Behavioral Ecology
doi:10.1093/beheco/ars091
Advance Access publication 16 July 2012

Original Article

Boldness affects foraging decisions in barnacle geese: an experimental approach

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Individuals foraging in groups constantly need to make decisions, such as when to leave a group, when to join a group, and when to move collectively to another feeding site. In recent years, it has become evident that personality may affect these foraging decisions, but studies where individuals are experimentally forced into different roles are still absent. Here, we forced individual barnacle geese, *Branta leucopsis*, differing in boldness scores, either in a joining or in a leaving role in a feeding context. We placed a food patch at the far end of a test arena and measured the arrival latency and number of visits of individuals to the patch either in the presence of a companion that was confined near the food patch ("joining context") or in the presence of a companion that was confined away from the food patch ("leaving context"). We also ran trials without a companion ("nonsocial context"). Bolder individuals arrived more quickly than shyer individuals in the "leaving" context, but there was no effect of boldness in the "joining" context, suggesting that boldness differences are important in explaining variation in leaving behavior but not in joining behavior. The difference in arrival latency between the "joining" and non-social context increased with decreasing boldness score, suggesting that shyer individuals are more responsive to the presence of other individuals (i.e., social facilitation). These results indicate that individual differences in boldness play a role in patch choice decisions of group-living animals, such as when to leave a flock and when to join others at a patch. *Key words:* boldness, foraging, joining, personality, social context, social facilitation. *[Behav Ecol]*

INTRODUCTION

Individuals constantly need to make decisions throughout their lives. For individuals foraging in groups, these decisions include when to leave a group, when to join a group, and when to move collectively to another feeding site. In recent years, it has become evident that conspecific individuals are not all alike in the decisions they make (Bergvall et al. 2011; Kurvers et al. 2011) but show variation in personality that affects their foraging decisions. Personality describes the phenomenon that differences in behavioral and physiological traits among individuals of the same species are consistent over time and context (Gosling and John 1999; Koolhaas et al. 1999; Carere and Eens 2005; Groothuis and Carere 2005; Réale et al. 2007; Biro and Stamps 2008; Sih and Bell 2008).

There is ample evidence that variation in personality affects foraging decisions in groups. For example, in groups that collectively move toward a feeding site, bolder individuals are more often found in the leading edge, with examples including guppies, *Poecilia reticulata* (Dyer et al. 2008), three-spined sticklebacks, *Gasterosteus aculeatus* (Harcourt et al. 2009), barnacle geese, *Branta leucopsis* (Kurvers et al. 2009), and zebra finches, *Taeniopygia guttata* (Beauchamp 2000; Schuett and Dall 2009). Also decisions regarding when to leave or join a group are known to be affected by variation in personality: in a study on barnacle geese, bolder individuals found more food in a producer–scrounger game than shyer barnacle geese which in turn scrounged more from the food discoveries of others (Kurvers et al. 2010a). Michelena et al. (2008) offered groups of female Scottish Blackface sheep, *Ovis aries*, an arena with 2 grass patches, one on each side. In groups of 6 and 8 sheep, bold individuals split more often in subgroups than shy sheep did, which stayed more often together. In addition, when leaving a patch, bold individuals were more likely to move to the other patch compared with shy individuals, who were more likely to return to the same patch.

These studies clearly demonstrate that personality can affect foraging decisions in groups, but causality cannot be inferred because individuals are not experimentally tested in a specific context (e.g., leader/follower or producer/scrounger). A second limitation arises due to the social context of this type of study. In a social context, the behavior of an individual may be affected by its own personality, the presence and behavior of other individuals, and the interaction between these factors (Harcourt et al. 2009). Disentangling these processes is challenging because it can be problematic to separate the individual choice from the social effect (see, e.g., Magnhagen and Staffan 2005; Van Oers et al. 2005; Webster et al. 2007; Magnhagen and Bunnefeld 2009; Schuett and Dall 2009) and therefore requires an experimental approach.

To overcome these problems, we performed a social foraging experiment, placing individuals with different boldness scores in 2 different standardized social environments. Individuals

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Received 16 July 2011; revised 5 January 2012; accepted 27 March 2012.

were allowed to approach a food patch placed at the far end of an arena, in which there was either a companion animal present at the food patch ("joining context") or a companion was held at the start of the arena, simulating a situation where individuals had to leave the group to search for food opportunities ("leaving context"). We also tested individuals in a similar nonsocial context (i.e., without a companion individual present) to study the behavioral change attributable to the social context (i.e., social facilitation).

