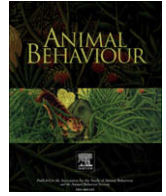


Contents lists available at [ScienceDirect](#)

Animal Behaviour

journal homepage: www.elsevier.com/locate/yanbe

Personality differences explain leadership in barnacle geese

Ralf H.J.M. Kurvers^{a,*}, Babette Eijkelenkamp^a, Kees van Oers^{b,1}, Bart van Lith^{c,2},
Sipke E. van Wieren^a, Ronald C. Ydenberg^a, Herbert H.T. Prins^a

^a Resource Ecology Group, Wageningen University

^b Department of Animal Population Biology, Netherlands Institute of Ecology

^c Department of Plant–Animal Interactions, Netherlands Institute of Ecology

ARTICLE INFO

Article history:

Received 2 April 2009

Initial acceptance 22 May 2009

Final acceptance 3 June 2009

Available online xxx

MS. number: 09-00213R1

Keywords:

barnacle goose

boldness

Branta leucopsis

group behaviour

leadership

personality

Personality in animal behaviour describes the observation that behavioural differences between individuals are consistent over time and context. Studies of group-living animals show that movement order among individuals is also consistent over time and context, suggesting that some individuals lead and others follow. However, the relationship between leadership and personality traits is poorly studied. We measured several personality traits and leadership of individual barnacle geese, *Branta leucopsis*. We measured body size and scored the dominance of individuals living in a stable group situation before subjecting them to an open-field test, an activity test, a novel-object test, and a leadership test in which the order of the movement of individuals in pairs towards a feeding patch was scored. We found high repeatability for activity and novel-object scores over time. Leadership was strongly correlated with novel-object score but not with dominance rank, activity or exploration in an open field. These results provide evidence that leadership is closely related to some aspects of personality. Interestingly, an individual's arrival at the food patch was affected not only by the novel-object score of the focal individual, but also by the novel-object score of the companion individual, indicating that movement patterns of individuals living in groups are affected by the personality traits of other group members and suggesting that movement patterns of a group may be shaped by the mix of personality types present in the group.

Crown Copyright © 2009 Published on behalf of The Association for the Study of Animal Behaviour by Elsevier Ltd. All rights reserved.

Personality in animal behaviour describes the observation that differences between individuals in behavioural and physiological traits are consistent over time and context (for reviews see Gosling & John 1999; Koolhaas et al. 1999; Carere & Eens 2005; Groothuis & Carere 2005). Different behavioural and physiological reactions are often correlated, suggesting that these differences are fundamental aspects of the behavioural organization of individuals and are the subject of natural (Dingemanse & Reale 2005; Smith & Blumstein 2008) or sexual selection (van Oers et al. 2008). The concept of interindividual differences has also been referred to as coping styles (Koolhaas et al. 1999), temperament (Reale et al. 2007) and behavioural syndromes (Sih et al. 2004a, b). Here we distinguish

between 'personality traits' for repeatable behaviours and 'personality' for a suite of these traits.

Studies of group-living animals show that the order in which individuals move between locations and initiate or follow group movements towards a new feeding site can also be consistent over time and context (Dumont et al. 2005). Certain individuals are observed to be consistently at the forefront of collective movements and these individuals have been described as 'leaders' (Beauchamp 2000; Dumont et al. 2005; Harcourt et al. 2009). Leadership can be affected by experience (Reebs 2000), motivation (Fischhoff et al. 2007) or dominance (Stahl et al. 2001) and can have important fitness consequences. For example, individuals on the leading edge are the first to arrive at new food patches and suffer less from depletion, but they may also face higher predation risk (Krause 1994; Stankowich 2003). These differences in potential costs and benefits and the consistency of movement order lead to the suggestion that leaders might be intrinsically different from followers in certain personality traits. Several studies have investigated whether behavioural variation associates with leadership, but to date only one study has looked at the relation between personality and leadership (Schuett & Dall 2009).

* Correspondence: R. H. J. M. Kurvers, Resource Ecology Group, Wageningen University, Droevendaalsesteeg 3a, 6708 PB Wageningen, The Netherlands.

E-mail address: ralf.kurvers@wur.nl (R.H.J.M. Kurvers).

¹ K. van Oers is at the Department of Animal Population Biology, Netherlands Institute of Ecology (NIOO-KNAW), Boterhoeksestraat 48, 6666 GA Heteren, The Netherlands.

² B. van Lith is at the Department of Plant–Animal Interactions, Netherlands Institute of Ecology (NIOO-KNAW), Rijksstraatweg 6, 3631 AC Nieuwersluis, The Netherlands.

In zebra finches, *Taeniopygia guttata*, more active (Beauchamp 2000) and explorative (Beauchamp 2000; Schuett & Dall 2009) individuals were the first to arrive at a food patch. In golden shiners, *Notemigonus crysoleucas*, individuals that led showed a very weak correlation with boldness measured as the willingness to pass through a dark U-shaped tube and no correlation with boldness measured as the willingness to emerge from a refuge (Leblond & Reebbs 2006). In three-spined sticklebacks, *Gasterosteus aculeatus*, individuals with a higher propensity to leave cover led more often in foraging trips of two individuals (Harcourt et al. 2009). These studies show that behavioural variation can associate with leadership, but they did not look directly at the relation between personality and leadership (but see Schuett & Dall 2009).

