Personality in a group living species

Social information, collective movements and social decision-making

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Personality in a group living species

Social information, collective movements and social decision-making

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Contents

Chapter 1

General introduction

Many animals live in groups either year round, or during large parts of the year. Groups are a collection of individuals and much work has been done to understand how and why individuals live in groups (Giraldeau & Caraco 1999; Krause & Ruxton 2002; Beauchamp 2010). An important aspect in group-living is the question whether individuals within groups are similar or dissimilar. The degree of (dis)similarity between individuals within groups can have important consequences for the functioning of groups on many different hierarchical levels. The degree of (dis)similarity between individuals may for example affect collective movements (Conradt & Roper 2009), group formation processes (Ranta *et al.* 1996) and social organization within groups (Krause *et al.* 2010). Therefore, understanding whether individuals within groups behave similar or not is of vital importance for many ecological processes. Differences between individuals in a group might arise as a result of dominance, sex or age and these differences can lead to differences in behaviour between individuals in groups but also to different outcomes at the level of the group. To illustrate, more dominant individuals may occupy positions in the centre of groups to profit more from food discoveries of other individuals (Barta *et al.* 1997; Monus & Barta 2008). In chacma baboons, *Papio ursinus*, males are more influential in the morning departures than females (Stueckle & Zinner 2008) and in several species it has been shown that adults predominantly initiate group movements (Rowell 1969; Lamprecht 1992; Sueur & Petit 2008, see also Petit & Bon 2010). Individuals of the same species might also differ in personality. Animal personality is a relatively new field in behavioural ecology and only recently started to receive considerable attention from behavioural and evolutionary ecologists (Réale *et al.* 2007). Surprisingly little attention, however, has been paid to the role of animal personality in the context of group-living. In this thesis I studied the importance of personality on various aspects of group-living focusing on leadership, collective movement, decision making and social information use.

Animal personality Personality in animal behaviour describes the phenomenon 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; Réale *et al.* 2007; Dingemanse *et al.* 2010). Different behavioural and physiological reactions are often correlated, suggesting that these differences are fundamental aspects of the behavioural organization of individuals. Personality traits are heritable (Drent *et al.* 2003, van Oers *et al.* 2005; Bell 2007; Fidler *et al.* 2007) and several studies show that animal personality is the subject of natural (Dingemanse & Réale 2005; Smith & Blumstein 2008) and sexual selection (van Oers *et al.* 2008; Schuett & Dall 2010). The concept of inter-individual differences has also been referred to as coping styles (Koolhaas *et al.* 1999), temperament (Réale *et al.* 2007) and behavioural syndromes (Sih *et al.* 2004a, b). Recently, there has been a sharp increase in studies reporting individual variation in behaviour between individuals within a population across a wide range of animal taxa (Réale *et al.* 2007; Biro & Stamps 2008; Sih & Bell 2008), including insects (Gyuris *et al.* 2011), reptiles (Cote *et al.* 2008), birds (Carere & Eens 2005; Groothuis & Carere 2005), fish (Schurch & Heg 2010), mammals (Michelena *et al.* 2009) and many more. A recent meta-analysis estimated that individual differences in behaviour explain > 30% of the phenotypic variance within populations (Bell *et al.* 2009). Around 35% of the variation among individuals in behaviour was explained by individual differences, though it has to be acknowledged that part of this variation might be explained by sex, age or dominance. This altogether illustrates that animal personality is widespread in the animal kingdom and an important process in evolutionary ecology.

Collective movements Predicting and understanding the movement of animal groups is an important goal for both ecology (Nathan *et al.* 2008; Holyoak *et al.* 2008) and conservation biology (Rubenstein & Hobson 2004; Struye *et al.* 2010). The movement of animal groups is ultimately the consequence of the behaviour of individuals. However, linking individual behaviour to group-level outcomes is still a major challenge, because it is often unknown how the behavioural rules of individuals translate into group-level outcomes, as well as which individuals contribute most to the up-scaling from individual behaviour to collective movements. One of the intriguing questions is which individuals contribute most to collective movements (Conradt & Roper 2009). The importance of individual differences on collective movements is illustrated by studies where information was provided to only a few individuals within a group. Both in fish and humans, a small minority of informed individuals were able to guide a group to a target destination (Reebs *et al.* 2000; Dyer *et al.* 2009; see also Couzin *et al.* 2005). An extreme example of the importance of individual variation on collective movements comes from chacma baboons. In this species alpha-males were able to steer a group towards a food source where few individuals besides the alpha-male were able to consume food (King *et al.* 2008). Examples of the importance of dominance come primarily from species with strong social group structure, like several species of monkeys, in which the highest ranked individuals have a strong influence over the behaviour of other individuals (Deaner *et al.* 2005; King *et al.* 2008; Sueur & Petit 2008). These studies show that variation between individuals in groups may have profound consequences on collective movements. Given that personality in animal behaviour describes the phenomenon that differences between individuals in behavioural and physiological traits are consistent over time and context, it leads to the question how important variation in personality is in collective movements. This is a remarkably poorly understood subject and in this thesis I investigated the role of animal personality on collective movements. More specifically, I studied whether variation in personality corresponded to variation in leadership and subsequently to collective movements. Leadership is the initiation of new directions of locomotion by one or more individuals, which are then followed by other group members (Krause *et al.* 2000).

Social information use One of the benefits of living in groups is that an individual has access to social information. Individuals might use two forms of information, either personal information, usually retrieved on a trial and error basis by interacting with the physical environment, or they might use information made available by other individuals, known as social information (Danchin *et al.* 2004; Dall *et al.* 2005). Social information use has been studied extensively in a wide variety of species and in many different contexts (Galef & Giraldeau 2001; Valone & Templeton 2002; Danchin *et al.* 2004; Valone 2007). Individuals use social information to decide with whom to mate (mate choice copying, Nordell & Valone 1998; Valone & Templeton 2002), where to breed (habitat copying, Danchin *et al.* 1998), where to forage (Drent & Swierstra 1977; Coolen *et al.* 2003), when to leave a food patch (Templeton & Giraldeau 1995, 1996), what food to eat (Galef 1990) and when to flee from a predator (Chivers & Smith 1998). Social information use indeed affects various important aspects of an individual's ecology, such as foraging, dispersal and space use (Seppänen *et al.* 2007).

Despite a rich tradition of studies on social information use the relationship between animal personality and social information use is poorly studied. In this thesis I studied whether variation in personality traits is correlated with variation in the use of social information. That the value of social information might be different for 2 individuals in a group can be illustrated by a simple example. Consider a group of 3 individuals with individual a dominant over b and c, and individual b dominant over c. If individual b finds a food patch which can be monopolized this information is valuable for individual a, as it can displace individual b and take over the food patch. However, for individual c the exact same information is not valuable since it cannot use the information as it can not displace individual b and access the food. This illustrates that within a group of individuals the value of social information might differ between individuals. Despite this obvious example, there are few studies which take an individual approach to social information use and generally it is assumed that social information is equally valuable to each individual in a population and consequently most studies focus on the conditions under which an animal is expected to use social information (Galef & Giraldeau 2001; Danchin *et al.* 2004; Kendal *et al.* 2005; Valone 2007). In this thesis I studied the relationship between social information use and personality in several different contexts to test if variation in personality reflects differences in the use of social information.

Maintenance of variation One of the major challenges in animal personality is to explain the evolution and maintenance of animal personality. Several (non-mutually exclusive) mechanisms have been suggested, including spatiotemporal variation in environmental conditions (Sih *et al.* 2003; Dall *et al.* 2004; Dingemanse *et al.* 2004; Smith & Blumstein 2008; Réale *et al.* 2010), differences in life-history trade-offs (Wolf *et al.* 2007; Gyuris *et al.* 2010; see also Biro & Stamps 2008; Réale *et al.* 2009) and sexual selection (Schuett *et al.* 2010). A fourth mechanism is negative frequency dependent selection (Wolf *et al.* 2008).

Negative frequency dependent selection operates against common phenotypes, thereby favouring the rarer phenotype in a population. The rarer phenotype for example suffers less from predation. Negative frequency dependent selection is used in many areas of evolutionary biology (Maynard Smith 1982) and is predicted to be important in generating variation in personality (Sih *et al.* 2004; Réale *et al.* 2007; Wolf *et al.* 2008; Wolf & Weissing 2010). However, there is currently very little experimental evidence of negative frequency dependent selection in maintaining variation in animal personality. The benefits of using social information are known to be negative frequency dependent in many situations. For instance, in producer–scrounger games where an individual can either produce food or scrounge from food discoveries of others, it is well-known that payoffs to the scrounging tactic are negative frequency dependent since the value of scrounging decreases with an increase in the proportion of scrounging tactic in the population (Barnard & Sibly 1981; Giraldeau *et al.* 1994; Mottley & Giraldeau 2000). If personality and social information use are linked, variation in personality might be maintained as a result of differences in information use between different personality types, resulting in the maintenance of variation in personality in a population. In this thesis I will test this idea both experimentally and theoretically.

Study species The barnacle goose, *Branta leucopsis,* is used as study species. The barnacle goose is a highly gregarious avian herbivore, occurring in large flocks throughout most of its lifetime (Ydenberg *et al.* 1983). Barnacle geese are selective foragers that use both food biomass and food quality in their patch choice (Ydenberg & Prins 1981; Teunissen *et al.* 1985; Vickery *et al.* 1994; Riddington *et al.* 1997; Hassall *et al.* 2001; Durant *et al.* 2004; Bos *et al.* 2005). They exploit the fresh growth of food plants (Prins *et al.* 1980; Ydenberg & Prins 1981) and their food resources are highly variable both in time and in space as a result of depletion, regrowth and change in quality. Therefore, information has to be regularly updated (Ydenberg *et al.* 1983) and it is known that geese switch habitats in the course of one season (Prins & Ydenberg 1985; Vickery *et al.* 1995). Indeed, barnacle geese have to decide frequently where to eat, when to leave a patch and whom to follow. Given the uncertainty of their food resources, their nature as selective foragers and their high gregariousness, the barnacle goose is an ideal study species to study collective movements and social information use. And indeed several studies demonstrate that geese move collectively (Lamprecht 1992; Ramseyer *et al.* 2009) and make use of social information. Drent & Swierstra (1977) showed in a field experiment that groups of artificial geese models attract barnacle geese, providing evidence that the presence of individuals is used in patch choice decisions, a phenomenon also known as local enhancement. Ydenberg *et al.* (1983) suggested that geese make use of post roost gatherings to collect social information of foraging opportunities in nearby areas. Stahl *et al.* (2001) showed that dominant barnacle geese keep track of the foraging success of subordinates. After subordinates discovered high quality patches they were quickly displaced by the dominant individuals, a system known as producer–scrounger game. Lastly, the function of alert behaviour (‘vigilance’) is suggested to function not only as anti-predator behaviour but also to keep informed about the foraging success of conspecifics (Drent & Swierstra 1977; Stahl *et al.* 2001).

