrounger tactic because the value of scrounging decreases with an increase in the proportion of scrounging tactic in the population (Giraldeau et al. 1994; Mottley and Giraldeau 2000). Payoffs of the producing tactic can be negatively, positively, or not frequency-dependent (Giraldeau and Dubois 2008).

Address correspondence to R.H.J.M. Kurvers. E-mail: ralf.kurvers@wur.nl.

Received 3 March 2011; revised 12 July 2011; accepted 28 July 2011.

In the current experiment, individuals were classified as shy or bold based on novel object tests. Then, we formed companion groups consisting of either bold or shy individuals and introduced these groups together with one focal individual (either bold or shy) in a producer–scrounger game and scored the foraging tactic and foraging success of the focal individual. We measured and controlled for a potential effect of dominance. An earlier study in barnacle geese (Kurvers, Prins, et al. 2010) showed that shy individuals had a higher frequency of joining than bold individuals, indicating that bold individuals rely more on the producing tactic, whereas shy individuals rely more on the scrounging tactic (see also Kurvers, van Oers, et al. 2010). Therefore, we expected in a situation with only bold companions that a shy individual would do better than a bold individual because it could profit more from the food discoveries of its bold companions due to its increased reliance on scrounging. In a situation with only shy companions, we expected a bold individual to do better than a shy individual because there was ample opportunity to produce food, as there was a low rate of producing patches by conspecifics.

## MATERIALS AND METHODS

### Study subjects

We used captive-born wing-clipped barnacle geese, each fitted with a uniquely coded leg ring for identification ( $n = 44$ , 20 females, 24 males). We measured tarsus and culmen length (to the closest 0.1 mm) using calipers 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 (PCs) analysis of tarsus, culmen, and wing lengths to derive a measure of body size. PC1 explained 79.8% 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 by 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 by 1 m) was present in the aviary, with continuous flowing water for bathing and drinking.

### Novel object test

We assessed the boldness level of individuals by performing novel object tests (see for details, Kurvers et al. 2009). We habituated individuals to an experimental arena ( $9 \times 3$  m). After habituation, we placed a novel object in the middle of the arena, introduced each goose for 10 min, and scored the minimal distance reached between the goose and the novel object as well as the approach latency (defined as the time elapsed before the goose came within 50 cm of the novel object). Each individual was tested twice in November or December 2008 (see Kurvers et al. 2009; Kurvers, Prins, et al. 2010). We calculated PCs of the test variables for each test as the novel object score. Including all individuals, PC1 explained 87% and 90% of the variation for test 1 and test 2, respectively. The correlations of both the minimal distance and the approach latency with PC1 were negative, implying that high values of PC1 correspond to bolder individuals. We determined the repeatability of the novel object test by calculating the mean squares from a one-way analysis of variance with individual as the main effect. Repeatability was calculated following Lessells and Boag (1987) and its standard error (SE) following Becker (1984). Repeatability of novel object score

was high (rep  $\pm$  SE =  $0.81 \pm 0.05$ ,  $n = 44$ ) indicating that individuals differed consistently in their boldness scores.

We ranked all individuals based on the average of the 2 novel object tests and selected the 14 boldest and 14 shyest individuals for the social foraging experiment (see below). All other individuals were housed in another compartment. Because the novel object tests took place (November–December 2008) approximately 1 year prior to the social foraging experiment (December 2009), we repeated the novel object tests 1 year after the social foraging experiment (November–December 2010) to confirm that boldness levels were consistent, which they were (repeatability score over all 4 tests:  $0.61 \pm 0.07$ ,  $n = 44$ ). For the final analysis, we used as boldness score for the focal individuals the average of all 4 novel object tests, which is probably the most adequate reflection of the boldness level during the social foraging experiment.

### Dominance

Prior to the social foraging experiment, we scored agonistic interactions within the flock of the 28 selected individuals (7–11 December 2009). We identified the participants of each interaction and scored the behavior each used. We considered an interaction as being won by an individual when the opponent turned and walked or ran away (Stahl, Tolsma, et al. 2001). In total, we scored 617 interactions (mean number per individual: 44; range: 10–110 interactions). We constructed a dominance matrix (using Matman 1.1; Noldus Information Technology, Wageningen, The Netherlands) because this takes into account the identity of each opponent and all the interactions and is built in such a way that the number of contests won by individuals lower in rank are minimized. The Kendall's coefficient of linearity ( $K = 0.32$ ,  $\chi^2 = 101.9$ ,  $P < 0.001$ ), Landau's index  $h$  ( $h = 0.33$ ), and the corrected index of linearity  $h'$  ( $h' = 0.37$ ,  $P < 0.001$ ) allowed the use of a linear order to rank individuals. In barnacle geese, dominance positively affected the proportion of successful joining (i.e., the chance that a joining attempt is successful), and dominance had a nonsignificant tendency to affect feeding time in an earlier producer–scrounger experiment (Kurvers, Prins, et al. 2010). To avoid a possible confounding effect of dominance on tactic use and feeding time (see also Stahl, Tolsma, et al. 2001), we used the dominance rank to assign individuals to either the companion group or the focal group during the social foraging experiment (see below).