To increase our understanding of the relationship between personality and leadership we measured three personality traits (exploration, activity and boldness) and leadership of individuals of the highly social barnacle goose, *Branta leucopsis*. We scored the dominance of individuals living in a stable group situation and subjected them to three personality tests: an open-field test (exploration), an activity test (activity) and a novel-object test (boldness). During the personality tests individuals were observed alone. To test their leadership we allowed the geese to move towards a feeding patch in pairs and measured which individual took the lead and how long it took for each individual to arrive. We calculated repeatability scores of replicate tests and correlated different behaviours. Additionally we studied the effect the personality of the companion had on the behaviour of the focal individual during the leadership test, because in group-living animals the behaviour of an individual might depend on the personality traits of its companions (e.g. Magnhagen & Staffan 2005; Sih & Watters 2005). We predicted that more explorative and bolder individuals (1) would lead more often and (2) would arrive more quickly at the food patch than less explorative and less bold individuals. Moreover, we predicted (3) that individuals paired with a more explorative and bolder companion would arrive more quickly at the food patch than individuals paired with a less explorative and less bold companion.

METHODS

Study Species

We used captive-born wing-clipped barnacle geese, each fitted with a uniquely coded white-coloured leg ring for identification. All of these individuals were born in 2007 ($N = 18$) and were unpaired. Birds were sexed by visual inspection of sexual organs in the cloaca (10 females, 8 males). Before the start of the experiment we measured tarsus and culmen length (± 0.1 mm) using callipers, wing length (± 1.0 mm) using a ruler, and body mass (± 1.0 g) using a digital balance (19 December 2007). One observer carried out all measurements to minimize observer bias. We used a principal components analysis of tarsus, culmen and wing lengths to derive a measure of body size. PC1 explained 76.6% of the variation. Body condition was calculated as the residual from a regression of body mass on PC1.

Housing and Experimental Arena

All geese were kept as one group in an outdoor enclosed area 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. In the outdoor enclosure was a large pond (6 by 1 m) with continuous flowing water for bathing and drinking. A fenced corridor connected this outdoor enclosure with the experimental arena. Experiments were

conducted in an arena of 3 by 9 m, built inside a greenhouse to reduce disturbance due to environmental factors. The arena was fenced with white plastic (height: 80 cm) and the floor covered with anti-root cloth. On the floor, a grid of 75 compartments enabled us to measure movement patterns in detail. Geese entered the arena through a wooden pen equipped with a sliding door, which could be operated from outside the greenhouse. The arena was visually but not acoustically isolated from the outdoor enclosure. Four cameras placed above the arena provided complete coverage. All trials were videotaped and the behaviour was analysed from the recordings afterwards.

Dominance Score

Prior to the experiments (19–27 December 2007) we scored agonistic interactions in the flock of 18 individuals. To avoid any human influence, we made observations using binoculars from a caravan. We defined an interaction as a direct confrontation between two birds, ranging from threats with lowered head and neck to active chases with flapping wings (Stahl et al. 2001). We scored the participants of the interaction as well as the outcome. 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 474 interactions (mean number per individual: 55.6; range: 27–86 interactions). Because the number of unknown relationships was small we constructed a dominance matrix, which is more precise under these conditions than using the dominance score (Poisbleau et al. 2006). A dominance matrix takes into account the identity of each opponent and all the interactions and it is built in such a way that inconsistencies are minimized (de Vries et al. 1993).

Experimental Procedure

All transportation was done without handling the geese. During each test geese were separated from each other in the early morning and placed as pairs in smaller holding enclosures to facilitate transport between the outdoor enclosure and the experimental arena. In the holding enclosures we provided water and a mixture of grain and pellets, which was refreshed each morning. Geese were kept in pairs in the holding enclosures. The holding enclosures were large enough (3 by 1 m) so that individuals were able to escape from aggressive behaviour of their companion, although aggressive behaviour was rarely observed.

To reduce the effect of social interactions in the cage on behaviour during trials, geese were separated from their fellows and held for 5 min in separate cages prior to each trial. After 5 min of habituation a goose was gently driven towards the wooden pen that served as the entrance to the experimental arena, where it was held for an additional 2 min before being admitted to the arena. All geese immediately entered the arena after the slide was opened. All experiments were done between 0900 and 1230 hours, local time. All animal experiments were approved by the animal ethical committees (Dier Experimenten Commissie) of both the Royal Netherlands Academy of Arts and Sciences and the Wageningen University (protocols 2007129.b and 2008094.b).

Open-Field Test

To study exploration behaviour we used an open-field test (Walsh & Cummins 1976). On 5 and 6 January 2007 we introduced each goose once for 10 min into the arena (see above). The experimental order was randomized. The geese had no previous experience with this arena. As a measure of exploration we scored how many grid compartments each goose visited throughout the 10 min.