Societal relevance The Netherlands is experiencing a spectacular increase in the number of wintering geese in the past few decades (van Eerden *et al.* 2005) most likely due to an increase in the availability of high quality grass (van Eerden *et al.* 2005) and a decrease in hunting pressure (Ebbinge 1991). As a result conflicts between farmers and geese have increased dramatically (van der Zee *et al.* 2009). In order to reduce conflicts accommodation areas have been assigned where geese are tolerated. The success of these areas varies. Some areas are visited throughout the whole winter whereas other areas are rarely visited (van der Zee *et al.* 2009). Social information can be of major importance in the distribution of individuals over a landscape (see for instance Hancock & Milner-Gulland 2006; Nocera *et al.* 2009; Nocera & Forbes 2010) and barnacle geese are not an exception to this as illustrated by their strong grouping behaviour and social attraction. Thus a better understanding of the mechanisms and functions of personal and social information can help us to better understand the distribution patterns of barnacle geese. Most current models on the distribution of geese do not include social factors in their models but only focus on resource quality (Percival & Percival 1997; Bos *et al.* 2005; Fox *et al.* 2006; Ely & Raveling 2011) and/or disturbance (Tamisier *et al.* 2003; Kahlert 2003; Tombre *et al.* 2005). One positive exception is the study by Amano *et al.* (2006) where the model with the assumption that there are benefits of group foraging gave the best fit with empirical data, suggesting that it is necessary to include social factors to understand distribution patterns. Thus understanding the role of social information and collective movements might help to understand the movement and distribution patterns of wild geese. Therefore, a better understanding of both the mechanisms and the functions of social foraging information is required. Experiments are a suitable way to gain insight in the role of social information because in an experimental setting it is possible to control (and manipulate) the available information and the available options for an individual. In the field it is much more difficult to control (or even understand) both the availability of information and the available options.

Outline of the thesis

In chapter 2 I performed several personality tests on barnacle geese to test for the presence of consistent individual behavioural differences. I show that individual barnacle geese differ consistently in their activity level and their reaction towards novel objects over a period of one year. Subsequently, I tested the importance of these differences in a social foraging task whereby a pair of individuals was allowed to approach a food patch. I show that the reaction towards the novel object (hereafter called boldness) is important in this foraging task. Bolder individuals walked more often in front and arrived more often and quicker at the food patch than shyer individuals. In addition, I show that the arrival of an individual did not only depend on its own boldness score, but also on the boldness score of the companion individual. When paired with a bold companion an individual arrived more often than when paired with a shy companion.

In chapter 3 I studied the importance of boldness on collective movements in the presence of informed individuals. I introduced naïve barnacle geese, differing in boldness score, in a labyrinth in groups with either one or three informed demonstrators to study if naïve individuals would make use of the social information of the demonstrators. The demonstrators possessed information about the route through the labyrinth. In pairs, the probability of choosing a route prior to the informed demonstrator increased with increasing boldness score: bolder individuals decided more often for themselves where to go compared with shyer individuals, whereas shyer individuals waited more often for the demonstrators to decide and followed this information. In groups of four individuals, however, there was no effect of boldness on decision making.

In chapter 4 I tested the social information use of different personality types. Individuals were allowed to watch two pairs of demonstrators. One pair of demonstrators received food, whereas the other pair of demonstrators did not receive any food. After an observation period the individual was allowed to join one of both demonstrator pairs. By scoring which individuals joined the foraging pair of demonstrators I was able to test if differences in boldness levels predicted the use of social information. I found that shyer individuals used social information more often than bold individuals. In chapter 5 I tested the use of social information in a more natural situation where individuals had to search for food in groups in a producer–scrounger game. Individuals could either search for food themselves (personal information, producing) or join food discoveries of other individuals (social information, scrounging). I show that the frequency of scrounging increased with decreasing boldness score. In chapter 6 I performed an experiment to disentangle the finding and joining role by experimentally forcing individuals differing in boldness score in either a finding or a joining role. I show that boldness affected the producing behaviour, with bolder individuals producing faster than shyer, whereas boldness did not affect the joining behaviour.

In chapter 7 I tested for negative frequency dependent feeding success of barnacle geese in a producer–scrounger experiment. I tested if the rare personality type enjoyed higher feeding success than the common type. I found no evidence for negative frequency dependent feeding success. Rather, I found that both bold and shy individuals enjoyed higher feeding success when foraging with bold than when foraging with shy companions. The higher feeding success of individuals in the presence of bold companions was explained by the higher number of joining events, and a higher joining proportion than when foraging with shy companions. In chapter 8 I studied the co-evolution of boldness and foraging tactic use using a genetic algorithm approach. In the simulations bold individuals evolved to play both producer and scrounger, whereas shy individuals remain confined to scrounging. For each parameter combination the genetic algorithm selected a single optimum level of boldness for all individuals demonstrating the absence of any negative frequency dependent selection of personality types in a producer–scrounger game. The results did however show that differences in ecological conditions (like predation or patch density) in a social foraging game may generate variation in boldness between populations. In the last chapter, chapter 9, I present a synthesis of the main findings and discuss the relationship between personality, social information use and collective movements.

Chapter 2

Personality differences explain leadership in barnacle geese

Ralf HJM Kurvers, Babette Eijkelenkamp, Kees van Oers, Bart van Lith, Sipke E van Wieren, Ronald C Ydenberg & Herbert HT Prins

Personality in animal behaviour describes the phenomenon 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 relation 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 movement of individuals in pairs towards a feeding patch was scored. We found high repeatability scores for activity and novel object score 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 is 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.

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Introduction

Personality in animal behaviour describes the phenomenon 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 inter-individual 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 leads 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).

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 relation 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, since in group living animals the behaviour of an individual might depend on the personality traits of their 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 to 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 biases. 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 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 video taped 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, observations were made 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 thereby 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). Since 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 which served as the entrance of 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 opening the slide. All experiments were done between 900 – 1230 hours, a.m. local time. 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 numbers 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 in the arena (see above). The experimental order was randomized. 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 Since activity is preferably measured in a familiar environment (Barnett & Cowan 1976), we introduced each goose four times in 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 in 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 geese did not arrive within close distance (50 cm) of the novel object they were 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. Since 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 one and test two 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 one and test two, respectively.

As a measure of exploration score 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 x 0.2 m). The first goose which arrived 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 9 trials per day and 153 trials in total over a period of 17 days (15 February - 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 as compared to 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 repeatabilities of activity and novel object score for period 1 and period 2 separately and for both periods combined. Since exploration score of an open field was performed only once during each period we could calculate repeatability only for both periods combined. We compared repeatabilities 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 indices vary from 0 (complete absence of linearity) to 1 (complete linearity). Statistical significance of *K* is calculated by a chi-squared 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 Pearson correlation coefficient (r) if the data were normally distributed or 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 analyze the effect on arrival yes/no, we used generalized linear mixed models with binomial errors and a logit-link function. (2) To analyze the effect on arrival time within the group of individuals which 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 dominance and the 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 non-significant terms ($P > 0.1$), starting with the highest-order interactions and / or the least significant term. To compare the explanatory power of two subsequent models we used a log-likelihood ratio test which follows a χ^2 distribution, with degrees of freedom equal to the difference in the number of parameters between the two models. We 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).

Table 2.1 Repeatability scores of different behaviours in January 2008 (period 1), in November 2008 (period 2), and both periods combined. Means ± SE are shown. $N = 18$. *t* statistics refer to the comparison of repeatabilities between period 1 and 2.

Behaviour	Period 1	Period 2	Both periods	*t* test	*P* value
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

Table 2.2 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.

	♂	♂	♂	♂	♂	♀	♂	♀	♀	♂	♂	♀	♀	♀	♀	♀	♀	♀
	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						$\underline{2}$			■		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								$\underline{2}$					■	4	11	7	1	13
B														■	1	2		
K				$\underline{1}$											■	1		3
5																■	2	
Y																	■	
9																		■

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 2.1). Repeatability of the open field exploration score was low (0.04) (Table 2.1).

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 (Table 2.2). Dominance rank was significantly correlated with body size (Table 2.3) but there was no correlation with body condition (Table 2.3). Males had on average higher dominance ranks than females ($U = 7$, $N_1 = 8$, $N_2 = 10$, $P < 0.01$) (see also Table 2.2).

Correlations between sex, behaviours and dominance Males had a larger body size (mean ± SD = 0.66 ± 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 2.3). Neither body size nor body condition were significantly correlated with exploration, activity or novel object score (Table 2.3). There were no significant correlations between the three behaviours (exploration, activity and novel object score; Table 2.3).

Table 2.3 Results of multiple correlations between dominance, body size, body condition, different behaviours and outcomes of the leadership test. Leader = the total number of trials an individual led. Arrival time = the average arrival time at the food patch. Shown are correlation coefficients (*r*). *P* values are sequential Bonferonni corrected.

	body size	body condition	exploration	activity	novel object	leader	arrival time
dominance	0.73***	-0.30	0.26	0.24	0.19	0.26	-0.04
body size		0.00	0.28	0.09	0.20	0.07	0.19
body condition			-0.27	-0.22	0.33	0.16	-0.20
exploration				0.59	0.42	0.23	-0.16
activity					0.15	0.11	-0.13
novel object						0.73***	-0.71**
leader							-0.89***

** $P < 0.01$, *** $P < 0.001$

Leadership Novel object score was significantly correlated with the leadership score (= number of trials leading; Table 2.3, Fig. 2.1). Likewise, individuals with a higher novel object score arrived at the food patch more quickly (Table 2.3). Leadership was not significantly correlated with dominance, exploration, activity, body size or body condition (Table 2.3). 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 2.3) 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 ($\chi^2 = 12.04$, $P < 0.001$; Fig. 2.2a) and that individuals paired to a companion with a higher novel object score also arrived more often ($\chi^2 = 5.20$, $P = 0.023$; Fig. 2.2b). None of the other variables were significant (all $P > 0.1$). Within the group of individuals which arrived, individuals with a high novel object score arrived earlier at the food patch ($\chi^2 = 4.86$, $P = 0.031$), but the novel object score of the companion did not significantly explain arrival time ($\chi^2 = 2.42$, $P = 0.12$). None of the other variables were 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 at the food patch. Moreover, individuals paired to a bolder companion had a higher chance to arrive at the food patch.

Repeatability scores of activity and boldness were high, both within a period and between periods. The only behaviour which 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) since the arena was identical, or that this test is not adequate to measure the exploration of an open field in barnacle geese. The high

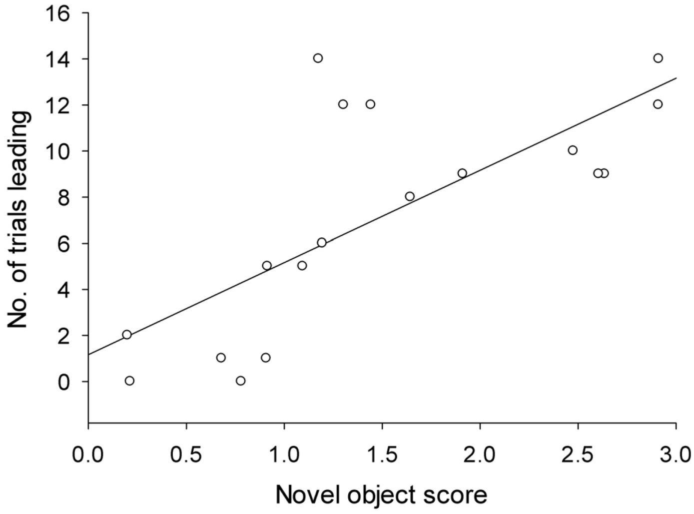

Figure 2.1 Individuals with a higher novel object score (i.e. bolder) were more often leading the group. $N = 18$. The line is a linear regression line. Shown are raw means.