### Social foraging experiment

The experimental arena consisted of an arena of  $5.5 \times 11$  m. The floor was covered with anti-root cloth, and we placed 99 flowerpots (height: 20 cm, diameter opening: 22 cm) equidistantly at 55 cm on the anti-root cloth. Flowerpots were empty or contained a  $5 \times 5$  sod of perennial ryegrass (*Lolium perenne*), cut to a height of 1 cm. This grass is an important food source of wild barnacle geese (Prins and Ydenberg 1985). We fastened the sod into the ground using a long nail stuck through the sod and pot.

To habituate the individuals to the experimental conditions, we supplied half of the pots with grass and introduced all geese as one group in the experimental arena. Thereafter, we gradually decreased the group size and the number of pots filled. Prior to the start of the experiment, all individuals had been introduced 6 times in the experimental arena. During experimental trials, we filled 9 randomly chosen pots with a sod of grass ("food"). Sodds were replaced after each trial if grazed on.

We used the 8 most dominant individuals from the bold and shy group as focal individuals ( $n = 16$ ). The remaining 6 individuals from the bold and shy group were used as companion animals ( $n = 12$ ). This assured that focal individuals were dominant over companion individuals, thereby excluding a potential effect of dominance on foraging tactic and feeding time. We formed 4 companion groups consisting of either 3 shy or 3 bold individuals. Companion group composition was randomized throughout the experiment to avoid strong habituation patterns between members of companion groups. Companion animals were used twice a day, and focal animals were used once per 2 days alternating between foraging in a bold or shy companion group. Each focal individual was tested 8 times, 4 times in a bold companion group, and 4 times in a shy companion group. We performed 8 trials per day resulting in a total of 128 trials performed in 16 days (16 December 2009–13 January 2010).

Each morning, the geese were placed in groups of 4 in smaller holding enclosures to facilitate transport between the outdoor enclosure and the experimental arena. Prior to a trial, the group of 4 geese was gently driven toward the wooden pen, which served as the entrance of the experimental arena. The group was held for 1 min in the wooden pen before being admitted to the arena for 10 min. All experiments were done between 9.00 and 13.00 h.

All trials were videotaped, and we scored the behavior of the focal individual from the recordings. Additionally, we scored the behavior of all companions to be able to quantify a possible difference between individuals in both companion groups. Feeding events were identified either as “finding” or “joining,” as we could not score the investment in tactic use directly (i.e., producing or scrounging, see also Coolen et al. 2001). 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). The number of unsuccessful joining was extremely low for the focal individuals ( $n = 3$  over all trials) reflecting that focal individuals were indeed dominant over companions. 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. 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.

### Statistical analysis

To test the effect of focal personality type and personality type of companions on focal tactic use, we used linear mixed effect models. For count data (i.e., number of findings and joinings), we used generalized linear mixed effect models (GLMMs) with Poisson distributions and a log-link function; for proportion data (i.e., joining proportion), we used GLMMs with binomial errors and a logit-link function. To analyze the effect on feeding time, 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 of the focal individual (continuous), boldness of the companion (bold or shy), body condition, body size, sex, and the interaction between boldness of the focal individual and boldness of the companion. A significant interaction would indicate that boldness of the focal individual had a different effect in the shy companion groups as compared with the bold companion groups, which could provide

evidence for negative frequency-dependent performance. We used similar statistical models to test the effect of the behavior of companion animals (i.e., number of findings and joinings) on focal tactic use (i.e., number of findings and joinings) and focal feeding time. To avoid pseudoreplication, we fitted focal individual as random effect in all models. We report full statistical models including estimates and SEs of all fixed factors. Significance levels of individual factors for GLMM were derived from the  $z$  values and associated  $P$  values. Significance levels of individual factors for general mixed models were derived by a Monte Carlo Markov Chain with 10 000 simulations using the package Language R. We used the package lme4 (Bates and Sarkar 2007) for GLMM procedures and nlme (Pinheiro et al. 2011) for general mixed models procedures in R (version 2.11.1, R Development Core Team 2008). For all other calculations, we used SPSS (version 15.0).

## RESULTS

### Companion individuals

Bold companions had on average 2.6 finding and 0.7 joining events per individual per trial with an average joining proportion of 0.21. Shy individuals had on average 1.4 finding and 0.3 joining events and a joining proportion of 0.19. Bold companions fed on average 67 s per trial, whereas shy companions fed 35 s.