Activity Test

Because activity is preferably measured in a familiar environment (Barnett & Cowan 1976), we introduced each goose four times into the arena on separate days for 10 min to habituate the geese to the experimental arena before continuing with the activity test. On 16 and 17 January 2007 each goose was introduced once into the experimental arena to measure activity levels. As a measure of activity we scored the total number of grid compartments visited. The same procedure was repeated on 18 and 19 January 2007.

Novel-Object Test

We conducted a novel-object test on 31 January and 1 February 2007. We use the term 'boldness' for the reaction towards a novel object (Frost et al. 2007), although it has been proposed to use the term 'exploration' for the reaction towards a novel object (e.g. Reale et al. 2007). We placed a novel object (green plastic mat) in the middle of the arena, introduced each goose once for 10 min, and scored the minimal 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. If the goose did not arrive within a close distance (50 cm) of the novel object it was assigned an approach latency of $600 + 1$ s. The test was repeated with another novel object (a brown deep-pile rug) on 7 and 8 February 2007. Because both minimal distance and approach latency may contain information about the reaction towards the novel object we calculated principal components (PCs) for each test as an independent measure of novel-object score. PC1 explained 83.0 and 76.0% of the variation for test 1 and test 2, respectively. The correlations of both variables with PC1 were negative, implying that high values of PC1 correspond to bolder individuals.

To study the repeatability of behaviours over time we repeated the three personality tests 10 months later (10–27 November 2008; termed period 2) following the same procedure. For period 2, PC1 of the novel-object test explained 90.2 and 89.9% of the variation for test 1 and test 2, respectively.

As a measure of exploration of an open field we averaged the two measurements of each individual. We averaged the four measurements of activity and novel-object score to obtain a composite measure of each behaviour for each individual. The activity score was log transformed to meet assumptions of normality.

Leadership Test

To test for leadership, we provided a food patch at the far end of the arena and we recorded which individual in a pair of two was the first to arrive at that food patch. As a food patch we used a patch of fresh grass (mainly consisting of *Lolium perenne*), which was refreshed each morning. To minimize possible confounding effects of dominance during arrival, we provided a fairly large patch (1.5×0.2 m). The first goose to arrive was given a score of 1, and the other a score of 0. In addition we scored whether each goose arrived at the food patch (yes/no) and, if yes, the time elapsed before arrival at the food patch (s). A trial was ended 1 min after both geese started to forage and lasted up to a maximum of 10 min. If both geese did not arrive at the food patch within 10 min both individuals received a score of 0 ($N = 25$ trials). Each goose was tested once against every other goose. Geese were used once a day, resulting in nine trials per day and 153 trials in total over a period of 17 days (between 15 February and 4 March 2008). The first day, geese were paired randomly. Thereafter, we used a rotating system to pair the couples. The order of introducing the couples on each day was randomized.

After the experiments the geese were kept in one group at the Netherlands Institute for Ecology for further behavioural experiments, as they are part of a larger research project on personality.

Statistics

Repeatability is a measure of the within-individual variance compared with the among-individual variance and gives the phenotypic variance explained by the individual. To calculate repeatability of behaviours we calculated 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 standard error following Becker (1984). We calculated repeatability of activity and novel-object score for period 1 and period 2 separately and for both periods combined. Because the score for exploration of an open field was calculated only once during each period we could calculate repeatability only for both periods combined. We compared repeatability between both periods using pairwise *t* test.

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). Both indexes vary from 0 (complete absence of linearity) to 1 (complete linearity). Statistical significance of *K* is calculated by a chi-square test. 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). Each bird was then assigned a rank from 1 (most subordinate) to 18 (most dominant).

Correlations between dominance, different behaviours, body size, body condition and leadership data were analysed using the Pearson correlation coefficient (*r*) if the data were normally distributed or the Spearman rank coefficient (*r_s*) if the data could not be normalized. From the leadership data we calculated the total number of trials an individual led and its average arrival time. Because of the many correlations we used a sequential Bonferroni test (Rice 1989) to control for a type 1 error. To test for differences in sex we used a *t* test or a Mann–Whitney *U* test.

To test the effect of dominance, body condition, and behavioural traits of the focal individual as well as the companion on (1) arrival (yes/no) and (2) arrival time (s) of the focal individual during the leadership test we used linear mixed-effect models. (1) To analyse the effect on arrival (yes/no), we used generalized linear mixed models with binomial errors and a logit-link function. (2) To analyse the effect on arrival time within the group of individuals that arrived, we used general linear mixed models. Arrival time was log transformed to meet the criteria of normality. As fixed effects in both models we fitted body condition, activity, novel-object score and the novel-object score of the companion, together with the interactions between dominance and novel-object score and between dominance and novel-object score of the companion. To avoid problems with pseudo-replication we fitted focal individual and companion individual as random effects. We started with full models containing all terms. Minimal adequate models were obtained by stepwise deletion of nonsignificant terms ($P > 0.1$), starting with the highest-order interactions or the least significant term. To compare the explanatory power of two subsequent models we used a log-likelihood ratio test, which follows a chi-square distribution, with degrees of freedom equal to the difference in the number of parameters between the two models. We inspected that

the error variation was normally distributed. We used the package *lme4* for generalized mixed-model procedures and *nlme* for general mixed-model procedures in R (version 2.7.2). For all other calculations we used SPSS (version 15.0).