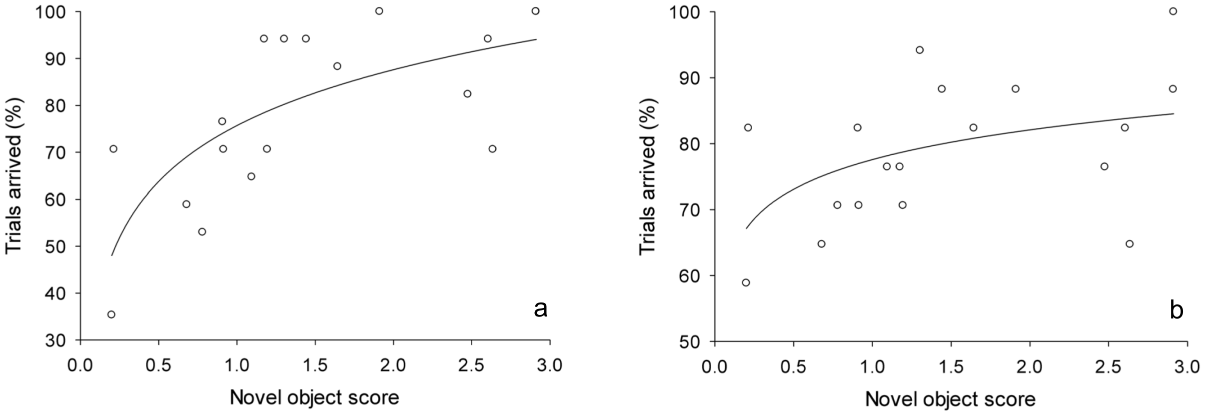

Figure 2.2 (a) Individuals with a higher novel object score (i.e. bolder) and (b) individuals paired to a companion with a higher novel object score (i.e. bolder) arrived more often at the food patch. $N = 18$. Lines are logit regression lines. Shown are raw means.

repeatability scores over time and the strong correlation between novel object score and leadership suggests 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 of an individual. 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 relation 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 was found in golden shiners (Leblond & Reebs 2006). However, these studies did not provide evidence that the individual variation in behaviour is repeatable over time and / or context and thus did not study personality but personality traits. Here we demonstrate 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. Firstly, the individuals were used to forage from such a patch in their outdoor enclosure. Hence, the individuals were familiar to the “object” itself. Secondly, 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 since there was a strong correlation between novel object score and leadership score during the first nine days as well as during the last eight days of the leadership test.

Whether or not 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 the companion. Individuals paired to 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 chance of 100 percent of arriving at the food patch, whereas in the presence of the shyest individual this probability was less than 60 percent (Fig. 2.2b). Thus, although personality has a genetic (van Oers *et al.* 2005) and 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 demonstrate that an independent personality trait measured in a non-social context affects the behaviour of other group members in a social context. A number of other studies have recently demonstrated 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, since the social context may alter the behavioural expression of individuals (as clearly demonstrated in this study). Harcourt *et al.* (2009) studied leadership in three-spined sticklebacks and demonstrated 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 conclude 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.* (2005) 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. They have, however, not investigated whether the focal individual followed the companion. Recently, Schuett & Dall (2009) demonstrated in pairs of zebra finches that the time the pair spent together at a feeder increased with increasing difference in exploratory behaviour between both individuals, suggesting that some characters may be better in forming stable groups.

Our study demonstrates that movement patterns of group-living animals can be highly affected by the personality types in the group. Our study 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 its 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, since our results demonstrate 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 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 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 personality of both itself as well as 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.

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Chapter 3

The effect of boldness on decision-making in barnacle geese is group-size-dependent

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In group-living species, decisions made by individuals may result in collective behaviours. A central question in understanding collective behaviours is how individual variation in phenotype affects collective behaviours. However, how the personality of individuals affects collective decisions in groups remains poorly understood. Here, we investigated the role of boldness on the decision-making process in different sized groups of barnacle geese. Naive barnacle geese, differing in boldness score, were introduced in a labyrinth in groups with either one or three informed demonstrators. The demonstrators possessed information about the route through the labyrinth. In pairs, the probability of choosing a route prior to the informed demonstrator increased with increasing boldness score: bolder individuals decided more often for themselves where to go compared with shyer individuals, whereas shyer individuals waited more often for the demonstrators to decide and followed this information. In groups of four individuals, however, there was no effect of boldness on decision-making, suggesting that individual differences were less important with increasing group size. Our experimental results show that personality is important in collective decisions in pairs of barnacle geese, and suggest that bolder individuals have a greater influence over the outcome of decisions in groups.

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Introduction

The benefits of group living for individual group members are well established and include reduced predation risk and sharing of information (Krause & Ruxton 2002). If the benefits of grouping outweigh the costs of splitting, animals with conflicting interest may face situations where they have to reach consensus decisions whereby they have to choose collectively between various alternatives (see Conradt & Roper 2009 for a review), for instance, choosing between different movement directions. Coordinated behaviour in such groups might arrive as a result of communal decisions ('democracy') (Prins 1996) or by following decisions of other individuals, so called 'leaders' ('despotism') (King & Cowlishaw 2009; King *et al.* 2009). Leadership has been explained by individual variation in dominance (Deaner *et al.* 2005; King *et al.* 2008; Sueur & Petit 2008; but see Leca *et al.* 2003), motivation (Krause 1993; Fischhoff *et al.* 2007; Sumpter 2009), relatedness (Sueur & Petit 2008; Sueur *et al.* 2009) and social relations (Sueur & Petit 2008; Ramseyer *et al.* 2009). Information might also be an important component for determining leadership. Providing a few individuals in a large crowd of humans with information can result in collective movements led by the informed humans (Dyer *et al.* 2009). Likewise, a minority of informed golden shiners, *Notemigonus crysoleucas* (Reebs 2000), were able to lead groups towards a food source. Also honeybee (Beekman *et al.* 2006) and ant migrations (Langridge *et al.* 2008) are led by a minority of informed individuals. When observing social information, individuals need to weigh this information against their personal information and an important mechanism in mediating this balance is quorum sensing. Quorum sensing implies that the probability of an individual performing a certain behaviour increases as a function of the number of conspecifics already demonstrating this behaviour (Sumpter & Pratt 2009). Individuals only follow information if they observe a certain threshold (or majority) of individuals performing a particular behaviour. Empirical examples include ants (Pratt *et al.* 2002), African buffalo, *Syncerus caffer* (Prins 1996) and three-spined sticklebacks, *Gasterosteus aculeatus*, where one replica conspecific was able to control the movement of a solitary individual but not of larger groups (Ward *et al.* 2008).

Recently, the role of personality in contributing to leadership has been acknowledged and this might therefore also directly influence collective movements. Personality describes the phenomenon that differences among individuals of the same species in behavioural and physiological traits are consistent over time and context (Gosling & John 1999; Koolhaas *et al.* 1999; Carere & Eens 2005; Groothuis & Carere 2005). Examples in guppies, *Poecilia reticulata* (Dyer *et al.* 2008), three-spined sticklebacks (Harcourt *et al.* 2009), barnacle geese, *Branta leucopsis* (chapter 2) and zebra finches, *Taenopygia guttata* (Beauchamp 2000; Schuett & Dall 2009), show that bolder individuals are more often found in the leading edge of moving groups. Although the role of personality in determining leadership is quite well established, the relationship between personality and collective decisions in groups remains poorly understood.

Here we studied whether the personality of an individual affected the way it reacts to different numbers of informed individuals and how this in turn affects collective group movements in barnacle geese. Barnacle geese are highly gregarious birds forming large flocks during foraging, roosting and migration. Boldness has been shown to be a good proxy for personality in barnacle geese (chapter 2, 4, 5). We introduced naive barnacle geese together with either one or three informed individuals (all of intermediate boldness level) in a labyrinth and studied the decision-making process in these groups, i.e., whether naive individuals decided where to go for themselves or not. Based on the observation that bolder barnacle geese walk in front towards a food source more often in pairs of geese as compared to shyer individuals (chapter 2) and that bold/fast individuals are less reactive to companions than shy/slow individuals (great tits, *Parus major,* van Oers *et al.* 2005; ravens, *Corvus corax,* Stöwe & Kotrschal 2007; three-spined sticklebacks, Harcourt *et al.* 2009), we expected that bolder individuals would make a decision on their own more often, whereas shyer individuals were expected to wait more often for the decision of the informed individual(s) and follow this decision.

Methods

Experimental subjects We used captive-born wing-clipped barnacle geese ($N = 42$), each fitted with a uniquely coded leg ring for identification. Birds were sexed by cloacal inspection (20 females, 22 males). We measured tarsus and culmen length (to the nearest 0.1 mm) using callipers and wing length (1.0 mm) using a ruler. One observer carried out all measurements to minimize observer biases. Prior to the decision experiment 1 we measured body mass on a digital balance (1.0 g). We used a principal components (PC) analysis of tarsus, culmen and wing lengths to derive a measure of structural body size. PC1 explained 75.6% of the variation. Body condition was calculated as the residuals from a linear regression of body mass on PC1 ($R^2 = 0.22$, $F_{1,\ 41} = 11.4$, $P = 0.002$). When not used for the experiment, all geese were kept as one group in an outdoor aviary of 12 by 15 m at the Netherlands Institute of Ecology in Heteren, the Netherlands. Throughout the experiments geese were fed ad libitum with a mixture of grains and pellets. A pond (6 by 1 m) was present in the aviary, with continuous flowing water for bathing and drinking.

Boldness We used a novel object test to assess boldness of all individuals (see for details chapter 2). We habituated individuals to an experimental arena. After habituation we placed a novel object in the middle of the arena, introduced each goose for 10 min and scored the minimal distance (cm) reached between the goose and the novel object, as well as the approach latency (defined as the time elapsed (s) before the goose came within 50 cm of the novel object). Each individual was tested twice in November or December 2008. We calculated principal components (PCs) of the test variables for each test as an independent measure of novel object score. PC1 explained 86.9% and 89.6% 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. Repeatability of novel object score was high (0.81) indicating that individuals differed consistently in their boldness scores (see also Fig. 3.1).

For the first decision experiment (see below) we selected the 15 boldest and the 15 shyest individuals as naive, focal individuals (Fig. 3.1), because we expected the largest differences in reaction towards an informed demonstrator between bold and shy individuals. We selected 5 intermediate individuals as demonstrators (see below). All remaining individuals (*N* = 7) were placed in a separate aviary. For the second decision experiment we took 12 intermediate individuals as demonstrators.

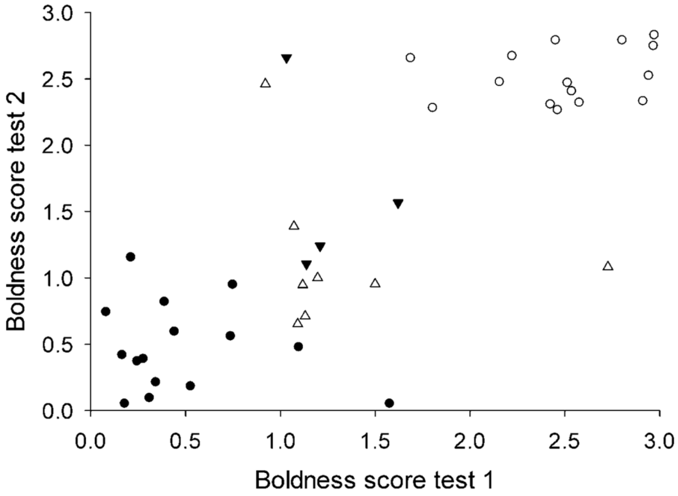

Figure 3.1 Relationship between the outcome of two novel object tests for all individuals (*N* = 42). Closed circles represent geese that were classified as shy (*N* = 15). Open circles represent geese that were classified as bold (*N* = 15). Triangles represent geese that were used as demonstrators (*N* = 12). Closed triangles represent geese that were used as demonstrators in experiment 1 and 2 (*N* = 4).

Decision experiment To study the effect of personality on the decision-making process, we used a labyrinth consisting of a starting area with two identical, mirrored corridors (Fig. 3.2). One corridor led to the end of the labyrinth and back to the home aviary, whereas the other corridor led towards a dead end. Individuals were walked gently towards a wooden pen that served as the entrance of the labyrinth (Fig. 3.2). Individuals were held for 2 min in the pen before introducing them to the arena by lifting a Plexiglas partition (from outside the experimental area to minimize disturbance).

For experiment 1 we trained five individuals (of intermediate boldness levels, see also Fig. 3.1) in the labyrinth. First, we introduced all five individuals (hereafter called: demonstrators) together, then in groups of two individuals and finally alone. The training period lasted five days with three training sessions (introductions) per demonstrator per day. One demonstrator did not learn the route, leaving a total of four demonstrators.