### Focal individuals

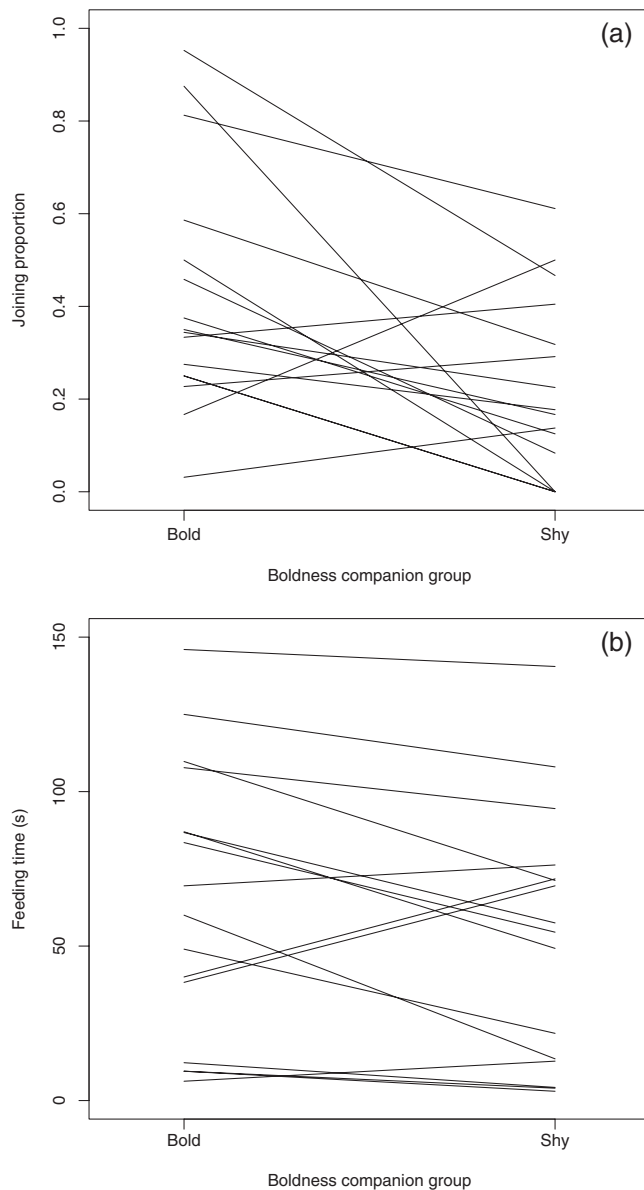
Focal individuals had a higher joining proportion in the presence of bold companions than in the presence of shy companions ( $z = -2.077$ ,  $P = 0.038$ , Table 1, Figure 1a), with the proportion being nearly twice as high (mean in bold group: 41.3%, in shy group: 21.9%). There was a tendency for shy individuals to have a higher joining proportion ( $z = -1.75$ ,  $P = 0.080$ , Figure 2). Body size, body condition, sex, and the interaction between boldness of the focal individual and the companion group did not affect the proportion of joining (Table 1).

Focal individuals had a higher feeding time in the bold companion groups (mean: 64.7 s) than in the shy companion groups (mean: 53.5 s) (Table 2, Figure 1b). Boldness of the focal individual did not affect its feeding time (Table 2) nor was there a significant interaction between boldness of the focal individual and boldness of the companion group (Table 2, Figure 3), indicating that there was no evidence that the rare type did better than the common type. There was no effect of body size, body condition, or sex on feeding time (Table 2). A post hoc power analysis of a linear regression using feeding time focal

**Table 1**  
Results of a generalized LMM analysis with the proportion of joining of the focal individual as response variable

	Estimate	SE	$z$ value	Pr(>  $z$  )
(Intercept)	-0.607	0.669	-0.908	0.364
Boldness focal	-0.424	0.242	-1.753	0.080
Sex	0.593	0.902	0.658	0.511
Body size	-0.569	0.415	-1.372	0.170
Body condition	-0.001	0.001	-0.598	0.550
Boldness companions	-0.964	0.464	-2.077	<b>0.038</b>
Focal $\times$ companions	-0.240	0.463	-0.518	0.605

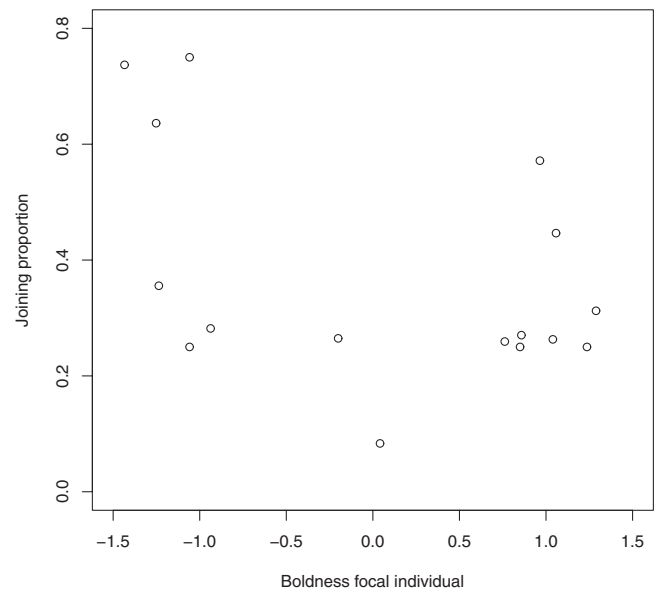
Focal  $\times$  companions represents the interaction between boldness score of the focal individual and boldness score of the companion group. Significant terms are given in bold.