We used barnacle geese as our study species. Individual barnacle geese differ consistently in boldness, and the boldness level of focal and companions is important in a social foraging task: in pairs, bolder individuals take the lead more often toward a food patch and arrive quicker than shyer individuals; moreover, individuals arrive at the food patch more often in the presence of a bolder conspecific (Kurvers et al. 2009). We predicted that (1) bolder individuals would arrive quicker in the nonsocial context, (2) bolder individuals would arrive quicker in the "leaving context" because boldness correlates positively with the propensity to go away from conspecifics, (3) shyer individuals would arrive quicker in the "joining context" because shyer barnacle geese use the scrounging tactic more often than bolder individuals (Kurvers et al. 2010a), and (4) the difference in arrival latency between the nonsocial and the social context would be larger for shyer individuals because several studies showed that shyer individuals are more reactive to the behavior of conspecifics than bolder individuals (Van Oers et al. 2005; Magnhagen and Bunnefeld 2009; Kurvers et al. 2010b).

METHODS

Experimental subjects

We used captive-born female barnacle geese (n = 20), all born in 2007, wing-clipped and fitted with a uniquely coded leg ring for identification. Because foraging behavior of geese may be affected by their size (Durant et al. 2004; Cope et al. 2005; Jonsson and Afton 2009) and/or condition (Durant et al. 2003; Heuermann et al. 2011), we also measured body size and body condition. We used the first axis of a principal component analysis (PC1, explaining 68.7% of the variation) of tarsus, culmen, and wing lengths to derive a structural measure of body size. Prior to the experiment, we measured body mass using a digital balance. Body condition was calculated as the residual from a regression of body mass on PC1. When not used for the experiment, all geese were kept as 1 group in an outdoor aviary of 12 × 15 m at the Netherlands Institute of Ecology (NIOO-KNAW) in Heteren, the Netherlands. Throughout the experiments, geese were fed *ad libitum* with a mixture of grains and pellets. We did not provide grass in the aviary during the experiments so that geese would be highly motivated in the experiments to start foraging on the available grass. Geese have a strong preference for grass above grains and pellets. A pond (6 × 1 m) was present in the aviary, with continuously flowing water for bathing and drinking. 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 2010037.a).

Boldness test

We assessed the boldness level of individuals by performing novel object tests. We habituated individuals to an experimental arena (9 × 3 m) by introducing them 5 times for 10 min. 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). If geese did not arrive within close distance (50 cm) of the novel object, they received an approach latency of 601 s. Each individual was tested twice in November or December 2008 (see Kurvers et al. 2009, 2010a) as part of a larger group of individuals (n = 46). Each individual was tested with 2 different novel objects: a green plastic mat and a brown deep-pile rug. Because both minimal distance and approach latency may contain information about the reaction toward the novel object, we calculated principal components (PCs) for each test as an independent measure of novel object score. Including all individuals, PC1 explained 87% and 90% of the variation for test one and test two, 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 following Becker (1984). Repeatability of novel object score was high (0.82) (see Kurvers et al. 2010a), indicating that individuals differed consistently in their boldness scores.

Foraging experiment

We used an experimental arena consisting of 2 compartments: one for the focal individual and one for the companion individual (see legend Figure 1 for details). In both compartments, a patch of grass (20 × 40 cm) was placed opposite of the entrance. We used commercially bought sods of perennial ryegrass, *Lolium perenne*, an important food source for barnacle geese in the wild (Prins and Ydenberg 1985). Focal individuals were able to move freely in their compartment. The companion individual, on the contrary, was restrained to a small compartment either at the far end of the arena (near the patch of grass) or at the entrance of the arena (see also Figure 1). We used a single individual (a female of intermediate boldness from the same flock) as the standard companion in all trials. The arena was contained within a greenhouse to reduce external disturbances, and a fenced corridor connected the arena with the outdoor aviary, so all transportation was done without handling the geese. During each test day, geese were isolated in smaller holding enclosures in the early morning to facilitate transport between the outdoor aviary and the arena. All trials were done between 07.00 and 12.30 h, local time (15 March–4 May 2010; summer time started 28 March 2010).

Experiment 1: joining context

All individuals were first tested in the experimental arena without a companion (nonsocial context, round 1), and we measured the time taken to arrive at the food patch. On the next day of the experiment, each focal individual was tested in the "joining" context (round 2) with the companion individual at the far end of the arena near the grass patch (see Figure 1a). We repeated this procedure thrice, alternating between the nonsocial and the social context, resulting in 6 trials per focal individual.