The experimental period lasted 10 days (1 – 10 May 2009). Each day we introduced every demonstrator three times on its own. If they chose the correct corridor for three times, and if they had also correctly chosen for three times the previous day, we performed one experimental run together with a naive individual. The average success rate of the demonstrators over the 10 days was 95%. For the first experimental run of each demonstrator we randomly picked a naive individual from either the bold or the shy group. After that we alternated between a shy and a bold companion. In total we ran 29 trials. One shy companion was not used in the experiment since it showed unusual behaviour in the home aviary (such as fleeing from the group and trying to jump over fences). One trial was excluded from the analysis since the naïve individual (from the bold group) managed to escape from the

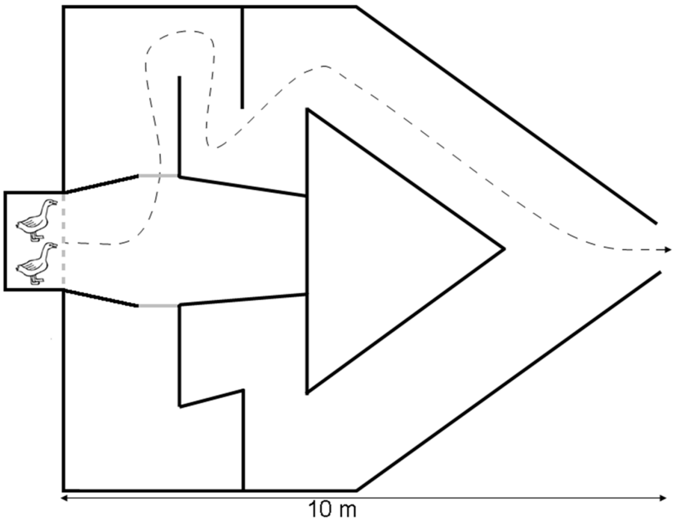

Figure 3.2 Schematic overview of the labyrinth used for the decision experiment. The black closed lines represent a wire, fenced with black anti-root cloth. The bottom of the arena was also covered with anti-root cloth. The dashed grey line represents a Plexiglas partition which was lifted 2 min after introduction of the geese. The dashed arrow represents the route that individuals had to take to arrive at the exit of the arena. The grey lines represent fictive lines. Crossing of one of both lines was used as the criterion for choosing a side.

labyrinth, leaving a total of 28 successful trials, 14 with a bold individual and 14 with a shy individual. Demonstrators were used between six and eight times each.

During each trial we scored (1) whether the naive individual was the first to enter one of both corridors (yes/no) (see also Fig. 3.2) and (2) when the naive individual was not the first to enter a corridor, whether the individual followed the demonstrator (yes/no). Following was defined as entering the same corridor within 5 s after the demonstrator.

Experiment 2 was performed eight months later. In this experiment we used groups of four individuals, containing three informed demonstrators and one naive individual. During the trainings phase, we trained four groups of three demonstrators. Since four of these 12 individuals were already used in experiment 1 as demonstrators and were possibly more experienced we assigned one of these four individuals to each demonstrator group to minimize variation between demonstrator groups. We trained the four demonstrator groups three times a day for a period of four days, after which the experimental period started. The experimental period lasted nine days (20 – 28 January 2010) and we used demonstrator groups between five and eight times following the same criteria and the same experimental protocol as in experiment 1. We used the same 28 naive individuals as in experiment 1, except for one shy individual which had died in between both experiments. This individual was replaced by another shy individual. We slightly rebuilt the arena (but keeping it the same dimensions) to avoid recognition of the arena by the naive individuals. During each trial we scored (1) whether the naive individual was the first to enter one of both corridors (yes/no), and when the naive individual was not the first to enter a corridor (2) whether it followed the demonstrator(s) (yes/no) and (3) which position in the group it occupied when entering a corridor.

Dominance Since dominance might affect collective movements, we established the dominance hierarchy for experiment 1 by scoring agonistic interactions within dyads in the flock of 34 individuals (15 – 28 May 2009). In total we scored 1185 interactions (mean number per individual: 69.7; range: 28 - 193 interactions). The value of Kendall's linearity index ($k = 0.48$), Landau's index and the corrected index of the sociometric matrix ($h = 0.48$, $h' = 0.51$) were moderate. We constructed a linear dominance hierarchy but to evaluate if this hierarchy reflected the pair-wise dominance relationships experienced between individuals in a pair, we also tested the dominance in all combinations of pairs we used during decision experiment 1. We introduced each pair in an arena (1 by 3 m), offering a small patch of grass (30 x 20 cm). During 30 min we scored each agonistic interaction (22 – 26 May 2009). The average number of interactions was 9.7 per trial (range 0 – 35) and all agonistic interactions, except two, were unidirectional. In 23 out of 28 trials we observed agonistic interactions. Of the winners, 22 out of 23 corresponded to the linear dominance hierarchy, indicating that the position in the linear dominance hierarchy is a good predictor for the pair-wise dominance. For these 23 pairs we used the outcome during the pair-wise interaction to establish the dominance, for the remaining five pairs we used the linear dominance hierarchy to establish which individual of the pair was dominant.

Statistics To test whether boldness affected an individual's decision to choose a corridor prior to the demonstrator we used 'naive individual first to choose a corridor' (yes/no) as a response variable in a generalized linear mixed model with binomial errors and a logit-link function. As fixed effects we fitted boldness score of the naive individual (on a continuous scale), dominance (dominant/subordinate), body condition (continuous) and sex (male/female). For experiment 1 we also included the boldness score of the demonstrator as a fixed effect to control for a possible effect of boldness differences between demonstrators. We constructed separate models for experiments 1 and 2. Prior to the mixed model analysis we used Spearman's rank correlations to study possible correlations between body condition, dominance rank and boldness. To test if there were sex differences in boldness score, body condition or dominance we used non-parametric Mann-Whitney U tests. There were no significant correlations between dominance rank, body condition and boldness (all $|r_s| < 0.17$, all $P > 0.3$, $N = 34$). There were no significant differences between males and females in boldness or body condition (all $U > 110$, $U_1 = 18$, $U_2 = 16$; all $P > 0.4$). Males, however, had a higher dominance rank than females ($U = 39$, $P < 0.001$). Since sex and dominance were not independent, we constructed three separate models: including (1) all terms, (2) all terms but excluding sex, and (3) all terms but excluding dominance, to study the effect of sex and dominance separately.

Since it has been shown that personality traits might affect the behaviour of other individuals (e.g., Harcourt *et al.* 2009, chapter 2), we analyzed whether the boldness score of the naive individual affected the decision time of the demonstrator in experiment 1, using all trials in which the demonstrator entered a corridor first. Likewise, we analyzed whether the boldness score of the demonstrator affected the decision time of the naive individual, using all trials in which the naive individual entered a corridor first.

To minimize pseudoreplication we included demonstrator(s) identity as a random effect in all mixed models. We started with full models containing all terms. Minimal adequate models were obtained by stepwise deletion of non-significant terms (*P* > 0.1), starting with the least significant term. To compare the explanatory power of two subsequent models we used a log-likelihood ratio test which follows a chi-square distribution, with degrees of freedom equal to the difference in the number of parameters between the two models. We present these chi-squared values and *P*-values as well as the estimate (est.) and standard errors (se) of the individual factors. In addition, we performed a separate analysis entering all fixed effects independent of one another. We used the package lme4 for mixed model procedures in R (version 2.11.1).

Results

For trials with one informed individual, the probability of a naive individual to choose a side prior to the demonstrator increased with increasing boldness score (est. = 0.87, se = 0.45, χ^2 = 3.97, *P* = 0.046; Fig. 3.3). There was no significant effect of dominance, body condition, sex or boldness score of the demonstrator (dominance: est. = 1.65, se = 1.20, χ^2 = 2.22, *P* = 0.14; body condition: est. = 0.002, se = 0.002, χ^2 = 1.68, *P* = 0.20; sex: est. = 0.42, se = 0.81, χ^2 = 0.25, *P* = 0.62; boldness demonstrator: est. = 0.38, se = 1.78, χ^2 = 0.04, *P* = 0.84). All three models (i.e., full model, excluding sex or excluding dominance) gave similar results, indicating that neither dominance, nor sex was significant. Likewise, we arrived at similar results when we entered factors independent of each other. When a demonstrator entered a corridor first, it always chose the correct route and in nearly all cases the naive individual followed the demonstrator (*N* = 15/17). When a naive individual moved first there was no preference for either corridor (χ^2 = 2.3, *P* = 0.13, *N* = 11), indicating that naive individuals did not have side preferences. In these trials, the informed demonstrator always followed if the naive individual entered the correct corridor. If the naive individual entered the incorrect

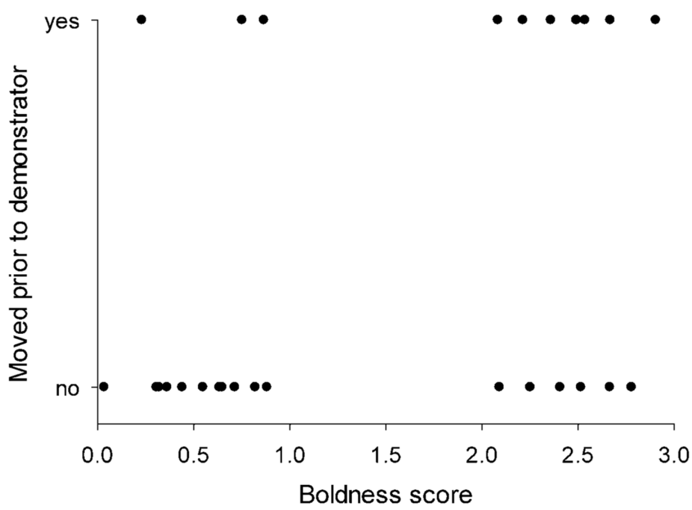

Figure 3.3 The probability of a naive individual to choose a side prior to the informed demonstrator increased with increasing boldness score of the naive individual during experiment 1 in groups with one informed demonstrator.

corridor, in two out of three cases the informed demonstrator waited for the naive individual to return to the entrance of the arena before walking together to the correct side, and in only one case the dyad split and chose different routes, indicating the strength of group cohesion in this species. The decision time of the demonstrator (mean ± se = 16.5 ± 5.9 sec, *N* = 17) was not affected by the boldness score of the naive individual ($\chi^2 = 0.23$, $P = 0.62$). Likewise, the decision time of the naive individual (mean ± se = 8.7 ± 2.3 sec, *N* = 11) was not affected by the boldness score of the demonstrator ($\chi^2 = 0.23$, $P = 0.63$).

For trials with three informed individuals, an informed demonstrator chose to move through the maze first on all but two occasions (*N* = 26/28), and were always seen to choose the correct route. There was no effect of boldness score on the probability of moving first (est. = 0.014, se = 0.74, $\chi^2 = 0.00$, $P = 0.98$), nor was there an effect of body condition or sex (body condition: est. = 0.0004, se = 0.003, $\chi^2 = 0.02$, $P = 0.89$; sex: est. = 0.000, se = 0.000, $\chi^2 = 0.00$, $P = 1$). Entering factors independent of each other gave similar results. When a demonstrator moved first, the naive individual always followed the demonstrator. In most trials (*N* = 22/28) the naive individual was walking either at the third or fourth position in the group and there was no effect of the boldness score of the naive individual on the position it occupied in the group ($\chi^2 = 0.09$, $P = 0.76$).