**Figure 1** Focal individuals had (a) a higher proportion of joining and (b) a higher feeding time when foraging in a group with bold companions than when foraging in a group with shy companions.

individual as dependent and boldness score of the focal individual as independent variable, split per boldness type of the companion group (see also Figure 3), revealed that the power was low (0.06 and 0.05, respectively), therefore, we have to treat these data with care.

Focal individuals had more joining events in bold companion groups (mean: 1.34 events) than in shy companion groups (mean: 0.73 events) ( $z = -3.40$ ,  $P = 0.001$ , Table 1 in Supplementary Material, Supplementary Appendix 1). There was no effect of the boldness of the focal individual ( $z = -1.32$ ,  $P = 0.19$ ) nor was the interaction between boldness of the focal individual and boldness of the companion group significant ( $z = -1.15$ ,  $P = 0.25$ , Table 1 in Supplementary Material, Supplementary Appendix 1). Males joined more than females ( $z = 2.02$ ,  $P = 0.044$ ), but there was no effect of body size or body condition (Table 1 in Supplementary Material, Supplementary Appendix 1).



**Figure 2** There was a tendency for bolder individuals to have a lower joining proportion ( $P = 0.080$ ).

There was no effect of the boldness of the companion groups or the boldness of the focal individuals on the number of finding events of the focal individuals nor was the interaction between boldness of the focal individual and boldness of the companion group significant (Table 2 in Supplementary Material, Supplementary Appendix 1). Males found more than females ( $z = 2.27$ ,  $P = 0.023$ ), but there was no effect of body size (Table 2 in Supplementary Material, Supplementary Appendix 1).

The number of finding events of companion animals positively affected the number of joining events of the focal individual ( $z = 4.53$ ,  $P < 0.001$ ) as well as its feeding time ( $P = 0.001$ ) but not its number of finding events ( $z = 0.77$ ,  $P = 0.44$ , Supplementary Material, Supplementary Appendix 2). The number of joining events of the companions did not affect the number of finding events, joining events, or the feeding time of the focal individual (Supplementary Material, Supplementary Appendix 2).

## DISCUSSION

Our results demonstrate that the boldness level of the companion individuals affected the foraging tactic and feeding success of focal individuals: focal individuals, independent of their own personality type, had a higher joining proportion and feeding time in the presence of bold companions as compared with shy companions. There was no effect of boldness of the focal individual on its feeding time, and there was only a weak tendency for shyer individuals to have a higher joining proportion ( $P = 0.080$ ).

In many species, a positive correlation between boldness and food intake rates has been reported (see for a review, Biro and Stamps 2008). Although we did not find a significant effect of boldness of the focal individual on feeding time, we did demonstrate that individuals profit from the presence of bold individuals because they increased their feeding time in bold companion groups as compared with shy companion groups. To the best of our knowledge, this is the first demonstration that individuals have higher foraging success in the presence of bolder individuals. The mechanism of increased feeding time is most likely due to the increased opportunity to

**Table 2**  
**Results of a general LMM analysis with feeding time of the focal individual as response variable**

	Estimate	MCMCmeanHP	D95lower	HPD95upper	pMCMC	Pr (> d )
(Intercept)	2.025	2.024	0.787	3.224	0.003	0.012
Boldness focal	0.048	0.048	-0.459	0.576	0.852	0.885
Sex	1.850	1.853	0.108	3.636	0.040	0.109
Body size	0.111	0.109	-0.693	1.006	0.787	0.842
Body condition	0.001	0.001	-0.001	0.003	0.408	0.524
Boldness companions	-0.568	-0.572	-1.025	-0.122	0.018	<b>0.010</b>
Focal × companions	-0.256	-0.255	-0.695	0.194	0.265	0.233