Experiment 2: leaving context

After experiment 1, we tested the focal individuals in the "leaving" context. As before, we started with the nonsocial context (round 7), introducing each focal individual separately without a companion. On the next day, we introduced each focal individual, with the companion individual placed

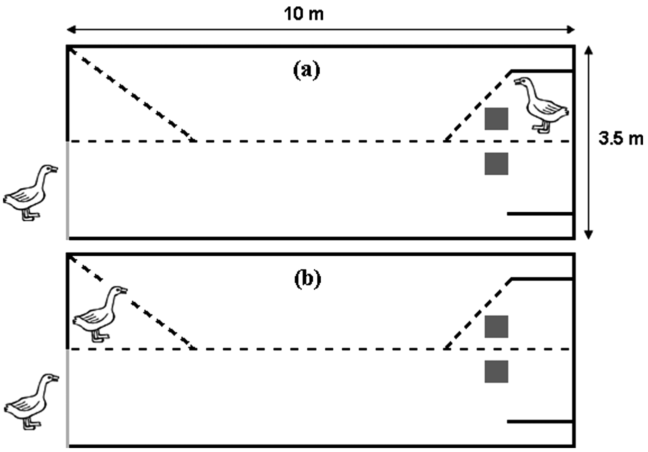

Figure 1
Schematic overview of the experimental arena used for the foraging experiment. The closed lines represent a wire-fence covered with white plastic (height: 80 cm). The dashed lines represent transparent wire netting. The grey squares represent grass patches. The grey lines represent a door, which served as the entrance for the focal individual. As shown, the companion animal was either placed (a) in the compartment at the far end of the arena with access to the grass patch (experiment 1; "joining context") or (b) in the compartment in the beginning of the arena, with no access to the grass patch (experiment 2; "leaving context").

at the beginning of the arena (see Figure 1b, round 8). As in experiment 1, we repeated this procedure thrice.

All trials were ended 1 min after the focal individual arrived at the food patch, up to a maximum of 10 min. We measured whether the focal individual arrived at the food patch (yes/no), and if yes, the time elapsed until arrival at the food patch (hereafter called: arrival latency). If individuals did not arrive at the patch, they were assigned an arrival latency of 601 s. Because the behavior of the companion individual could affect the arrival latency of the focal individual (see van Oers et al. 2005), we scored the activity of the companion in each social trial (i.e., a trial in which there was a companion individual present). We calculated an "activity score" for each social trial ranging between 0 (companion individual did not move for the entire length of the trial) and 1 (companion individual was moving for the entire length of the trial). All trials were videotaped, and the arrival latency of the focal individual and the activity score of the companion were measured from the recordings afterwards.

Statistical analysis

We tested for an effect of boldness on arrival latency in the different contexts using generalized linear mixed models (GLMMs) with binomial errors and a logit-link function (logistic regression). We chose for a binomial data analysis because the data of arrival latency did not follow a normal distribution but consisted of data spread over nearly the full range of arrival latencies (14–601 s) with a peak in the data distribution at an arrival latency of 601. To obtain proportional data for binomial data analysis, we divided the arrival latency by the maximum arrival latency (601 s). By doing this, we conform to the consideration for a binomial data analysis while maintaining the variation in arrival latency in the data. A binomial data analysis using arrival success as a binary variable (yes/no) would remove this variation. We constructed separate models for the joining and leaving context. Arrival latency was used as response variable, and we fitted boldness score, treatment (social/nonsocial condition), the interaction between boldness score and treatment, round, body size, and body condition as fixed factors. We also included companion activity score as a fixed factor, only including social trials (because in nonsocial trials, there was no companion activity score). Again, we constructed separate models for the joining and leaving context. We included individual identity as a random effect in all mixed models. We report full statistical models including estimates and standard errors (se) of all fixed factors. Significance levels of individual factors were derived from the z-values and associated P values. We used the package lme4 for mixed model procedures in R (version 2.11.1, R Development Core Team 2008). Additionally, we performed a stepwise backward deletion procedure by removing individual factors, starting with the least significant term. This procedure rendered qualitative similar results as the full model procedure and is therefore not reported in the results.

To test whether individuals of different boldness scores differed in their behavioral change between a nonsocial and a social context, we calculated for each individual the average difference in arrival latency between the nonsocial and the social trials for each context (i.e., joining and leaving). The average difference in arrival latency was used as the response variable in a GLM, with boldness, context, and the interaction between boldness and context as fixed factors and individual as random term. Significance levels of individual factors were derived by a Monte Carlo Markov Chain with 10 000 simulations using the package LanguageR.

The arrival (yes/no) and arrival latencies measured in the 3 nonsocial trials in experiments 1 and 2 were compared to test whether individuals reacted differently between these trials (e.g., due to a habituation effect). We compared arrival (yes/no) using GLMMs with binomial errors and a logit-link function, fitting experiment (1 or 2) as fixed effect and individual identity as random effect. We compared the average arrival latencies using a Wilcoxon matched-pairs test. We also compared the average arrival latency of each individual in experiment 1 with its average arrival latency in experiment 2 using a Spearman rank correlation.