Discussion

As expected, the probability of moving first increased with increasing boldness score, although this effect was dependent on the number of geese: in pairs of geese boldness affected decision-making, whereas in groups of four individuals there was no effect of boldness. There is little known about the extent to which personality affects collective decision-making. In foraging groups of sheep bold and shy individuals show different spatial distribution patterns over resource patches with shy individuals showing a lower tendency to split into smaller subgroups than bold individuals (Michelena *et al.* 2008). The observed patterns of spatial distribution have been explained by individual variation in social attraction which results in emerging collective choices through the nonlinear dynamics of interactions between individuals of different boldness levels (Michelena *et al.* 2009). Likewise, in fish shy individuals have a higher shoaling tendency (Budaev 1997; Ward *et al.* 2004; Dyer *et al.* 2008). Next to a higher sociability, shy individuals also have a lower tendency to explore by themselves, which is confirmed by several studies showing that mainly bolder individuals take the role of leader (Beauchamp 2000; Dyer *et al.* 2008; Harcourt *et al.* 2009; Schuett & Dall 2009; chapter 2). Here we show that in pairs the probability of waiting for the decision of an informed conspecific decreased with increasing boldness score of the naive individual, suggesting that bolder individuals have a greater influence over the outcome of decisions in groups. In barnacle geese boldness is not correlated with either activity or exploration of a novel environment (chapter 2), hence our results cannot be explained by differences in activity levels between individuals, or by differences in exploration rate of a novel environment.

To what extent personality traits measured in isolation have consequences for behavioural differences between individuals in groups is important for understanding the impact of personality differences in an ecological context. In groups, individual behaviour can be affected both by individual differences, like personality (Magnhagen & Bunnefeld 2009; chapter 5), but also by social influences (van Oers *et al.* 2005; Dyer *et al.* 2008; Magnhagen & Bunnefeld 2009; chapter 2). In larger groups the feedback and interaction processes between traits may alter and it has been hypothesized that individual behavioural differences (owing to, for example, personality traits) in larger groups become more pronounced (by self-organization, Hemelrijk & Wantia 2005) or, in contrast, become less pronounced (by consensus decisions, Sumpter *et al.* 2008). Our results show that personality differences were important in pairs of geese, but not in groups of four individuals, suggesting that individual differences became less important with increasing group size. However, both experiments differed in an important aspect which forces us to be cautious about a direct comparison between both experiments. In experiment 1 there was only one informed individual, whereas in experiment 2 there were three informed individuals. A key difference is the number of informed individuals and this could have consequences if geese use a form of quorum sensing. The number of individuals demonstrating the correct entrance was higher in experiment 2 than in experiment 1, and this might help explain our observation that boldness was important in pairs (with one informed individual) but not in groups of four individuals (with three informed individuals). Most naive individuals in experiment 2 were walking either in third or fourth position which seems to suggest that the probability of following increased with the number of individuals entering a certain corridor. If this is due to a minimum threshold or a majority rule (see also King & Cowlishaw 2007) cannot be discriminated in our experiments. Careful experimental manipulation of group size, number of informed individuals and boldness differences could investigate this matter further and explore whether individuals differing in boldness follow similar quorum sensing rules, or whether boldness differences also result in different quorum sensing rules. Nonetheless, the observation that individual variation in boldness did not result in behavioural differences in groups with three informed individuals (whereas it did in groups with one informed group mate) highlights the need to study the expression of personality in larger, more natural groups. For instance, most studies showing that personality affects leadership are done in very small groups like pairs (e.g., Beauchamp 2000; Harcourt *et al.* 2009; Schuett & Dall 2009; chapter 2). An evaluation of the expression of personality in larger, more natural groups is important to understand the importance of personality in a natural situation.

Nomakuchi *et al.* (2009) performed a similar experiment to ours in which they trained three-spined sticklebacks to follow a route through a maze and introduced these informed individuals together with naive individuals differing in exploration score. They found that more explorative individuals followed the informed individual to a larger extent than less explorative individuals. Unfortunately, they used the same maze to study exploration behaviour and following behaviour making it difficult to assess if the increased tendency to follow demonstrators by more explorative individuals is not a result of an increased tendency to explore the maze. Here, we assessed individual boldness levels in a completely different context by challenging individuals with a novel object to show that this reaction correlates with the tendency to explore a route in the presence of an informed individual. This result is opposite to the findings of Nomakuchi *et al.* (2009). An important difference between our findings and Nomakuchi *et al.* (2009) is that in their study the demonstrators were always the first to enter the maze, whereas in our study naive individuals did not always wait for the informed demonstrator.

Dominance was not related to individual contribution to group movement decisions in our experiment. Several studies showed that more dominant individuals have a stronger say in determining group movements (e.g., Deaner *et al.* 2005; King *et al.* 2008; Sueur & Petit 2008; but see Leca *et al.* 2003). These examples are primarily from species with strong social group structure, like several species of monkeys, in which the highest ranked individuals have a strong influence over the behaviour of other individuals. For instance, alpha-males in chacma baboons, *Papio ursinus*, were able to steer a group towards a food source where few individuals besides the alpha-male were able to consume food (King *et al.* 2008). In species with a less strong social group structure, like the barnacle geese, the role of dominance on travel directions is probably less strong, as is also confirmed by an absence of a relation between dominance and leadership in domestic goats (Stewart & Scott 1947) cattle and sheep (Ramseyer *et al.* 2009).

Next to dominance, also motivation has been shown to be important in collective movements, in particular individuals with a higher need for resources are predicted to lead groups (Rands *et al.* 2003; Conradt *et al.* 2009; Sumpter 2009). Empirical support comes from studies in fish where food deprived fish were seen more often in front positions than well-fed fish (Krause 1993) and plains zebra, *Equus burchellii*, where lactating females were more likely to initiate group movements compared to non-lactating females (Fischhoff *et al.* 2007). Likewise in African buffalo where mostly adult females, mainly with offspring, initiate group movements (Prins 1996). In our study we did not find an effect of body condition on individual contribution to group movement decisions. Most likely the individual differences in terms of energy requirements were small in our experiment, as no individuals were food deprived, or in a stage where they would face high energy requirements (e.g., moult), explaining the lack of a possible effect of body condition.

In conclusion, personality affected individual contribution to group movement decisions in pairs of geese with bolder individuals deciding more often by themselves on travel direction as compared to shyer individuals, suggesting that bold individuals have a greater influence over the outcome of collective decisions. The effect of personality disappeared in groups of four individuals, suggesting that individual differences were less important with increasing group size.

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Chapter 4

Personality predicts the use of social information

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The use of social information is known to affect various important aspects of an individual's ecology, such as foraging, dispersal and space use and is generally assumed to be entirely flexible and context dependent. However, the potential link between personality differences and social information use has received little attention. Here we studied whether use of social information was related to personality, using barnacle geese, *Branta leucopsis*, where boldness is a personality trait known to be consistent over time. We found that the use of social information decreased with increasing boldness score of the individuals. Individuals had lower feeding times when they did not follow the social information and this effect was unrelated to boldness score. When manipulating social information, thereby making it incorrect, individuals irrespective of their boldness score, learned that it was incorrect and ignored it. Our results show that social information use depends on the personality type of an individual, which calls for incorporation of these personality-related differences in studies of spatial distribution of animals in which social information use plays a role.

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Introduction

Individuals constantly need to make decisions such as where to forage, with whom to mate and when to migrate. To decide effectively, individuals rely on information about the potential outcomes of different alternatives. Information might be obtained in two distinct ways: individuals might use personal information, usually retrieved on a trial and error basis by interaction with the physical environment, or they might use information made available by other individuals, which is referred to as social information (Danchin *et al.* 2004). The use of social information has been demonstrated in a wide variety of species (Galef & Giraldeau 2001; Danchin *et al.* 2004; Valone 2007) and is known to affect various important aspects of an individual's ecology, such as foraging, dispersal and space use (Seppänen *et al.* 2007). For instance, in patch selection individuals may use the presence (Drent & Swierstra 1977) or performance (Coolen *et al.* 2003) of other individuals. The role of social information use in the spatial distribution of animals has received considerable attention (see examples in Valone & Templeton 2002; Seppänen *et al.* 2007; Valone 2007), but in nearly all studies to date personality is not taken into account. This absence reflects a broader phenomenon in ecology, namely that ecologists thus far showed little interest in personality (Réale *et al.* 2007). This is surprising since personality traits may have profound affects on ecological processes like social organization, dispersal and spatial distribution (see studies in Réale *et al.* 2007).

Animal personality describes the phenomenon that differences among individuals of the same species in behavioural and physiological traits are consistent over time and context (Gosling & John 1999; Carere & Eens 2005; Groothuis & Carere 2005). Different behavioural and physiological reactions have a genetic basis (van Oers *et al.* 2005a) and are often phenotypically and genetically correlated. This suggests that these differences are fundamental aspects of the behavioural organization of individuals and are the subject of natural (Dingemanse & Réale 2005; Smith & Blumstein 2008) and sexual selection (van Oers *et al.* 2008).

The relationship between personality and social information use is poorly studied (Marchetti & Drent 2000; Nomakuchi *et al.* 2009) and it is generally assumed that individuals are flexible in their use of social information and that it is context dependent. Consequently, most studies focus on the conditions under which an animal is expected to use social information (Galef & Giraldeau 2001; Danchin *et al.* 2004; Kendal *et al.* 2005; Valone 2007). Beyond doubt social information use is partly flexible (van Bergen *et al.* 2004; Kendal *et al.* 2004) but there is reason to believe that individuals may consistently differ in the way they process and use cues from conspecifics. Firstly, several studies have demonstrated that shy/slow individuals are more reactive to companions than bold/fast individuals (van Oers *et al.* 2005b; Stöwe & Kotrschal 2007; Harcourt *et al.* 2009), suggesting that shy/slow individuals pay more attention to the behaviour of conspecifics, consequently collecting more social information. Secondly, some studies provide indirect evidence that personality affects social information use: In barnacle geese, *Branta leucopsis*, shy individuals used the scrounging tactic more often compared to bold individuals in a producer scrounger game (chapter 5) and in great tits, *Parus major*, fast exploring birds copied the behaviour of tutor birds more readily than slow exploring birds (Marchetti & Drent 2000). Lastly, Beauchamp (2001) showed that in zebra finches, *Taenopygia guttata,* individuals differed consistently in their tactic use in a producer scrounger game with less efficient foragers having higher levels of scrounging (Beauchamp 2006).

To specifically test the hypothesis that shy individual make more use of social information compared to bolder individuals we conducted a social foraging experiment with barnacle geese. Barnacle geese, differing in boldness score, which we use as a proxy for personality (see chapter 2 and 5), were allowed to watch two pairs of demonstrators which revealed the location of a food resource for the observing goose. After an observation period, individuals were given the opportunity to join one of the pairs, thereby revealing whether they used the social information. In our first experiment we examined whether geese differing in boldness score used reliable social information in choosing a foraging site. In a second experiment, we manipulated the social information, thereby making it incorrect, whereby we expected that individuals would learn that the social information was incorrect, with shy individuals being the faster learners.

Methods

Experimental subjects We used captive-hatched wing-clipped barnacle geese (N = 20), each fitted with a uniquely coded leg ring for identification. Birds were sexed by cloacal inspection (13 females, 7 males) and were all unpaired. Before the start of the experiment we measured tarsus and culmen length (to the nearest 0.1 mm) using calipers and wing length (1.0 mm) using a ruler. Body mass was measured on a digital balance (1.0 g). We used a principal components (PC) analysis of tarsus, culmen and wing lengths to derive a measure of body size. PC1 explained 79.8% of the variation. 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 one group in an outdoor aviary of 12 by 15 m at the Netherlands Institute of Ecology in Heteren, the Netherlands. Throughout the experiments geese were fed ad libitum with a mixture of grains and pellets. A pond (6 by 1 m) was present in the aviary, with continuous flowing water for bathing and drinking.