RESULTS

Repeatability

Repeatability of activity and novel-object scores was generally high, ranging from 0.56 to 0.85, and did not vary between periods (Table 1). Repeatability of the open-field exploration score was low (0.04) (Table 1).

Dominance

The value of Kendall's linearity index ($K = 0.61$, $P < 0.001$), Landau's index and the corrected index of the sociometric matrix were high ($h = 0.62$, $h' = 0.65$, $P < 0.001$), allowing the use of a linear order to rank the individuals (Fig. 1). Dominance rank was significantly correlated with body size (Table 2), but there was no correlation with body condition (Table 2). Males had on average higher dominance ranks than females ($U = 7$, $N_1 = 8$, $N_2 = 10$, $P < 0.01$) (see also Fig. 1).

Correlations Between Sex, Behaviours and Dominance

Males had a larger body size ($\bar{X} \pm SD = 0.66 \pm 1.04$) than females (-0.53 ± 0.59) ($t_{16} = 3.06$, $P < 0.01$), but there was no significant difference in body condition (males: -68.4 ± 137.7 ; females: 54.7 ± 133.4 ; $t_{16} = -1.91$, $P = 0.08$). There were no sex differences in behaviour during the personality tests (exploration, activity and novel object all $P > 0.1$).

Dominance rank was not significantly correlated with exploration, activity or novel-object score (Table 2). Neither body size nor body condition were significantly correlated with exploration, activity or novel-object score (Table 2). There were no significant correlations between the three behaviours (exploration, activity and novel-object score; Table 2).

Leadership

Novel-object score was significantly correlated with the leadership score (=number of trials leading; Table 2, Fig. 2). Likewise, individuals with a higher novel-object score arrived at the food patch more quickly (Table 2). Leadership was not significantly correlated with dominance, exploration, activity, body size or body condition (Table 2). There was no sex difference in leadership ($U = 38$, $P > 0.1$). There was no significant correlation between arrival time and dominance, exploration, activity, body size or body condition (Table 2) and there was no sex effect ($t_{16} = -0.689$, $P > 0.1$). To study if the effect of novel-object score on leadership score diminished over time we performed a separate analysis for the first 9 days and the last 8 days of the leadership test. In both periods there was a strong positive correlation between novel-object score

and leadership score (first 9 days: $r = 0.83$, $P < 0.001$; last 8 days: $r = 0.61$, $P = 0.008$).

Mixed-model analysis revealed that individuals with a high novel-object score arrived at the food patch more often ($\chi^2_1 = 12.04$, $P < 0.001$; Fig. 3) and that individuals paired with a companion with a higher novel-object score also arrived more often ($\chi^2_1 = 5.20$, $P = 0.023$; Fig. 4). None of the other variables was significant (all $P > 0.1$). Within the group of individuals that arrived, individuals with a high novel-object score arrived earlier at the food patch ($\chi^2_1 = 4.86$, $P = 0.031$), but the novel-object score of the companion did not significantly explain arrival time ($\chi^2_1 = 2.42$, $P = 0.12$). None of the other variables was significant (all $P > 0.1$).

DISCUSSION

Our data show that activity and boldness are consistent in individual barnacle geese. Bold individuals led the group and arrived at the food patch more often, and they arrived sooner. Moreover, individuals paired with a bolder companion had a higher chance of arriving at the food patch.

Repeatability scores of activity and boldness were high, both within a period and between periods. The only behaviour that appeared not to be repeatable over time was the exploration of an open field. This could indicate that the individuals recognized the arena during the second period (nearly one year later), because the arena was identical, or that this test is not adequate to measure the exploration of an open field in barnacle geese. The high repeatability scores over time and the strong correlation between novel-object score and leadership suggest the presence of personality variation in barnacle geese. Dominance was not correlated with exploration, activity or boldness. Likewise, males and females did not differ in exploration, activity and boldness score. This is in agreement with the general finding that differences in personality traits are usually independent of social status and sex (Drent et al. 2003). Boldness was not correlated with activity, suggesting that an individual's reaction towards a novel object was not merely a reflection of its activity level, but that these behaviours are different traits. Bold individuals did not have a higher exploration score in the open-field test. In great tits, *Parus major*, there is a strong correlation between the behaviour of an individual in both tests (Verbeek et al. 1994) and sometimes the behaviour in both tests is added up to represent one personality trait (e.g. Martins et al. 2007). However, because of the low repeatability of an individual's exploration score during the open-field test and the absence of a correlation between both tests we decided to treat these outcomes as different aspects of barnacle goose personality.