RESULTS

Experiment 1: Joining

In the joining context, there was a significant effect of treatment and boldness score on arrival latency (treatment: est ± se = −3.10 ± 0.54, z = −5.74, $P < 0.001$; boldness: est ± se = −0.99 ± 0.39, z = −2.53, $P = 0.011$) and no effect of round, body size, and body condition (all $P > 0.1$). Because the interaction between treatment and boldness score was close to significant (est ± se = 0.94 ± 0.56, z = 1.69, $P = 0.090$), we analyzed the effect of all fixed factors on arrival latency for both treatments separately. In the nonsocial context, arrival latency decreased with increasing boldness score (est ± se = −1.13 ± 0.47, z = −2.39, $P = 0.017$; Figure 2a). There was no effect of round, body size, or body condition (all $P > 0.1$). In the social context, however, there was no effect of boldness score on arrival latency (est ± se = −0.07 ± 0.45, z = −0.15, $P = 0.88$; Figure 3a), nor was there an effect of companion activity score, round, body size, or body condition (all $P > 0.1$).

Experiment 2: leaving

In the leaving context, there was a significant effect of boldness score (est ± se = −1.08 ± 0.51, z = −2.11, $P = 0.035$) and body size (est ± se = −1.10 ± 0.44, z = −2.49, $P = 0.013$) on the arrival latency and no effect of treatment, round, and body condition (all $P > 0.09$). Arrival latency decreased with increasing boldness score. In addition, larger individual had

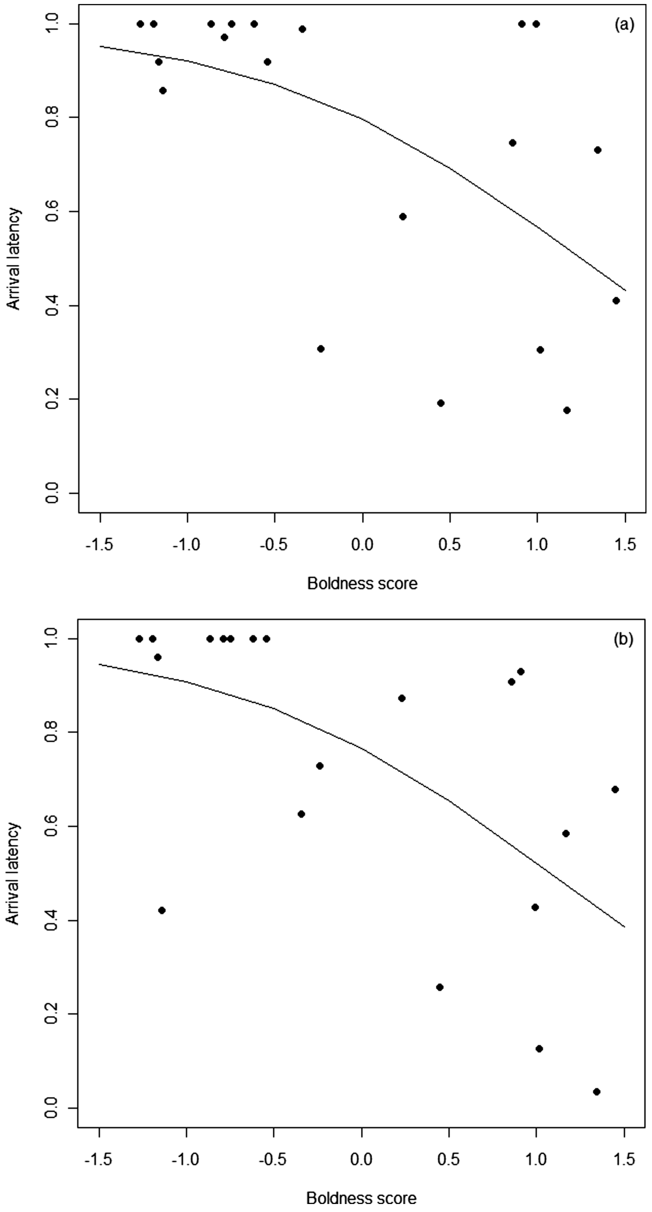

Figure 2
The arrival latency at the food patch decreased with increasing boldness score during the nonsocial context in (a) experiment 1 and (b) experiment 2. Lines are logistic regression lines.

