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Personality differences explain leadership in barnacle geese

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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.

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).

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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 & Reebs 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 ($\pm$0.1 mm) using callipers, wing length ($\pm$1.0 mm) using a ruler, and body mass ($\pm$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.