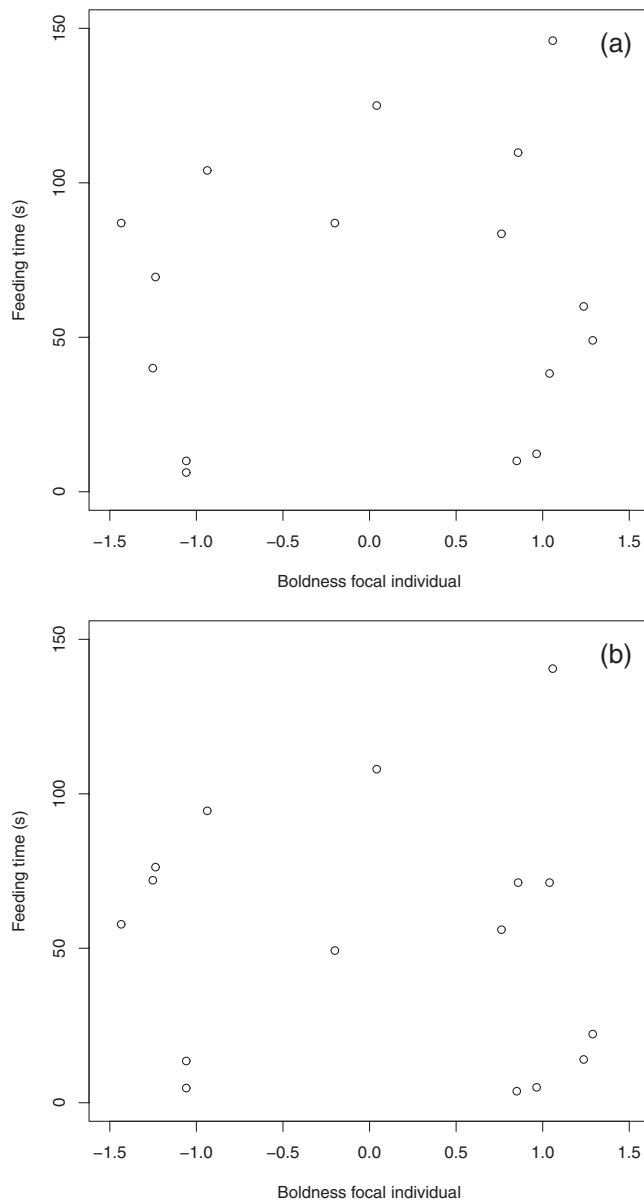
Focal × companions represents the interaction between boldness score of the focal individual and boldness score of the companion group. Significant terms are given in bold. *P* values were derived using a Monte Carlo Markov Chain (MCMC) with 10 000 simulations.

join food discoveries as illustrated by the higher number of joining events (and joining proportion) of focal individuals in the bold companion groups and the positive effect of the number of findings of the companions on the number of joining events of the focal individual. The number of finding events of the focal individuals, by contrast, was not affected by the personality type or the number of findings events of the companions. Our demonstration that associating with bold individuals offers foraging benefits, for bold and shy individuals, can help explain why there is a preference for individuals, regardless of personality or hunger state, to join groups consisting of bold individuals rather than groups of shy individuals, as illustrated in 3-spined sticklebacks, *Gasterosteus aculeatus* (Harcourt, Sweetman, et al. 2010).

In focal individuals, there was a weak tendency for shyer individuals to have a higher joining proportion ( $P = 0.080$ ), confirming an earlier found patterns in this species (Kurvers, Prins, et al. 2010). Several other studies suggest that personality traits determine producer–scrounger roles or social information use (Marchetti and Drent 2000; Dyer et al. 2008; Kurvers, van Oers, et al. 2010, but see Webster et al. 2007; Harcourt, Biau, et al. 2010a; for a review, see Webster and Ward 2011). Because shyer individuals were expected to use the scrounging tactic more often, they were expected to profit more from the presence of bold (producing) individuals than bolder individuals. However, this was not found because focal individuals, independent of their own boldness score, profited from the presence of bold companions (see Figure 1). This is not totally unsurprising because all individuals do use the scrounging tactic to some extent and therefore increase their feeding success when there are more opportunities to scrounge. As a result, we did not find evidence for negative frequency–dependent feeding success as outlined in the introduction, though the power of the test was low. Because we only tested the feeding performance under one food condition, we cannot yet generalize our conclusions. Numerous factors are known to affect scrounging frequency, including the cost of producing (Giraldeau et al. 1994; Beauchamp and Giraldeau 1997), patch richness (Giraldeau and Livoreil 1998; Coolen et al. 2001; Coolen 2002; Beauchamp 2008), group size (Barnard and Sibly 1981; Vickery et al. 1991; Coolen 2002), and predation risk (Mathot and Giraldeau 2008). All these factors shape the foraging payoffs, and it is possible that certain parameter combinations allow negative frequency–dependent feeding performance. A modeling exercise varying these parameters could elucidate this. Up to date, there have been few studies that manipulated group composition based on personality types to study the effect of group composition on individual fitness (but see Sih and Watters 2005; Dyer et al. 2008). Clearly, more experimental work is necessary in order to understand the ecological implications of personality types in group living animals and to answer the question if negative frequency dependence is an important factor for the maintenance of animal personality.