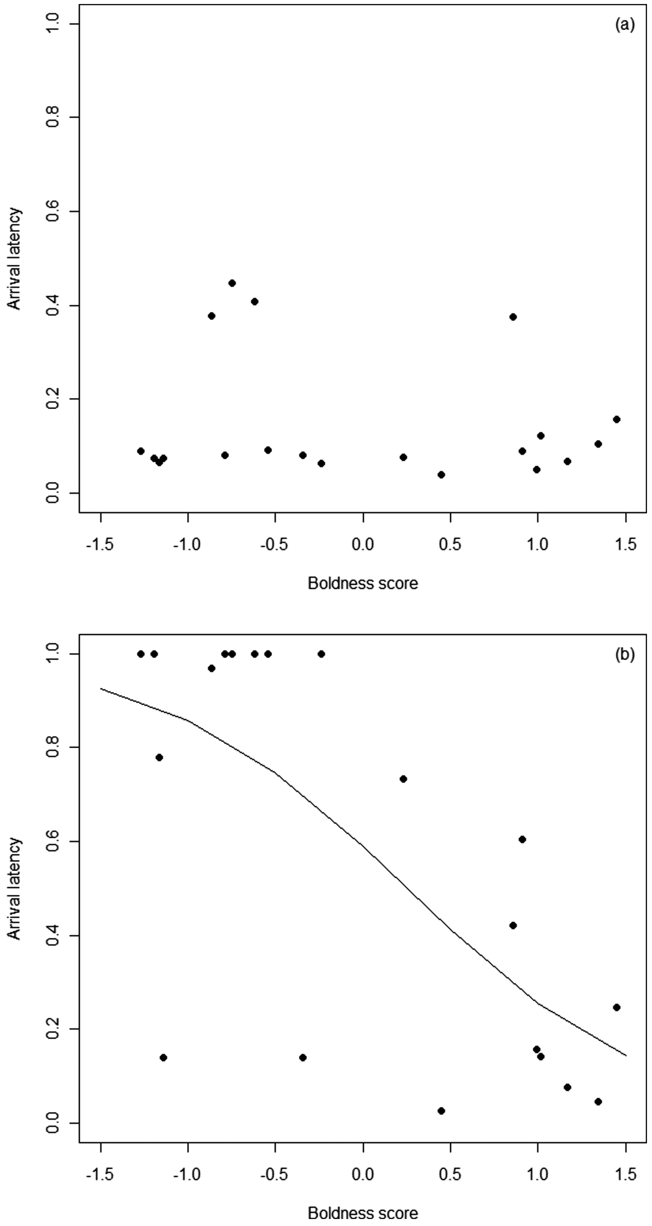

Figure 3
Arrival latency at the food patch during the social foraging experiments: (a) in the presence of a companion that was already present at the food patch, there was no effect of boldness on the arrival latency ("joining context" of experiment 1) and (b) in the presence of a companion that was restrained at the beginning of the arena, the arrival latency decreased with increasing boldness score ("leaving context" of experiment 2). Line is a logistic regression line.

lower arrival latencies. The interaction between treatment and boldness score was far from significant ($z = -0.72$, $P = 0.48$). Both in the nonsocial ($z = -2.26$, $P = 0.024$; Figure 2b) and social context ($z = -3.00$, $P = 0.003$; Figure 3b), arrival latency decreased with increasing boldness score. In the social context, there was no effect of companion activity score on the arrival latency of the focal individual ($z = -0.41$, $P = 0.68$).

Difference between social and nonsocial trials

There was a significant interaction between boldness and context ($P < 0.001$) on the difference in arrival latency between the social and nonsocial trials. In the joining context, the difference in arrival latency decreased with increasing boldness score (GLM: est ± se = −98.88 ± 37.00, $t = -2.67$, $P = 0.016$; Figure 4). In the leaving context, there was a trend of an effect of boldness on the difference in arrival latency between the social and nonsocial trials, but the effect was in the opposite direction (est ± se = 58.90 ± 28.60, $t = 2.06$, $P = 0.054$; Figure 4).

Repeatability

There was no significant difference in the number of arrivals between experiments 1 and 2 during the nonsocial context ($\chi^2_1 = 0.05$, $P = 0.80$) nor was there a significant difference in arrival latency ($z = -0.17$, $P = 0.87$), suggesting that individuals did not habituate to the experimental challenge. There was a strong positive correlation ($r_s = 0.66$, $P = 0.001$; repeatability score ± se = 0.56 ± 0.15, $n = 20$) between the average

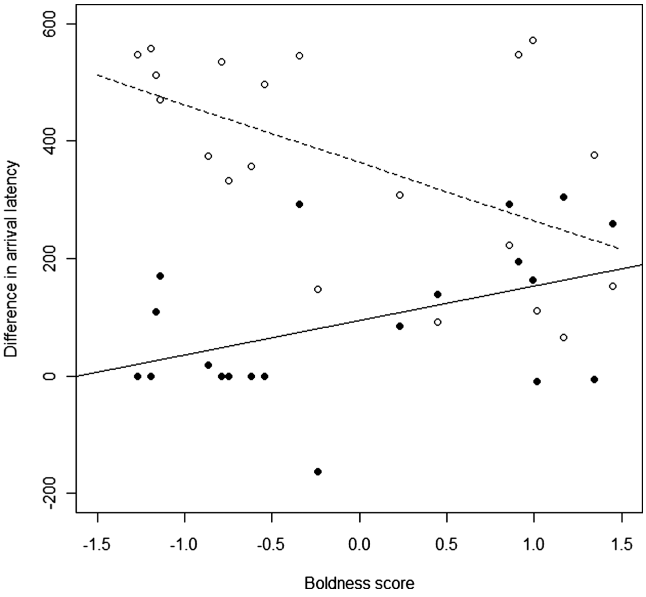

Figure 4
Difference in arrival latency between the nonsocial and social context. Open circles and dotted line represent the difference in experiment 1 (with a companion animal already present at the food patch, joining context). In the joining context, the difference in arrival latency between the nonsocial and social context increased with decreasing boldness score. The closed circles and line represent the difference in experiment 2 (with a companion present that was restrained at the beginning of the arena, leaving context). In the leaving context, the difference in arrival latency increased with increasing boldness score although this effect was nonsignificant ($P = 0.054$). Positive values indicate that individuals became faster in the social context compared with the nonsocial context. Lines are linear regression lines.

arrival latency in experiments 1 and 2 during the nonsocial context, indicating that individual differences in arrival latency were consistent.