Leadership was best predicted by the novel-object score. Bolder individuals led the pair more often compared to shyer individuals; they arrived more often at the food patch and arrived there earlier. Few studies thus far have studied the relationship between behavioural variation and leadership: in zebra finches (Beauchamp 2000; Schuett & Dall 2009) and three-spined sticklebacks (Harcourt et al. 2009) more explorative (bolder) individuals led more often, but no evidence for this was found in golden shiners (Leblond & Reebbs 2006). However, these studies did not provide evidence that the individual variation in behaviour is repeatable over time or context and thus did not study personality but personality traits. Here we show that several aspects of individual behaviour in barnacle geese are repeatable over time and that one of these aspects of personality, namely novel-object approach, is a predictor of leadership. One could argue that the patch of grass during the leadership test was treated as a novel object. We have two reasons to believe that this was not the case. First, the individuals were used to foraging from such a patch in their outdoor enclosure. Hence, the individuals were familiar to the 'object' itself.

Table 1
Repeatability scores of various behaviours in January 2008 (period 1), November 2008 (period 2), and both periods combined

Behaviour	Period 1	Period 2	Both periods	<i>t</i> test	<i>P</i>
Open-field score	—	—	0.04±0.24	—	—
Activity score	0.60±0.15	0.77±0.10	0.56±0.12	-0.94	0.52
Novel-object score	0.64±0.14	0.85±0.07	0.72±0.09	-1.34	0.41

Means ± SE are shown. $N = 18$. *t* statistics refer to the comparison of repeatability between period 1 and period 2.

	♂	♂	♂	♂	♂	♀	♂	♀	♀	♂	♂	♀	♀	♀	♀	♀	♀	♀
	L	A	6	U	T	J	N	=	4	C	E	2	1	B	K	5	Y	9
L			3		5	4	4	6	10	4	11	1	2	7	3	5	5	3
A			6		3	3	8	2	7	3	6	3	4	5	1	4	2	6
6				1	4	1	4			2	1	2	4	1		2		1
U					9	4	5		3	5	6	5	4					
T						11	2	2	4	5	10		3	6 / 2	2	3	5	5
J							4						1	3	1	2		4
N								3	1	1	2 / 2			2	4	8	7	5
=									5	3	5	3	1	1		3		
4						2						1	10 / 2	5	3	5	1	2
C												2	8	3	3	1	6	8
E													8	2	4	1	3	2
2														1		3	4 / 2	
1								2							4	11	7	13
B																1	2	
K				1														3
5																		
Y																		
9																		

Figure 1. Dominance matrix for the 18 barnacle geese ($N = 474$ interactions). The geese are ordered according to the dominance rank that best fitted the linear hierarchy. The left number in each filled cell indicates the number of encounters won by the bird in that row over the bird in that column and the number on the right indicates the number of encounters won by the bird in that column over the bird in that row. The underlined numbers, below the diagonal, indicate pair-specific inconsistencies that did not fit the linear hierarchy.

Second, the leadership test was performed over a period of 17 days, using each individual once per day. If there was a strong effect of novelty then we would expect that the effect of the novel-object score would diminish over time. However, this appeared not to be the case because there was a strong correlation between novel-object score and leadership score during the first 9 days as well as during the last 8 days of the leadership test.

Whether a goose arrived at the food patch was affected not only by the novel-object score of the focal individual but also by the novel-object score of its companion. Individuals paired with a bolder companion arrived more often at the food patch. This effect was very pronounced: in the presence of the boldest companion the focal individual had a 100% chance of arriving at the food patch, whereas in the presence of the shyest individual this probability was less than 60% (Fig. 4). Thus, although personality has a genetic (van Oers et al. 2005a) and a rigid underlying physiological mechanism (Koolhaas et al. 1999), and traits are genetically correlated (van Oers et al. 2004), the expression of the behaviour in a social context depends strongly on the behaviour of other members. To our knowledge, this is one of the few studies that show that an independent personality trait measured in a nonsocial context affects the behaviour of other group members in a social context. A number of other studies have recently shown that the behaviour of an individual changes according to the personality

type of the group members, but most studies use personality measurements assessed in a social context (Magnhagen & Staffan 2005; Sih & Watters 2005; Dyer et al. 2008; Michelena et al. 2008) thereby providing no independent measure of a personality trait, because the social context may alter the behavioural expression of individuals (as clearly shown in this study). Harcourt et al. (2009) studied leadership in three-spined sticklebacks and showed that the tendency to follow another individual increased with the boldness score of the partner and the tendency to follow was greater with decreasing boldness in the following individual. They concluded that leadership emerges from differences in personality traits. However, boldness and leadership were measured in the same context and in similar ways, so they did not provide an independent measure of a personality trait. van Oers et al. (2005b) showed that the correlation between exploratory behaviour and risk-taking behaviour in great tits is dependent on the personality of a nearby companion that visibly foraged in a separate compartment. Slow-exploring males became bolder in the presence of a companion, and this effect was larger with increasing boldness of the companion, whereas fast-exploring males did not change their behaviour in reaction to the presence of a companion. These authors, however, did not investigate whether the focal individual followed the companion. Recently, Schuett & Dall (2009) showed in pairs of zebra finches that the time the pair spent

Table 2

Results of multiple correlations between dominance, body size, body condition, behaviours and outcomes of the leadership test