Dominance To establish the dominance hierarchy we scored agonistic interactions in the flock (December 2007, for details see chapter 2). In total we scored 474 interactions (mean number per individual: 55.6; range: 27 - 86 interactions). 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. Individuals were used either as observers or as demonstrators in the social information experiment (see below) based on the dominance hierarchy. Individuals lowest in rank ($N = 8$, all females) were used as demonstrators in order to assure that observers ($N = 12$) would not be aversive to use information provided by the demonstrators.

Boldness test We used a novel object test to assess boldness (see for details chapter 2). We habituated individuals to an experimental arena. 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. We tested each individual twice in February 2008 and twice in November 2008. We calculated principal components (PCs) of the test variables for each test as an independent measure of novel object score. We use the term ‘boldness’ for the reaction towards a novel object, although sometimes the term ‘exploration’ is used (e.g., Réale *et al.* 2007), since we think that the term boldness describes the willingness to take risks in absence of a food reward.

Social information experiment We used a test arena with an observer area, and two demonstrator areas (see legend Fig. 4.1 for details). This arena was built inside a greenhouse to minimize external disturbance. Based on the dominance hierarchy individuals were used as either demonstrators (subordinates, $N = 8$) or observers (dominants, $N = 12$). An observer was allowed to watch two pairs of demonstrators behind a Plexiglas partition. After 90 sec we allowed the observer to join one pair of demonstrators (the one of its choice) by pulling up the partition (from outside the greenhouse as to avoid disturbance). After joining one of the demonstrator pairs, individuals were able to switch to the other side, but they had to walk around a fence to get to the other side (see Fig. 4.1). The trials were ended 90 sec after pulling up the partition. The observer and the demonstrator areas were separated from each other by wire-netting and both pairs of demonstrators were visually isolated from each other by opaque plastic. Each pair of demonstrators had one trough (10 x 100 x 10 cm) which either contained food or was empty. The observer had two different troughs to choose from, one on each side and in front of one of the demonstrator troughs (see also Fig. 4.1). We used commercially bought sods of perennial ryegrass, *Lolium perenne*, cut to a height of 1 cm as food. This grass is an important food source for wild barnacle geese (Prins & Ydenberg 1985). During the

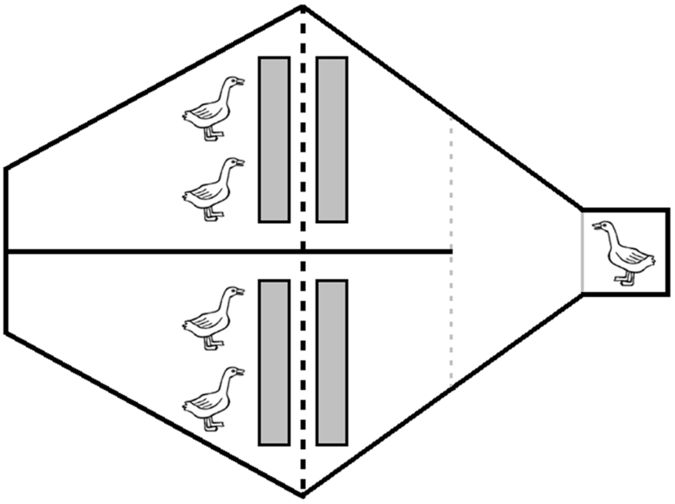

Figure 4.1 Schematic overview of the experimental arena used for the social information experiment. The closed lines represent a wire fenced with white plastic. The black dashed line represents a wire netting. The goose on the right hand side was the observer goose and was allowed to watch the behaviour of the two pairs of demonstrators before choosing a side. The grey line represents a Plexiglas partition which was pulled up after the observation period (90 sec). The grey dashed line represents a taped line on the floor and was used as the criterion of which side the observer chose. The rectangles represent troughs that either contained food or were empty. For the first experiment we filled one of the troughs of the demonstrators and the observer could find the food on the same side (e.g., both the upper troughs filled). For the second experiment we filled one of the troughs of the demonstrators but the observer could find food on the opposite side (e.g., the upper left trough and the bottom right trough filled). For the third experiment (control) we filled no troughs of the demonstrators and one trough for the observer.

experimental period geese were only offered grass during the experiments (and grains and pellets for the rest of the day). If given a choice barnacle geese show a strong preference for grass as food over grains or pellets (personal observation RHJM Kurvers, HHT Prins, SE van Wieren & RC Ydenberg). Geese were well motivated to consume their preferred resource during the experiments. The demonstrators, for instance, foraged nearly continuously when they had a filled trough.

Prior to the experiment we trained all demonstrators to start foraging upon introduction in the arena. Demonstrators were introduced in fixed pairs (*N* = 4 pairs) in the experimental arena offering always food in their troughs the first days. Thereafter we provided food in only half of their entries to habituate them to the condition that food would not always be present. We always used two extra individuals (not used in the remainder of the experiment) as observers to habituate the demonstrators to the presence of a conspecific in the observer area and the lifting of the Plexiglas partition. Demonstrators were introduced at least 20 times in the experimental arena prior to the experiment. Observers were also trained in order to habituate them to the experimental conditions. First, we introduced each observer four times in groups of six geese in the arena, followed by introducing them four times in the arena in groups of three. In half of these eight introductions food was provided on one side and in the other half on the other side in order to familiarize the observers with the unpredictability of the location of the food. We placed one demonstrator (individuals not used in the remainder of the experiment) on each demonstrator location without food in order to habituate the observers to the presence of conspecifics.

During the experiments we randomly assigned one side as the ‘food side’ each day, with the condition that we had a maximum of two consecutive days with the same ‘food side’ and the condition that in each experiment (see below) both sides were in total equally often used as ‘food side’. Each demonstrator pair was used an equal number of sessions during each experiment. In each experiment, we balanced the appearance of the demonstrator pairs in such a way that each observer met each pair of demonstrators an equal number of times, equally divided between encounters with and without food to prevent any association between demonstrator pair and food presence.

Experiment 1: Correct social information To test the relationship between personality and the use of social information we provided the pair of demonstrators on one side with food, whereas the pair on the other side faced an empty trough. In the observer area, food was provided in the trough at the same side as those in the demonstrator area. In this situation the information provided by the demonstrators was completely correct showing the actual place of the accessible food. We tested 12 observers, differing in boldness score, once per day for a period of 12 days and scored whether the observer followed the social information (i.e., joined the foraging pair) identified as entering one of the two demonstrator pair compartments by crossing a line (see also Fig. 4.1) (7 - 21 April 2008).

To investigate the possible cost of a loss of feeding time when making an incorrect decision and whether this cost varied for individuals of different boldness scores, we also scored feeding time defined as the total time an individual had its head in the filled trough.

Since individuals were used multiple times in this experiment there was a possibility that an individual formed a routine. We therefore tested for each trial whether the individual chose the same side as it had chosen the previous day. If individuals often chose the same side in subsequent trials, we assume that they formed routines.

Experiment 2: Incorrect social information In order to test if observers were able to assess the reliability of social information we again provided only one pair of demonstrators with food. In contrast to experiment 1, the observer received food in the trough situated at the side of the demonstrator pair that received no food. The information given by the demonstrators was thus consistently incorrect. We used the six most successful individuals from experiment 1 (average success rate: 9.17, range 7 - 11) since the other six individuals did not follow the social information so testing their reaction towards incorrect information would be irrelevant. We tested the six observers once per day for a period of 12 days and scored whether the observer followed the social information (i.e., joined the foraging pair) (23 April – 4 May 2008).

Experiment 3: No social information Lastly, we performed a control experiment to test if observers could locate the food without receiving any social information. Both pairs of demonstrators did not receive food and the observers received food on one side. We tested six observers (the same as used in experiment 2) once per day for a period of 8 days. We scored if the observer chose the side where we provided food (6 – 15 May 2008).

Statistical analysis To test whether observers followed the social information in experiment 1 we used 'choice of the observers' (left/right) as a response variable in a generalized linear mixed model (GLMM) with binomial errors and a logit-link function. As fixed effect we fitted 'food side' (the social information). To test the effect of personality on the use of social information in experiment 1 we used 'correct choice' (yes/no) as a response variable in GLMMs with binomial errors and a logit-link function. As fixed effects we fitted boldness score as well as body condition, day, side chosen by the observer, the identity of the demonstrator pair with food, and the interaction between boldness score and day. A significant interaction between boldness score and day with a negative estimate would imply that shyer individuals use more social information than bold individuals over time which, in turn, would suggest the presence of social learning.

We used a paired t-test to compare the average feeding time when individuals chose correctly and chose incorrectly. We correlated the percentage of feeding time lost per individual when choosing incorrectly (feeding time incorrect divided by feeding time correct) with boldness score using a Pearson correlation coefficient.

To test whether there was an effect of boldness on choosing the same side as the previous day we used 'choosing same side as previous day' (yes/no) as a response variable in GLMMs with binomial errors and a logit-link function. As fixed effect we fitted boldness score.

To test if individuals would continue following the social information in experiment 2 we used 'choice of the observers' (left/right) as a response variable in GLMMs with binomial errors and a logit-link function. As fixed effects we fitted ‘food side demonstrators’ (the social information) and boldness score. Since there could be a learning effect we also included period (two levels (1: first half of the experiment; 2: second half of the experiment)) as a fixed effect and the interaction between period and ‘food side demonstrators’. A significant interaction would indicate that the effect of the social information on the choice of the observers would be different between the first and the second half of the experiment. In addition, we included the interaction between boldness score and period. A significant interaction would imply that there were differences in learning between individuals of different boldness scores.

We tested if geese were able to establish the location of the food without social information in experiment 3, by using ‘choice of the observers’ (left/right) in GLMMs with binomial errors and a logit-link function. As fixed factors we fitted boldness score and ‘food side’. A positive effect of ‘food side’ would indicate that the observers could establish the location of the food without using the social information provided by the demonstrators.

In all mixed models we also included ‘food side previous day’ as a fixed effect. A positive significant effect would indicate that the observers used information from the previous day (‘personal information’). To avoid pseudoreplication we included observer identity as a random effect in all mixed models. For all models, we started with full models containing all terms. Minimal adequate models were obtained by stepwise deletion of non-significant terms ($P > 0.1$), starting with the least significant term. To compare the explanatory power of two subsequent models we used a log-likelihood ratio test which follows a chi-square distribution. We used the package lme4 for mixed model procedures in R (version 2.7.2).

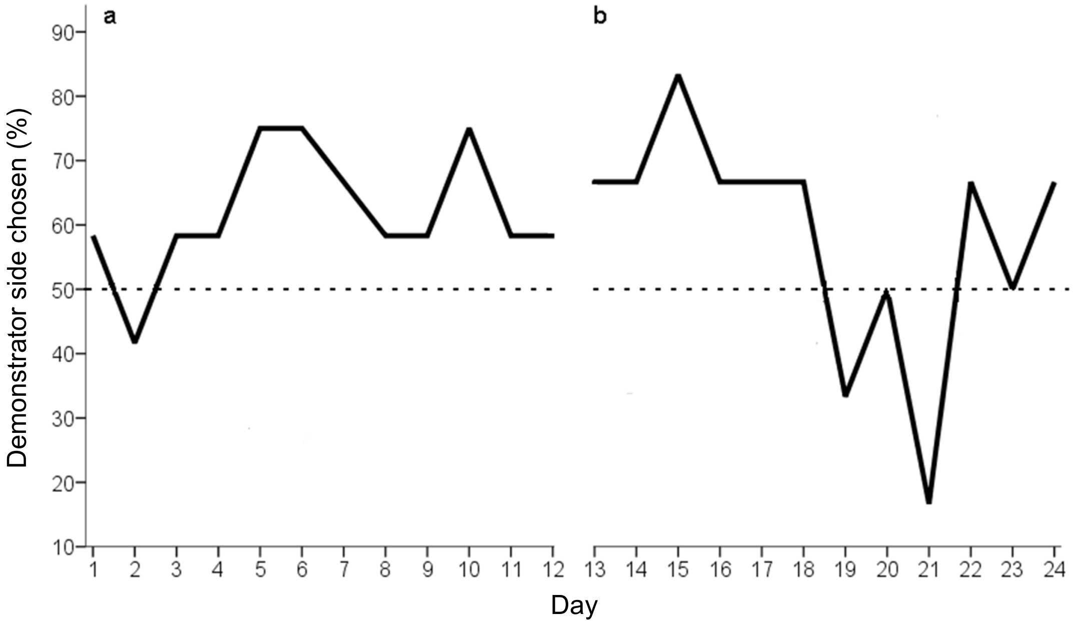

Figure 4.2 (a) Results of experiment 1 where the food for the demonstrator and the observer were on the same side (correct social information). Shown are the percentages per day individuals chose the side where demonstrators were foraging / which contained food over a period of 12 days ($N = 12$). (b) Results of experiment 2 where the food for the demonstrator and the observer were on the opposite side (incorrect social information). Shown are the percentages per day individuals chose the side where demonstrators where foraging / which did not contain food over a period of 12 days ($N = 6$). Dashed line represents expectation based on random choice.