DISCUSSION

In the situation where a companion individual was already present at the food patch (“joining context”), variation in arrival latency was not associated with boldness. However, when the companion was far from the food patch (“leaving context”), bolder individuals arrived faster at the food patch than did shyer individuals. Shyer individuals showed larger differences in arrival latency when comparing the nonsocial and social context.

Our study demonstrates experimentally that bolder individuals are indeed more prone to initiate a new direction of movement by an increased tendency to leave the group. Several studies showed that bolder individuals are more often found in the leading edge of moving groups (Beauchamp 2000; Dyer et al. 2008; Harcourt et al. 2009; Kurvers et al. 2009; Schuett and Dall 2009). We did not study leadership directly because companion animals did not follow the focal individual, as they were restrained at the entrance of the arena and therefore the second requirement of the definition of leadership is not met (“the initiation of new directions of locomotion by one or more individuals, which are then followed by other group members” (Krause et al. 2000)). We believe a similar manipulation can be used to study the role of personality in leadership and followership directly, which could increase our understanding of collective movements, leader–follower dynamics and the role of animal personality therein. The recent introduction of robotic animals (Halloy et al. 2007; Faria et al. 2010) offers one possibility by actually letting the robotic animal follow decisions of focal individuals or initiating new movement directions themselves.

For individuals living in groups, it is important to understand if and how personality traits (often measured in social isolation) are expressed in a social context (see Webster and Ward 2011 for a review) as this can determine to what extent natural selection can act on these personality traits. One of the difficulties is that individuals affect each other, so that these interaction processes are difficult to disentangle. Here, we standardized the social context, by restraining the companion animal at either side of the arena, thereby prohibiting the companion animal from approaching or leaving the food patch, thus excluding or reducing a possible interaction process between individuals. Boldness of the focal individual was expressed in the arrival latency at the food patch only when a companion was restrained at the entrance of the arena far away from the food patch. There were no such effects of boldness when there was a companion already present at the food patch. The most unambiguous explanation for the effect of social context on the expression of boldness is that in experiment 2 (“leaving context”), individuals had to approach the food patch on their own, which probably required overcoming some fear. In experiment 1 (“joining context”), the companion was already present at the food patch, perhaps signaling that the food patch was a safe place.

When studying the importance of personality traits in a social context, it is important also to look at the behavior in a comparable nonsocial context to understand how different personality types actually adjust their behavior toward the social context. Social facilitation occurs when the presence of other individuals causes the focal individual to show different behavior or to perform behavior at a different rate than when measured in isolation (for a review on the relation between social facilitation and personality, see Webster and Ward 2011). Van Oers et al. (2005) showed that slow-exploring male great tits, *Parus major*, became bolder in the presence of a companion, whereas fast-exploring males did not change their behavior in reaction to the presence of a companion. Magnhagen and Bunnefeld (2009) tested boldness of individual perch, *Perca fluviatilis*, both alone and in groups of 4 individuals. They found that individuals in groups were bolder compared with individuals when tested alone, and that shy individuals showed the largest change in behavior (i.e., became much bolder) when comparing a social and nonsocial context, whereas bold individuals changed their behavior less between treatments (see also Magnhagen and Staffan 2005). Similar to these studies, we found in the “joining context” that the difference in arrival latency between the social and nonsocial context increased with decreasing boldness score, suggesting that normally shy individuals were emboldened by the presence of a companion and that the effect of social facilitation is larger for shyer individuals. From these studies, a general pattern emerges in which shyer individuals are more reactive to the presence (and behavior) of other individuals (see also Kurvers et al. 2010b). In experiment 2, however, there was no evidence that shyer individuals showed a larger behavioral difference, indicating that a more reactive behavior of shyer individuals does depend on the nature of the social context (and it may also depend on the species under investigation, e.g., Webster et al. 2007; Schuett and Dall 2009). Next to boldness, other personality traits, for instance sociability, might affect joining and leaving decisions. “Sociability” is the tendency to stay close to conspecifics, and Côte and Clobert (2007) showed that in common lizards (*Lacerta vivipara*) individuals that dispersed from high-density populations were mainly asocial, whereas individuals that dispersed from low-density populations were mainly social. Our experiment was not an independent test of sociability because next to a social component it also contained a food component. However, our results do suggest that bolder individuals have a lower degree of sociability, though a test without food would be required to test this relationship unambiguously. Lastly, social network relationships might affect joining and leaving decisions (King and Cowlishaw 2009). The companion individual was part of the same flock as the focal individuals and social relationships might, thus, have played a role. We could not evaluate its importance because we had no recent data on social relationships.