Although bold companion individuals seemed to have higher feeding rates and more finding events, there was no effect of the boldness score of the focal individual on its feeding time. This leads to the question to what extent individuals can express their personality when they are in groups of different personality types. It is known that in this (Kurvers et al. 2009) and other species (Magnhagen and Staffan 2005; van Oers, Klunder, et al. 2005; Harcourt et al. 2009; Magnhagen and Bunnefeld 2009; Schuett and Dall 2009), individuals are affected in their behavior by the personality of companions (see also Webster and Ward 2011 for a review). In pairs of barnacle geese, the arrival time at a food patch depends on the personality type of the companion, with individuals arriving quicker in the presence of bold companions (Kurvers et al. 2009). Therefore, we can speculate that perhaps focal individuals were highly affected by the personality type of their companions in their feeding time. In addition, differences in boldness might relate to differences in plasticity. There is a recent interest in differences in plasticity (or responsiveness) as a mechanism to explain variation in animal personality (Wolf et al. 2011). Morand-Ferron et al. (2011) tested the same individuals under different food conditions in a producer–scrounger game and found significant individual differences in plasticity. These individual differences were consistent over a period of 6 months. Our study was not designed to specifically test for potential differences in behavioral plasticity but the observation that both bold and shy focal individuals increased their scrounging frequency in bold companion groups suggest that there is not a direct link between boldness level and level of plasticity. A related issue is to what extent the focal individuals changed their time investment in producing and scrounging tactic between both companion groups. Though focal individuals joined more in bold companions groups, this does not necessarily mean that they also invested more time in searching for joining opportunities because we did not directly measure time investments (see Coolen et al. 2001). We predict that focal individuals in the bold companion groups increased their investment in searching for joining opportunities because an increase in the number of producers or producing events should increase the scrounging frequency (Vickery et al. 1991).

Our results suggest that it is better to join bold individuals than shy individuals to increase feeding time. This confirms earlier observations that bolder individuals approach food sources quicker (Beauchamp 2000; Dyer et al. 2008; Harcourt et al. 2009; Kurvers et al. 2009; Schuett and Dall 2009), thereby offering potential foraging benefits for their companions. Dyer et al. (2008) suggest that it can also be beneficial for individuals to join shy individuals because the increased vigilance behavior of shy individuals can have antipredator benefits. This would suggest that in risky areas, it is more beneficial to join shy individuals, whereas in low risk areas, it is better to join bold individuals. This hypothesis awaits



**Figure 3**  
Boldness level of the focal individual did not affect its feeding time in the presence of (a) bold companions or (b) shy companions. There was no significant interaction between boldness of the focal individual and boldness of the companion group.

empirical scrutiny. An intriguing question is whether barnacle geese are able to discriminate between different boldness types. Drent and Swierstra (1977) showed that groups of artificial geese models can attract wild barnacle geese and that groups containing a higher percentage of geese models with their head down (“grazing”) were more attractive than groups containing a higher percentage of geese models with their head up (“vigilant”). If boldness corresponds to differences in vigilance behavior, then this could be a potential mechanism how searching individuals can use the boldness of other individuals in patch choice decisions. Next to boldness, other factors might play a role in the decision to join or leave a foraging flock in a natural environment. Stahl, Drent, et al. (2001) showed that family status predicts how frequently barnacle geese switch between foraging groups. Paired geese with young change less often between foraging groups than paired

geese without young and unpaired individuals change most frequently. Most likely unpaired geese are outcompeted because they have a lower dominance status than paired geese (Stahl, Tolsma, et al. 2001) and will therefore suffer more from resource depletion. Rowcliffe et al. (2004) showed that the most successful foragers in barnacle geese flocks were largely unaffected by resource depletion over time, whereas the least successful foragers experienced severe depletion. Thus, most likely in a natural situation, dominance interacts with family status causing unpaired subordinate birds to leave foraging groups quicker and search for new food opportunities. In our experiment, family status was not important because there were no pair bonds and no parent–offspring relationships. Furthermore, dominance was controlled for by assuring that all focal individuals were dominant over all companion group members.

To conclude, we showed that individuals, independent of their own boldness score, enjoyed higher feeding success when foraging with bold companions than when foraging with shy companions. Individuals foraging with bold companions had a higher number of joining events and a higher joining proportion than when foraging with shy companions explaining their higher foraging success. Our results provide no evidence for negative frequency-dependent performance of personality types because all individuals performed better when foraging with bold companions.

#### SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>.

#### FUNDING

Faunafonds and Koninklijke Nederlandse Jagers Vereniging (KNJV).

We thank Kees van Oers, Bonne Beerda, and Bart Nolet for helpful comments on the experimental design and Kees van Oers, Candy Rowe, and 2 anonymous reviewers for helpful comments on the manuscript. We thank Bart van Lith for his assistance during the experiments. We thank Jan Baar and Chantal Althuisen for conducting the second personality tests. 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 2009111.a).

#### REFERENCES

- Barnard CJ, Sibly RM. 1981. Producers and scroungers—a general model and its application to captive flocks of house sparrows. *Anim Behav.* 29:543–550.
- Bates D, Sarkar D. 2007. lme4: linear mixed-effects models using Eigen and syntax. R package version 0.9975-13. [cited 2011 May 24]. <http://CRAN.R-project.org/>.
- Beauchamp G. 2000. Individual differences in activity and exploration influence leadership in pairs of foraging zebra finches. *Behaviour.* 137:301–314.
- Beauchamp G. 2008. A spatial model of producing and scrounging. *Anim Behav.* 76:1935–1942.
- Beauchamp G, Giraldeau LA. 1997. Patch exploitation in a producer–scrounger system: test of a hypothesis using flocks of spice finches (*Lonchura punctulata*). *Behav Ecol.* 8:54–59.
- Becker WA. 1984. *Manual of quantitative genetics*. 4th ed. Pullman (WA): Academic Enterprises.
- Biro PA, Stamps JA. 2008. Are animal personality traits linked to life-history productivity? *Trends Ecol Evol.* 23:361–368.
- Carere C, Eens M. 2005. Unravelling animal personalities: how and why individuals consistently differ. *Behaviour.* 142:1149–1157.