	Body size	Body condition	Exploration	Activity	Novel object	Leader	Arrival time
Dominance	$r_S = 0.732$ $P < 0.001$	$r_S = -0.301$ $P = 0.23$	$r_S = 0.260$ $P = 0.29$	$r_S = 0.240$ $P = 0.34$	$r_S = 0.193$ $P = 0.44$	$r_S = 0.256$ $P = 0.31$	$r_S = -0.036$ $P = 0.89$
Body size		$r = 0.000$ $P = 1.00$	$r = 0.283$ $P = 0.25$	$r = 0.088$ $P = 0.73$	$r = 0.195$ $P = 0.44$	$r = 0.066$ $P = 0.79$	$r = 0.187$ $P = 0.46$
Body condition			$r = -0.272$ $P = 0.27$	$r = -0.222$ $P = 0.38$	$r = 0.332$ $P = 0.18$	$r = 0.155$ $P = 0.54$	$r = -0.198$ $P = 0.43$
Exploration				$r = 0.587$ $P = 0.010$	$r = 0.419$ $P = 0.083$	$r = 0.229$ $P = 0.36$	$r = -0.164$ $P = 0.52$
Activity					$r = 0.145$ $P = 0.57$	$r = 0.105$ $P = 0.68$	$r = -0.129$ $P = 0.61$
Novel object						$r = 0.730$ $P < 0.001$	$r = -0.706$ $P = 0.001$
Leader							$r = -0.888$ $P < 0.001$

Leader was calculated from the total number of trials an individual led. Arrival time was the average arrival time at the food patch. P values are sequential Bonferroni corrected. Significant results are given in bold.

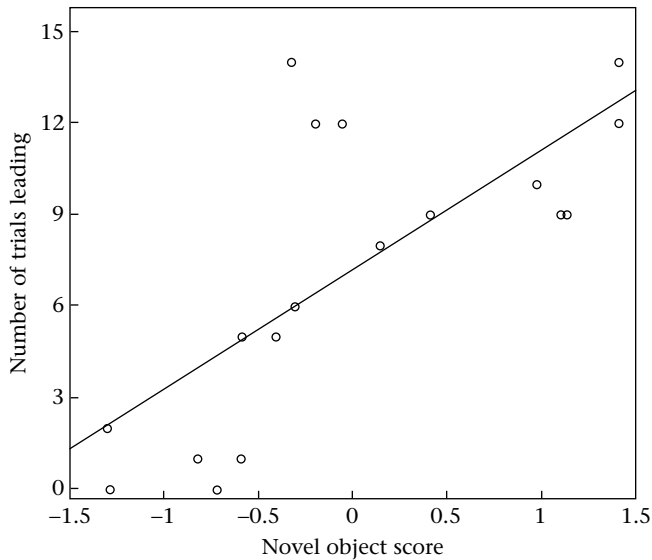


Figure 2. Individuals with a higher novel-object score (i.e. bolder) led the group more often. $N = 18$. The line is a linear regression line. Shown are raw means.

together at a feeder increased with increasing difference in exploratory behaviour between both individuals, suggesting that some characters may be better at forming stable groups.

Our study shows that movement patterns of group-living animals can be highly affected by the personality types in the group. It suggests that individuals may possess information about a food location but that the ability to use this information may be dependent on the personality types of the group members. This effect might be bigger when the cost of leaving a group is high (e.g. Prins 1996). Detailed experiments whereby an individual is informed about the location of a feeding site and tested together with the presence of different personality types might illuminate this topic. Moreover, because our results show that bolder individuals more often take the lead, it would be interesting to study how information provided by different personality types is treated. One might expect that the information of bolder individuals is more

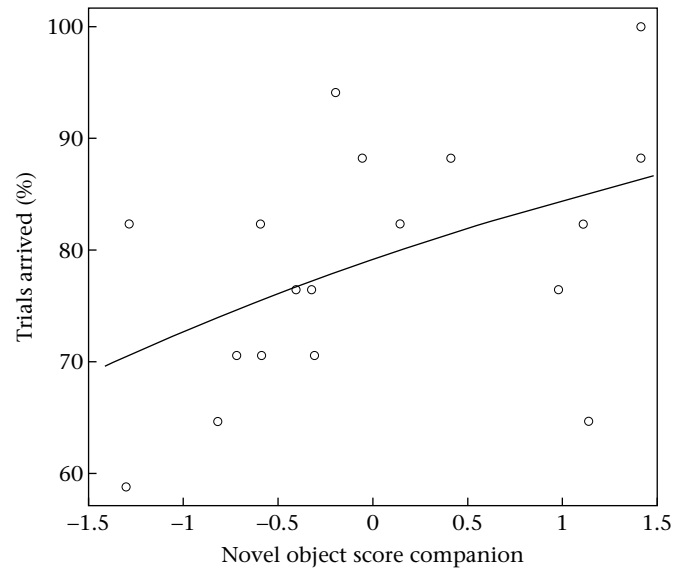


Figure 4. Individuals paired with a companion with a higher novel-object score (i.e. bolder) arrived more often at the food patch. $N = 18$. The line is a logit regression line. Shown are raw means.

readily used, given their ability to lead a group. In other words, the value of an individual's personal information in the decision of the group on where to go next might depend on its personality. A deeper understanding of collective action can thus be gained by studying the differences in the behaviour of individuals (Harcourt et al. 2009).