Several studies on geese in the wild have reported individual differences in foraging behavior. Prop and Deerenberg (1991) showed that dominant brent geese, *Branta bernicla*, consumed a higher proportion of the most profitable plants compared with subordinate geese. Stahl et al. (2001b) showed that subordinate barnacle geese are more likely to find experimentally enriched food patches but are then replaced by more dominant individuals. Next to dominance, foraging decisions can also be shaped by individual differences in body condition (Prop et al. 2003; Prop and Quinn 2004) and experience (Prop and Quinn 2004). In a natural situation, geese frequently switch between different foraging flocks, and there are large individual differences in mobility (Ganter 1994). Stahl et al. (2001a) 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 et al. 2001b) 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. Lastly, Lamprecht (1991, 1992) showed that age, family status, and time of the year affected which geese initiated departures. In our experiment, age and family status were not important because all birds had a similar age and there were no pair bonds or parent–offspring relationships. Furthermore, a possible confounding effect of dominance was to a large extent excluded because the focal individual and the companion individual did not compete directly for food because they both had access to different grass patches. Though many field studies show a rich diversity of factors affecting foraging behavior and leadership-related aspects in geese, the role of animal personality in wild geese remains currently unexplored. Based on the results of this study, we hypothesize that, in the wild, shy geese switch less often between foraging flocks.

One could criticize our study because all individuals started with a trial in a nonsocial context, followed by a social context, and because the experiment in which the companion animal was present at the food patch (i.e., experiment 1) took place prior to the experiment in which the companion was present away from the food patch (i.e., experiment 2). However, individual differences in arrival latency were very consistent, when comparing the nonsocial trials of experiments 1 and 2, and there was no significant difference in average arrival latency (or number of trials arrived) between the nonsocial trials of experiments 1 and 2. Individual boldness scores were still predictive for how quickly individuals approached the food patch in the nonsocial trials of experiment 2, even after numerous introductions. In addition, in all our mixed models, we included "round" (with round 1 being the first trial for each individual and round 12 the last trial for each individual) as a fixed factor to control for a potential habituation effect. However, "round" was not significant in any of our models, providing more evidence that the birds did not habituate to the experimental challenge. Lastly, because we always alternated between a nonsocial and a social context, the context itself always differed between subsequent trials.

To conclude, individual variation in boldness did not explain differences in arrival latency at a food patch when there was already a companion animal present at the food patch. However, boldness was important in predicting arrival latency in a situation where a companion animal was far from the food patch, with bolder individuals visiting the food patch faster than shyer individuals, suggesting that boldness differences are important when individuals decide to leave a group but not when they decide to join a group. Shyer individuals had a larger difference in arrival latency when comparing the nonsocial and social context, suggesting that shyer individuals are more responsive to the presence of other individuals.

FUNDING

Faunafonds; Koninklijke Nederlandse Jagers Vereniging (KNJV).

We thank Bart van Lith and Erica Ras for practical assistance during the experiments. We thank Sip van Wieren for valuable comments. 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 2010037.a). This is publication 5251 from the Netherlands Institute of Ecology (NIOO-KNAW).

REFERENCES

Beauchamp G. 2000. Individual differences in activity and exploration influence leadership in pairs of foraging zebra finches. *Behaviour.* 137:301–314.

Becker WA. 1984. *Manual of quantitative genetics. 4th ed.* Pulman (WA): Academic Enterprises.

Bergvall UA, Schäpers A, Kjellander P, Weiss A. 2011. Personality and foraging decisions in fallow deer, *Dama dama. Anim Behav.* 81:101–112.

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.

Cope DR, Loonen M, Rowcliffe JM, Pettifor RA. 2005. Larger barnacle geese (*Branta leucopsis*) are more efficient feeders: a possible mechanism for observed body size-fitness relationships. *J Zool.* 265:37–42.

Côte J, Clobert J. 2007. Social personalities influence natal dispersal in a lizard. *Proc R Soc B.* 274:383–390.

Durant D, Fritz H, Blais S, Duncan P. 2003. The functional response in three species of herbivorous Anatidae: effects of sward height, body mass and bill size. *J Anim Ecol.* 72:220–231.

Durant D, Fritz H, Duncan P. 2004. Feeding patch selection by herbivorous Anatidae: the influence of body size, and of plant quantity and quality. *J Avian Biol.* 35:144–152.

Dyer JRG, Croft DP, Morrell LJ, Krause J. 2008. Shoal composition determines foraging success in the guppy. *Behav Ecol.* 20:165–171.