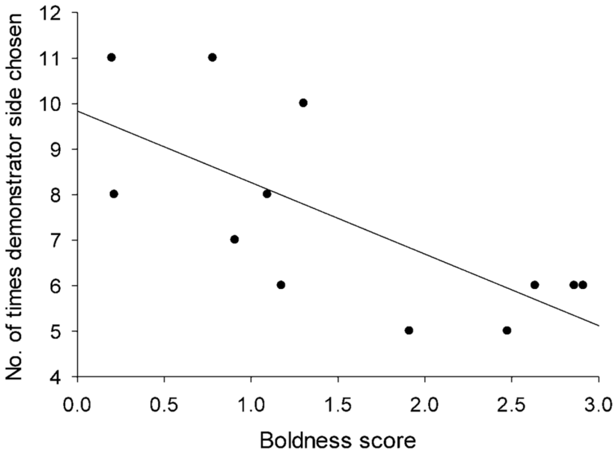

Figure 4.3 Social information use decreased with increasing boldness. Successful joining of foraging demonstrators decreased with increasing boldness during experiment 1. Shown are the total number of times each observer goose ($N = 12$) joined the foraging demonstrators. Line is a regression line.

Results

Boldness test For all four novel object tests PC1 explained between 76% and 90% of the variation. 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. All loading factors were between -0.89 and -0.95 indicating that both measurements are highly correlated with PC1 and that loading factors were similar across trials. Repeatability of novel object score was high (0.72 over the four tests; see also chapter 2) indicating that individuals differed consistently in their boldness scores. We averaged the four measurements of novel object score to derive a composite boldness measure for each individual.

Correct social information There was a significant positive effect of social information on the choice of the observers ($\chi^2 = 12.92$, $P < 0.001$): over 12 days observers joined 89 times the demonstrators which received food and 55 times the food deprived demonstrators (Fig. 4.2a), indicating that the observers followed the social information. There was no effect of 'food side previous day' ($P > 0.1$). There was a negative effect of boldness score on social information use ($\chi^2 = 8.23$, $P = 0.004$; Fig. 4.3): the number of times the observer joined the demonstrators which received food increased with decreasing boldness score of the observer, implying that shyer individuals made more use of the available social information. There was no effect of body condition, day, side chosen by the observer and the identity of the demonstrator pair with food (all $P > 0.1$). Moreover, there was no significant interaction between boldness score and number of days since the start of the experiment ($\chi^2 = 0.01$, $P > 0.9$).

Individuals had higher feeding times when choosing correctly (mean ± SD = 25.4 ± 12.0 sec) than when choosing incorrectly (8.1 ± 7.7; $t_{11} = 4.83$, $P = 0.001$). There was no significant correlation between boldness score and feeding time lost when choosing incorrectly ($r = 0.43$, $P = 0.16$). There was a positive effect of boldness on the number of times individuals chose the same side as they chose the previous day ($\chi^2 = 5.81$, $P = 0.016$).

Incorrect social information There was a significant period-'food side' interaction on the choice of the observers (χ^2 = 4.33, *P* = 0.038; Fig. 4.2b), indicating that there was a different effect of the social information on the choice of the observers between the first and the second half of experiment 2, so we tested both periods separately. In the first half of the experiment there was a significant positive effect of social information on the choice of the observers (χ^2 = 9.25, *P* = 0.002), indicating that the observers continued to join the demonstrator pair which received food (i.e., followed the social information) (day 13 – 18 in Fig. 4.2b). In the second half of the experiment there was no effect of social information on the choice of the observers anymore (χ^2 = 0.68, *P* = 0.41), indicating that the observers did not join the demonstrator pair which received food more often than the pair which received no food (day 19 - 24 in Fig. 4.2b). In all models there was no effect of 'food side previous day' (all *P* > 0.1). Additionally, there was no significant interaction between boldness score and period (*P* > 0.7) and no effect of boldness score (*P* > 0.2).

No social information There was no effect of the presence of the food on the side chosen by the observers (χ^2 = 0.82, *P* = 0.37; Fig. 4.4), indicating that the observers were not able to establish the location of the food without the presence of any social information. There was no effect of 'food side previous day' and no effect of boldness score (all *P* > 0.1).

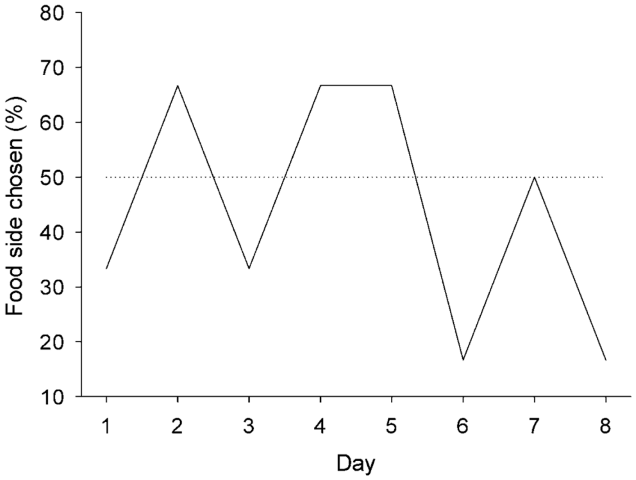

Figure 4.4 Results of experiment 3 where there was no food for the demonstrators and food on one side for the observers (no social information). Shown are the percentages per day individuals (*N* = 6) chose the side which contained food over a period of 8 days. Dashed line represents expectation based on random choice.

Discussion

Our results show that the use of social information decreased with increasing boldness. This result is particularly striking, given that the observers were only able to collect social information, since it was impossible for observers to collect personal information during the observation period (as was revealed by experiment 3). Moreover, the information in experiment 1 was completely reliable and there was no cost associated with collecting social information and no cost of aggression (since the observers and demonstrators had separate troughs and all the observers were dominant over all demonstrators). Importantly, we were able to discriminate between the use of social information and the motivation to be close to conspecifics ('sociability') since both demonstrator pairs were of the same group size. It has been shown that shy individuals have a stronger tendency to stay close to conspecifics (Budaev 1997; Ward *et al.* 2004; Michelena *et al.* 2008) making it difficult to judge whether a higher use of social information by shy individuals is merely the result of their higher tendency to stay close to others, or whether it is an active strategy (Sih & Bell 2008; chapter 5).

The observation that individuals within a species differ in their reaction to social information can have important implications for the spatial distribution patterns of individuals. Most models on spatial distribution patterns of individuals assume that each individual has an equal chance of being attracted to conspecifics or pay equal attention to the behaviour of conspecifics. Our observation that personality affects social information use and the many recent examples of the presence of personality in a wide variety of species (Gosling & John 1999; Koolhaas *et al.* 1999; Carere & Eens 2005; Groothuis & Carere 2005) questions this general assumption and stresses the need to include consistent behavioural variation in models of the spatial distribution of a species.

When studying group formation processes it is often difficult to reveal the exact reason for social attraction between individuals. The benefits of joining a group are generally assumed to be an increase in safety and/or an increase in foraging information (Ydenberg *et al.* 1983; Giraldeau & Caraco 2000; Krause & Ruxton 2002). It is often difficult to disentangle for which reason individuals join a flock. For example, in experiment 1, observers could have chosen to join the foraging individuals because they received information on the food availability of the patch or, alternatively, because they perceived the patch of the feeding demonstrators as safer due to the lower vigilance level of the foraging demonstrators. We were able to distinguish between both alternatives since if observers followed the lower vigilance level of the foraging demonstrator pair then we expected that the observers in experiment 2 continued to join the foraging demonstrators. However, observers decided not to continue joining the foraging demonstrators during the second half of experiment 2 (when the social information was incorrect), indicating that in experiment 1 the observers were using information related to foraging opportunities, ruling out predation avoidance as a motivational factor in our experiment. In the field, it has been shown that barnacle geese are attracted to plastic models of barnacle geese (Drent & Swierstra 1977) and that the posture of the models ('grazing' and 'alert' posture) affects the level of attraction: groups with a higher percentage of grazing models attract more barnacle geese than groups with a lower percentage of grazing models (Drent & Swierstra 1977). This observation suggests that barnacle geese use the posture of other individuals in patch decision rules and we show here that personality can play a role in such patch decision rules and consequently group formation and composition processes. The question, however, remains why individuals within one species differ in their social information use.

Firstly, bolder individuals might have had a lower loss of feeding time when choosing incorrectly since bolder individuals are known to explore the environment more readily.

Individuals indeed lost feeding time when they chose incorrectly, but there was no effect of boldness score on feeding time lost indicating that our observed relationship between boldness and social information use is not due to an absence of costs for bolder individuals. Secondly, bolder individuals may form routines more quickly, thereby neglecting social information around them. Several studies show that more explorative/proactive individuals (Benus *et al.* 1990; Verbeek *et al.* 1994; Koolhaas *et al.* 1999; Carere *et al.* 2005) are more prone to form routine like behaviour. In agreement with these studies we found that the probability that individuals chose the same side as the previous day increased with increasing boldness, suggesting that the bolder individuals formed more routine like behaviour, whereas shyer individuals depended more on the social information and were more flexible in their side choice. This suggests that in a field situation bolder individuals may rely more on previous experiences / information, whereas shy individuals rely more on social information. Individual variation in social information use may be maintained by a frequency dependent selection process, whereby a given tactic does better when it is rare in a population. For instance, the individual benefits of using social information are expected to be higher when fewer individuals are using the same information (e.g., in a producer scrounger context). The next step would be to test our observed variation in social information use in a field situation to study the ecological implications in terms of movement behaviour and fitness consequences.

Few other studies have examined the relationship between social information use and personality. Marchetti & Drent (2000) found that birds selected from fast exploring lines copied the behaviour of tutor birds faster than slow birds. Likewise, Nomakuchi *et al.* (2009) found evidence that in three-spined sticklebacks, *Gasterosteus aculeatus,* fast explorers used social information to a larger extent by following informed demonstrators further through a maze. The key difference with both these studies is that in our study individuals were allowed to watch the behaviour of other individuals and hence were, during that time, not able to collect personal information, whereas in the previous studies individuals were given the opportunity to collect personal information from the start of the experiment. Additionally, we were able to separate the effect of social information use and sociability (flocking tendency), which was not possible in both previous studies.