In conclusion we have shown that activity and boldness are highly repeatable in the barnacle goose and the personality of an individual is predictive for the leadership towards a food patch. The arrival probability of an individual was strongly affected by the personality both of itself and of its companion, suggesting that movement patterns of the group as a whole can be affected by the mix of personality types present in the group.

Acknowledgments

The authors are very grateful to Bart Nolet and Marcel Klaassen for facilitating the animal holding facilities. We thank Bart Nolet and Piet Drent for advice on the design of the experiment. We thank Erica Ras for practical assistance during the whole course of the experiment, Henk van der Jeugd for sexing the geese, and Rudy Jonker for taking morphological measurements and advice on the statistical analysis. We thank the Faunafonds and the Koninklijke Nederlandse Jagers Vereniging for financial support. Last, we thank two anonymous referees and one editor for their constructive and helpful comments on the manuscript. This is publication 4549 of the Netherlands Institute of Ecology.

References

- Barnett, S. A. & Cowan, P. E. 1976. Activity, exploration, curiosity and fear—ethological study. *Interdisciplinary Science Reviews*, **1**, 43–62.
- Beauchamp, G. 2000. Individual differences in activity and exploration influence leadership in pairs of foraging zebra finches. *Behaviour*, **137**, 301–314.
- Becker, W. A. 1984. *Manual of Quantitative Genetics*, 4th edn. Pullman, Washington: Academic Enterprises.
- Carere, C. & Eens, M. 2005. Unravelling animal personalities: how and why individuals consistently differ. *Behaviour*, **142**, 1149–1157.
- Dingemanse, N. J. & Reale, D. 2005. Natural selection and animal personality. *Behaviour*, **142**, 1159–1184.
- Drent, P. J., van Oers, K. & van Noordwijk, A. J. 2003. Realized heritability of personalities in the great tit (*Parus major*). *Proceedings of the Royal Society B*, **270**, 45–51.

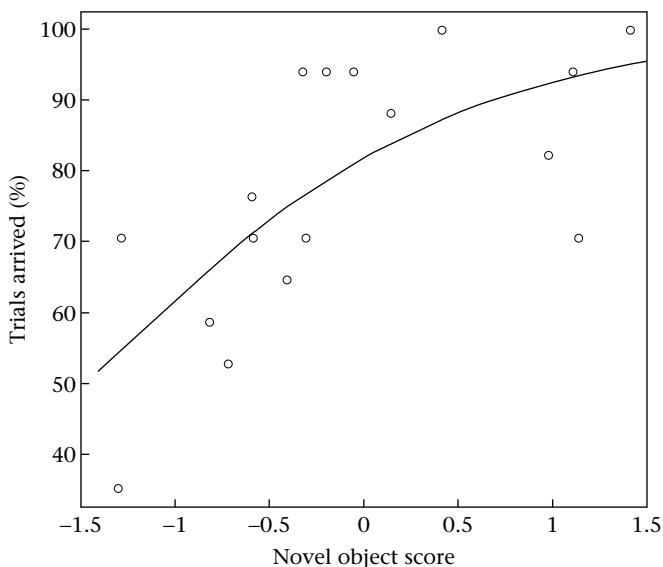


Figure 3. Individuals with a higher novel-object score (i.e. bolder) arrived more often at the food patch. $N = 18$. The line is a logit regression line. Shown are raw means.