Faria J, Dyer J, Clément R, Couzin I, Holt N, Ward A, Waters D, Krause J. 2010. A novel method for investigating the collective behaviour of fish: introducing "Robofish". *Behav Ecol Sociobiol.* 64:1211–1218.

Ganter B. 1994. Site-tenacity and mobility of staging barnacle geese. *Ardea.* 82:231–240.

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.

Halloy J, Sempo G, Caprari G, Rivault C, Asadpour M, Tache F, Said I, Durier V, Canonge S, Ame JM, et al. 2007. Social integration of robots into groups of cockroaches to control self-organized choices. *Science.* 318:1155–1158.

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.

Heuermann N, van Langevelde F, van Wieren SE, Prins HHT. 2011. Increased searching and handling effort in tall swards lead to a Type IV functional response in small grazing herbivores. *Oecol.* 166:659–669.

Jonsson JE, Afton AD. 2009. Time budgets of Snow Geese *Chen caerulescens* and Ross's Geese *Chen rossii* in mixed flocks: implications of body size, ambient temperature and family associations. *Ibis.* 151:134–144.

King AJ, Cowlishaw G. 2009. Leaders, followers and group decision-making. *Commun Integr Biol.* 2:147–150.

Koolhaas JM, Korte SM, De Boer SF, 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.

Krause J, Hoare D, Krause S, Hemelrijk CK, Rubenstein DI. 2000. Leadership in fish shoals. *Fish Fish.* 1:82–89.

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, Prins HHT, van Wieren SE, van Oers K, Nolet BA, Ydenberg RC. 2010a. The effect of personality on social foraging: shy barnacle geese scrounge more. *Proc R Soc B.* 277:601–608.

Kurvers RHJM, van Oers K, Nolet BA, Jonker RM, van Wieren SE, Prins HHT, Ydenberg RC. 2010b. Personality predicts the use of social information. *Ecol Lett.* 13:829–837.

Kurvers RHJM, Adamczyk VMAP, van Wieren SE, Prins HHT. 2011. The effect of boldness on decision making in barnacle geese is group-size-dependent. *Proc R Soc B.* 278:2018–2024.

Lamprecht J. 1991. Factors influencing leadership – a study of goose families (*Anser-indicus*). *Ethology.* 89:265–274.

Lamprecht J. 1992. Variable leadership in Bar-headed geese (*Anser-indicus*) – an analysis of pair and family departures. *Behaviour.* 122:105–120.

Lessells CM, Boag PT. 1987. Unrepeatable repeatabilities - a common mistake. *Auk.* 104:116–121.

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.

Magnhagen C, Bunnefeld N. 2009. Express your personality or go along with the group: what determines the behaviour of shoaling perch? *Proc R Soc B.* 276:3369–3375.

Michelena P, Sibbald AM, Erhard HW, McLeod JE. 2008. Effects of group size and personality on social foraging: the distribution of sheep across patches. *Behav Ecol.* 20:145–152.

Prins HHT, Ydenberg RC. 1985. Vegetation growth and a seasonal habitat shift of the Barnacle goose (*Branta-leucopsis*). *Oecol.* 66:122–125.

Prop J, Deerenberg C. 1991. Spring staging in brent geese *Branta-Bernicla* - feeding constraints and the impact of diet on the accumulation of body reserves. *Oecol.* 87:19–28.

Prop J, Black JM, Shimmings P. 2003. Travel schedules to the high arctic: barnacle geese trade-off the timing of migration with accumulation of fat deposits. *Oikos.* 103:403–414.

Prop J, Quinn JL. 2004. Interference competition, foraging routines and reproductive success in red-breasted geese: fight or flight? In: Food finding: on the trail to successful reproduction in migratory geese. PhD Thesis J Prop. University of Groningen.

R Development Core Team. 2008. R: a language and environment for statistical computing [Internet]. Vienna (Austria): R Foundation for Statistical Computing. Available from: http://www.R-project.org.

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.

Sih A, Bell AM. 2008. Insights for behavioral ecology from behavioral syndromes. *Adv Stud Behav.* 38:227–281.

Stahl J, Drent RH, van der Jeugd H. 2001a. Opportunistic underlings try their fortune elsewhere: inter-flock exchange in wintering barnacle geese. In: Limits to the co-occurrence of avian herbivores. PhD thesis J Stahl. University of Groningen.

Stahl J, Tolsma PH, Loonen M, Drent RH. 2001b. Subordinates explore but dominants profit: resource competition in high Arctic barnacle goose flocks. *Anim Behav.* 61:257–264.

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.

Webster MM, Ward AJW, Hart PJB. 2007. Boldness is influenced by social context in threespined sticklebacks (*Gasterosteus aculeatus*). *Behaviour.* 144:351–371.

Webster MM, Ward AJW. 2011. Personality and social context. *Biol Rev.* 86:759–773.