- Coolen I. 2002. Increasing foraging group size increases scrounger use and reduces searching efficiency in nutmeg mannikins (*Lonchura punctulata*). *Behav Ecol Sociobiol.* 52:232–238.
- Coolen I, Giraldeau LA, Lavoie M. 2001. Head position as an indicator of producer and scrounger tactics in a ground-feeding bird. *Anim Behav.* 61:895–903.
- Dall SRX, Houston AI, McNamara JM. 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecol Lett.* 7:734–739.
- Dingemanse NJ, Both C, Drent PJ, Tinbergen JM. 2004. Fitness consequences of avian personalities in a fluctuating environment. *Proc R Soc Lond B Biol Sci.* 271:847–852.
- Drent RH, Swierstra P. 1977. Goose flocks and food finding: field experiments with Barnacle geese in winter. *Wildfowl.* 28:15–20.
- Dyer JRG, Croft DP, Morrell IJ, Krause J. 2008. Shoal composition determines foraging success in the guppy. *Behav Ecol.* 20:165–171.
- Fitzpatrick MJ, Feder E, Rowe L, Sokolowski MB. 2007. Maintaining a behaviour polymorphism by frequency-dependent selection on a single gene. *Nature.* 447:210–215.
- Giraldeau LA, Dubois F. 2008. Social foraging and the study of exploitative behavior. *Adv Study Behav.* 38:59–104.
- Giraldeau LA, Livoreil B. 1998. Game theory and social foraging. In: Dugatkin LA, Reeve HK, editors. *Game theory and animal behavior*. New York: Oxford University Press. p. 16–37.
- Giraldeau LA, Soos C, Beauchamp G. 1994. A test of the producer-scrounger foraging game in captive flocks of spice finches, *Lonchura punctulata*. *Behav Ecol Sociobiol.* 34:251–256.
- Gosling SD, John OP. 1999. Personality dimensions in nonhuman animals: a cross-species review. *Curr Dir Psychol Sci.* 8:69–75.
- Groothuis TGG, Carere C. 2005. Avian personalities: characterization and epigenesis. *Neurosci Biobehav Rev.* 29:137–150.
- Gyuris E, Feró O, Tartally A, Barta Z. 2010. Individual behaviour in firebugs (*Pyrhocoris apterus*). *Proc R Soc Lond B Biol Sci.* 278:628–633.
- Harcourt JL, Ang TZ, Sweetman G, Johnstone RA, Manica A. 2009. Social feedback and the emergence of leaders and followers. *Curr Biol.* 19:248–252.
- Harcourt JL, Biau S, Johnstone R, Manica A. 2010. Boldness and information use in three-spined sticklebacks. *Ethology.* 116:440–447.
- Harcourt JL, Sweetman G, Johnstone RA, Manica A. 2010. Personality counts: the effect of boldness on shoal choice in three-spined sticklebacks. *Anim Behav.* 77:1501–1505.
- Koolhaas JM, Korte SM, De Boer SE, Van der Vegt BJ, Van Reenen CG, Hopster H, De Jong IC, Ruis MAW, Blokhuis HJ. 1999. Coping styles in animals: current status in behavior and stress-physiology. *Neurosci Biobehav Rev.* 23:925–935.
- Kurvers RHJM, Eijkelenkamp B, van Oers K, van Lith B, van Wieren SE, Ydenberg RC, Prins HHT. 2009. Personality differences explain leadership in barnacle geese. *Anim Behav.* 78:447–453.
- Kurvers RHJM, van Oers K, Nolet BA, Jonker RM, van Wieren SE, Prins HHT, Ydenberg RC. 2010. Personality predicts the use of social information. *Ecol Lett.* 13:829–837.
- Kurvers RHJM, Prins HHT, van Wieren SE, van Oers K, Nolet BA, Ydenberg RC. 2010. The effect of personality on social foraging: shy barnacle geese scrounge more. *Proc R Soc Lond B Biol Sci.* 277:601–608.
- Lessells CM, Boag PT. 1987. Unrepeatable repeatabilities—a common mistake. *Auk.* 104:116–121.
- Magnhagen C, Bunnefeld N. 2009. Express your personality or go along with the group: what determines the behaviour of shoaling perch? *Proc R Soc Lond B Biol Sci.* 276:3369–3375.
- Magnhagen C, Staffan F. 2005. Is boldness affected by group composition in young-of-the-year perch (*Perca fluviatilis*)? *Behav Ecol Sociobiol.* 57:295–303.
- Marchetti C, Drent PJ. 2000. Individual differences in the use of social information in foraging by captive great tits. *Anim Behav.* 60:131–140.
- Mathot KJ, Giraldeau LA. 2008. Increasing vulnerability to predation increases preference for the scrounger foraging tactic. *Behav Ecol.* 19:131–138.
- Maynard Smith J. 1982. *Evolution and the theory of games*. Cambridge (UK): Cambridge University Press.