- Dumont, B., Boissy, A., Achard, C., Sibbald, A. M. & Erhard, H. W. 2005. Consistency of animal order in spontaneous group movements allows the measurement of leadership in a group of grazing heifers. *Applied Animal Behaviour Science*, **95**, 55–66.
- Dyer, J. R. G., Croft, D. P., Morrell, L. J. & Krause, J. 2008. Shoal composition determines foraging success in the guppy. *Behavioral Ecology*, **20**, 165–171.
- Fischhoff, I. R., Sundaresan, S. R., Cordingley, J., Larkin, H. M., Sellier, M. J. & Rubenstein, D. I. 2007. Social relationships and reproductive state influence leadership roles in movements of plains zebra, *Equus burchellii*. *Animal Behaviour*, **73**, 825–831.
- Frost, A. J., Winrow-Giffen, A., Ashley, P. J. & Sneddon, L. U. 2007. Plasticity in animal personality traits: does prior experience alter the degree of boldness? *Proceedings of the Royal Society B*, **274**, 333–339.
- Gosling, S. D. & John, O. P. 1999. Personality dimensions in nonhuman animals: a cross-species review. *Current Directions in Psychological Science*, **8**, 69–75.
- Groothuis, T. G. G. & Carere, C. 2005. Avian personalities: characterization and epigenesis. *Neuroscience and Biobehavioral Reviews*, **29**, 137–150.
- Harcourt, J. L., Ang, T. Z., Sweetman, G., Johnstone, R. A. & Manica, A. 2009. Social feedback and the emergence of leaders and followers. *Current Biology*, **19**, 248–252.
- Koolhaas, J. M., Korte, S. M., De Boer, S. F., Van Der Vegt, B. J., Van Reenen, C. G., Hopster, H., De Jong, I. C., Ruis, M. A. W. & Blokhuis, H. J. 1999. Coping styles in animals: current status in behavior and stress-physiology. *Neuroscience and Biobehavioral Reviews*, **23**, 925–935.
- Krause, J. 1994. Differential fitness returns in relation to spatial position in groups. *Biological Reviews*, **69**, 187–206.
- Leblond, C. & Reeb, S. G. 2006. Individual leadership and boldness in shoals of golden shiners (*Notemigonus crysoleucas*). *Behaviour*, **143**, 1263–1280.
- Lessells, C. M. & Boag, P. T. 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*)? *Behavioral Ecology and Sociobiology*, **57**, 295–303.
- Martins, T. L. F., Roberts, M. L., Giblin, I., Huxham, R. & Evans, M. R. 2007. Speed of exploration and risk-taking behavior are linked to corticosterone titres in zebra finches. *Hormones and Behavior*, **52**, 445–453.
- Michelena, P., Sibbald, A. M., Erhard, H. W. & McLeod, J. E. 2008. Effects of group size and personality on social foraging: the distribution of sheep across patches. *Behavioral Ecology*, **20**, 145–152.
- van Oers, K., Drent, P. J., de Goede, P. & van Noordwijk, A. J. 2004. Realized heritability and repeatability of risk-taking behaviour in relation to avian personalities. *Proceedings of the Royal Society B*, **271**, 65–73.
- van Oers, K., de Jong, G., van Noordwijk, A. J., Kempenaers, B. & Drent, P. J. 2005a. Contribution of genetics to the study of animal personalities: a review of case studies. *Behaviour*, **142**, 1185–1206.
- van Oers, K., Klunder, M. & Drent, P. J. 2005b. Context dependence of personalities: risk-taking behavior in a social and a nonsocial situation. *Behavioral Ecology*, **16**, 716–723.
- van Oers, K., Drent, P. J., Dingemans, N. J. & Kempenaers, B. 2008. Personality is associated with extrapair paternity in great tits, *Parus major*. *Animal Behaviour*, **76**, 555–563.
- Poisbleau, M., Jenouvrier, S. & Fritz, H. 2006. Assessing the reliability of dominance scores for assigning individual ranks in a hierarchy. *Animal Behaviour*, **72**, 835–842.
- Prins, H. H. T. 1996. *Ecology and Behaviour of the African Buffalo: Social Inequality and Decision-Making*. London: Chapman & Hall.
- Reale, D., Reader, S. M., Sol, D., McDougall, P. T. & Dingemans, N. J. 2007. Integrating animal temperament within ecology and evolution. *Biological Reviews*, **82**, 291–318.
- Reeb, S. G. 2000. Can a minority of informed leaders determine the foraging movements of a fish shoal? *Animal Behaviour*, **59**, 403–409.
- Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution*, **43**, 223–225.
- Schuett, W. & Dall, S. R. X. 2009. Sex differences, social context and personality in zebra finches, *Taeniopygia guttata*. *Animal Behaviour*, **77**, 1041–1050.
- Sih, A. & Watters, J. V. 2005. The mix matters: behavioural types and group dynamics in water striders. *Behaviour*, **142**, 1417–1431.
- Sih, A., Bell, A. & Johnson, J. C. 2004a. Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution*, **19**, 372–378.
- Sih, A., Bell, A. M., Johnson, J. C. & Ziemba, R. E. 2004b. Behavioral syndromes: an integrative overview. *Quarterly Review of Biology*, **79**, 241–277.
- Smith, B. R. & Blumstein, D. T. 2008. Fitness consequences of personality: a meta-analysis. *Behavioral Ecology*, **19**, 448–455.
- Stahl, J., Tolsma, P. H., Loonen, M. & Drent, R. H. 2001. Subordinates explore but dominants profit: resource competition in high Arctic barnacle goose flocks. *Animal Behaviour*, **61**, 257–264.
- Stankowich, T. 2003. Marginal predation methodologies and the importance of predator preferences. *Animal Behaviour*, **66**, 589–599.
- Verbeek, M. E. M., Drent, P. J. & Wiepkema, P. R. 1994. Consistent individual differences in early exploratory behaviour of male great tits. *Animal Behaviour*, **48**, 1113–1121.
- de Vries, H. 1995. An improved test of linearity in dominance hierarchies containing unknown or tied relationships. *Animal Behaviour*, **50**, 1375–1389.
- de Vries, H. 1998. Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. *Animal Behaviour*, **55**, 827–843.
- de Vries, H., Netto, W. J. & Hanegraaf, P. L. H. 1993. MatMan—a program for the analysis of sociometric matrices and behavioural transition matrices. *Behaviour*, **125**, 157–175.
- Walsh, R. N. & Cummins, R. A. 1976. Open-field test—critical review. *Psychological Bulletin*, **83**, 482–504.