- Morand-Ferron J, Varennes E, Giraldeau LA. 2011. Individual differences in plasticity and sampling when playing behavioural games. *Proc R Soc Lond B Biol Sci.* 278:1223–1230.
- Mottley K, Giraldeau LA. 2000. Experimental evidence that group foragers can converge on predicted producer-scrounger equilibria. *Anim Behav.* 60:341–350.
- van Oers K, de Jong G, van Noordwijk AJ, Kempenaers B, Drent PJ. 2005. Contribution of genetics to the study of animal personalities: a review of case studies. *Behaviour.* 142:1185–1206.
- van Oers K, Klunder M, Drent PJ. 2005. Context dependence of personalities: risk-taking behavior in a social and a nonsocial situation. *Behav Ecol.* 16:716–723.
- Pinheiro J, Bates D, DebRoy S, Sarkar D. R Development Core Team. 2011. nlme: linear and nonlinear mixed effects models. R package version 3.1-101. [cited 2011 May 24] <http://CRAN.R-project.org/>.
- Prins HHT, Ydenberg RC. 1985. Vegetation growth and a seasonal habitat shift of the barnacle goose (*Branta leucopsis*). *Oecologia.* 66:122–125.
- R Development Core Team. 2008. R: a language and environment for statistical computing, R package version 2.11.1. [cited 2011 May 24]. Vienna (Austria): R Foundation for Statistical Computing. Available from: <http://www.R-project.org>.
- Réale D, Garant D, Humphries MM, Bergeron P, Careau V, Montiglio PO. 2010. Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philos Trans R Soc B Biol Sci.* 365:4051–4063.
- Réale D, Martin J, Coltman DW, Poissant J, Festa-Bianchet M. 2009. Male personality, life-history strategies and reproductive success in a promiscuous mammal. *J Evol Biol.* 22:1599–1607.
- Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ. 2007. Integrating animal temperament within ecology and evolution. *Biol Rev.* 82:291–318.
- Rowcliffe JM, Pettifor RA, Carbone C. 2004. Foraging inequalities in large groups: quantifying depletion experienced by individuals in goose flocks. *J Anim Ecol.* 73:97–108.
- Schuett W, Dall SRX. 2009. Sex differences, social context and personality in zebra finches, *Taeniopygia guttata*. *Anim Behav.* 77:1041–1050.
- Schuett W, Tregenza T, Dall SRX. 2010. Sexual selection and animal personality. *Biol Rev.* 85:217–246.
- Sih A, Bell A, Johnson JC. 2004. Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol Evol.* 19:372–378.
- Sih A, Kats LB, Maurer EF. 2003. Behavioural correlations across situations and the evolution of antipredator behaviour in a sunfish-salamander system. *Anim Behav.* 65:29–44.
- Sih A, Watters JV. 2005. The mix matters: behavioural types and group dynamics in water striders. *Behaviour.* 142:1417–1431.
- Smith BR, Blumstein DT. 2008. Fitness consequences of personality: a meta-analysis. *Behav Ecol.* 19:448–455.
- Stahl J, Drent RH, van der Jeugd H. 2001. Opportunistic underlings try their fortune elsewhere: inter-flock exchange in wintering barnacle geese. Limits to the co-occurrence of avian herbivores [PhD thesis]. Groningen, the Netherlands: Groningen University.
- Stahl J, Tolsma PH, Loonen M, Drent RH. 2001. Subordinates explore but dominants profit: resource competition in high Arctic barnacle goose flocks. *Anim Behav.* 61:257–264.
- Vickery WL, Giraldeau LA, Templeton JJ, Kramer DL, Chapman CA. 1991. Producers, scroungers, and group foraging. *Am Nat.* 137:847–863.
- Webster MM, Ward AJW. 2011. Personality and social context. *Biol Rev.* doi:10.1111/j.1469-185X.2010.00169.x.
- Webster MM, Ward AJW, Hart PJB. 2007. Boldness is influenced by social context in three-spine sticklebacks (*Gasterosteus aculeatus*). *Behaviour.* 144:351–371.
- Wolf M, van Doorn GS, Leimar O, Weissing FJ. 2007. Life-history trade-offs favour the evolution of animal personalities. *Nature.* 447:581–584.
- Wolf M, van Doorn GS, Weissing FJ. 2008. Evolutionary emergence of responsive and unresponsive personalities. *Proc Natl Acad Sci U S A.* 105:15825–15830.
- Wolf M, Van Doorn GS, Weissing FJ. 2011. On the coevolution of social responsiveness and behavioural consistency. *Proc R Soc Lond B Biol Sci.* 278:440–448.
- Wolf M, Weissing FJ. 2010. An explanatory framework for adaptive personality differences. *Philos Trans R Soc B Biol Sci.* 365:3959–3968.