Few studies have investigated the role of personality in individual differences in learning (Sih & Bell 2008). Pfeffer *et al.* (2002) showed that more innovative greylag geese excreted higher levels of faecel corticosterone. Corticosterone excretion is a measurement of the stress response of an individual and relatively large corticosterone responses are associated with reactive individuals (Cockrem 2007). In alignment with this, less proactive mice and great tits change their search pattern faster than proactive individuals as a reaction to a change in environment (Benus *et al.* 1987; Verbeek *et al.* 1994). However, several studies reported a positive correlation between boldness and learning speed (see Guilette *et al.* 2009 and references therein). In our experiment 1 we did not find evidence that there was a learning effect over the course of the experiment, since there was no effect of day and no significant interaction between day and boldness score on correct choice. This suggests that our results are not due to a difference in learning speed between bold and shy individuals, but that shy individuals use more social information during the whole course of the experiment. In experiment 2 individuals learned that the behaviour of the demonstrators did not correspond to the location of the food for the observers anymore. This was unrelated to boldness, although the variation in boldness score of the observers in experiment 2 was low. There are some other examples of individuals which stop relying on unreliable social information. Vervet monkeys, *Cercopithecus aethiops,* learned to ignore playbacks of a call of an unreliable signaller (Cheney & Seyfarth 1988). A similar mechanism has been demonstrated in Richardson's ground squirrels, *Spermophilus richardson* (Hare & Atkins 2001). Our results show that barnacle geese are able to stop relying on social information when reinforcement stopped. However, in the time given, they were not able to reverse the information by going consistently to the opposite side from where demonstrators where feeding.

To conclude, we have demonstrated that the use of social information decreased with increasing boldness and that bolder individuals paid a lower cost when not following the correct social information. In addition, we have shown that barnacle geese can assess the quality of social information by showing that they neglected the social information if it was not correct anymore. Our results emphasize the importance of including personality differences (or individual variation) in the theory of social information use and challenge the traditional view of social information use as an entirely flexible and context dependent entity. This indicates that personality differences can affect behavioural decisions related to spatial distribution and group formation processes when these are linked to the use of social information in natural populations and therefore calls for incorporation of these personality-related differences in studies of the spatial distribution of animals in which social information use plays a role.

Acknowledgements

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Chapter 5

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

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

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Introduction

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

Personality in animal behaviour describes the phenomenon that differences between individuals in behavioural and physiological traits are consistent over time and context (Gosling & John 1999; Koolhaas *et al.* 1999; Carere & Eens 2005; Groothuis & Carere 2005). Different behavioural and physiological reactions have a genetic basis (van Oers *et al.* 2005) and are often correlated. This suggests that these differences are fundamental aspects of the behavioural organization of individuals and are the subject of natural (Dingemanse & Reale 2005; Smith & Blumstein 2008) or sexual selection (van Oers *et al.* 2008). The concept of inter-individual differences is also known as temperament (Reale *et al.* 2007), coping styles (Koolhaas *et al.* 1999) and behavioural syndromes (Sih *et al.* 2004a, b).

One of the best studied personality traits in a wide range of taxa is boldness. Several studies have demonstrated that bolder individuals are more often found in the leading edge of moving groups (Beauchamp 2000; Harcourt *et al.* 2009; Schuett & Dall 2009; chapter 2). In foraging groups, animals located on the edges are more likely to play producer (Barta *et al.* 1997; Mónus & Barta 2008). Taken together, these observations suggest that boldness might also predict the use of tactic in a producer – scrounger context. However, to our knowledge, no study to date has tested for a relationship between personality and producer-scrounger foraging tactic use.

We studied the relationship between the personality trait boldness and foraging tactic use in barnacle geese, *Branta leucopsis*. Boldness has been shown to be repeatable over time and to correlate with movement order towards a food patch in this species (chapter 2). We scored the boldness status of individuals by performing two novel object tests. Based on the outcomes of these tests we defined individuals as either bold individuals, shy individuals or intermediate individuals. We formed groups of one bold, one shy and two intermediate individuals and scored the frequency of producing and scrounging and the feeding time of the bold and shy individuals in a producer – scrounger game. As bold individuals are more often found in the leading edge of a moving group, we expected that shy individuals would have a higher percentage of scrounging than bold individuals. We scored the dominance of individuals living in a stable group situation prior to the producer – scrounger experiment, to control for any confounding dominance effect. In some species a relationship between the outcome of a novel object test and dominance has been reported (e.g., Verbeek *et al.* 1996, 1999; Sundström *et al.* 2004), but not in others (e.g., Freeman *et al.* 2004; Fox *et al.* 2009). In barnacle geese there is no relationship between the novel object score and dominance (chapter 2).

Methods

Study subjects We used captive-born wing-clipped barnacle geese, each fitted with a uniquely coded leg ring for identification ($N = 28$). Birds were sexed by cloacal inspection (14 females, 14 males) and were all unpaired. Before the start of the experiment we measured tarsus and culmen length (to the closest 0.1 mm) using callipers and wing length (1.0 mm) using a ruler. One observer carried out all measurements to minimize observer biases. Body mass was measured on a digital balance (1.0 g). We used a principal components (PC) analysis of tarsus, culmen and wing lengths to derive a measure of body size. PC1 explained 79.8% of the variation. Body condition was calculated as the residual from a regression of body mass on PC1. All geese were kept as one group in an outdoor aviary of 12 by 15 m at the Netherlands Institute of Ecology in Heteren, the Netherlands. Throughout the experiments geese were fed *ad libitum* with a mixture of grains, pellets and grass. A pond (6 by 1 m) was present in the aviary, with continuous flowing water for bathing and drinking.

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

Novel object test The novel object test used the procedure described in chapter 2. In short, we habituated individuals to an experimental arena of 3 x 9 m by introducing each individual seven times for 10 min in the arena (1 – 12 December 2008). After habituation we placed a novel object (a green plastic mat) in the middle of the arena, introduced each goose once for 10 min, and scored the minimal distance (cm) reached between the goose and the novel object, as well as the time elapsed (s) before the goose came within 50 cm of the novel object (15 – 16 December). If geese never approached within 50 cm of the novel object they were assigned an approach latency of 601 s. The test was repeated with another novel object (a brown deep-pile rug) on 17 and 18 December 2008. We calculated principal components (PCs) for each test as an independent measure of novel object score. PC1 explained 85.3% and 90.9% of the variation for test one and test two respectively. The correlations of both variables with PC1 were negative, implying that high values of PC1 correspond to bolder individuals. We used the average novel object score over the two tests as a measure of boldness.

Based on the outcomes of the novel object tests we assigned individuals to different groups. Individuals with the highest average novel object score were defined as bold individuals (*N* = 7), individuals with the lowest average novel object score were defined as shy individuals (*N* = 7). All other individuals were defined as intermediates (*N* = 14) (see also Fig. 5.1). Bold and shy individuals were given an extra colour ring for identification. We formed seven pairs of focal individuals, consisting of one bold and one shy individual and seven pairs of companion individuals, consisting of two intermediate individuals.

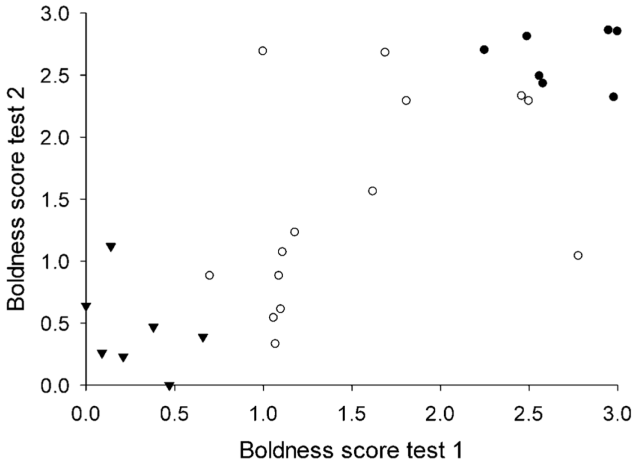

Figure 5.1 Relationship between the novel object score during two novel object tests for all individuals (*N* = 28). Triangles represent geese that were classified as shy (*N* = 7). Open circles represent geese that were classified as intermediate (*N* = 14). Filled circles represent geese that were classified as bold (*N* = 7).

Foraging experiment

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

To habituate the individuals to the experimental conditions we supplied half of the pots with grass and introduced all the geese as one group in the experimental arena. Thereafter, we gradually decreased the group size and the number of pots filled. Prior to the start of the experiment all individuals had been introduced eight times in the experimental arena. During experimental trials we filled 10 randomly chosen pots with a sod of grass (“food”). Sods were replaced after each trial if grazed upon. We removed the food from the aviary at 17.00h the day preceding each experiment.

During each trial we formed groups of four individuals, consisting of one pair of focal individuals (one bold and one shy) and one pair of companion individuals (two intermediates). The first day we randomly assigned one focal pair to one companion pair.

Thereafter we used a rotating system to pair the couples. The order of introducing the groups on each day was randomized. Geese were used once a day resulting in 7 trials per day and each focal pair was tested twice against each companion pair, resulting in 98 trials over a period of 14 days (5 – 20 February 2009).

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

All trials were video taped and we scored the behaviour of the two focal individuals from the recordings. Feeding events were identified either as ‘finding’ or ‘joining’. We did not use the terms producing and scrounging because we observed the actual feeding events and not the tactic use directly, i.e., whether a bird was searching as a producer or scrounger (Mottley & Giraldeau 2000; Coolen *et al.* 2001; Liker & Barta 2002). In a ‘finding event’ an individual discovered a filled pot at which no other individual was present and fed from it. In a ‘joining event’ an individual attempted to start feeding at a filled pot where another individual was foraging at the arrival of the focal individual. We distinguished between ‘successful joining’ (individual actually fed from the pot) and ‘unsuccessful joining’ (individual was not successful in feeding from the pot). We calculated the joining proportion for each individual for each trial as the total number of joining events divided by the sum of the total number of finding events plus the total number of joining events. We calculated the proportion of successful joining events as the number of successful joining events divided by the total number of joining events. We included the unsuccessful joining attempts in our calculation of proportion joined since the number of unsuccessful joining attempts contains important information on the foraging tactic an individual is following (regardless whether this tactic is successful or not). Excluding the cases of unsuccessful joining attempts would result in a less accurate estimation of the actual foraging tactic use. In addition we scored the total feeding time (s). Feeding time was defined as the total time a focal individual had its head in a filled pot. We could not measure the bite rate from our recordings. In addition we scored the order of arrival on the food patch and the number of different sods visited. Based on the linear dominance hierarchy each focal individual was rated a dominance score unique for each trial ranging from 1 (most dominant in the group of four) to 4 (most subordinate in the group of four) (see details below).

In a few trials (*N* = 12) not all four individuals foraged, which clearly affected the behaviour of other group members. Since we know that the foraging success of barnacle geese depends on the behaviour of other group members (chapter 2) and the reluctance to forage might affect the joining opportunities of other group members we excluded these trials from our analyses, leaving a total of 86 trials in which all individuals foraged.

Statistics We organized all observed dominance interactions between individuals in a sociometric matrix. To test for linearity we calculated Kendall’s coefficient of linearity *K*, Landau’s index *h* and the index of linearity *h’* using Matman 1.1 (Noldus Information Technology, Wageningen; and see de Vries *et al.* 1993). Statistical significance of *K* is calculated by a chi-squared test. Both indices vary from 0 (complete absence of linearity) to 1 (complete linearity). The index *h'* is based on *h* and takes into account the existence of unknown relationships. Statistical significance of *h'* is provided by a resampling procedure using 10,000 randomizations (de Vries 1995). If the dominance is linear Matman calculates a rank order most consistent with a linear hierarchy by minimizing the number of inconsistencies and then minimizing the total strength of inconsistencies (de Vries 1998).

We determined the repeatability of the novel object test by calculating the mean squares from a one-way analysis of variance (ANOVA) with individual as the main effect. Repeatability was calculated following Lessells & Boag (1987) and its standard error following Becker (1984). We compared differences between bold and shy individuals in dominance, body size and body condition using a t-test.

To test the effect of personality type and dominance on the use of tactic we used linear mixed effect models. To analyze the effect on proportion joined and on proportion successful joining events, we used generalized linear mixed models with binomial errors and a logit-link function. To analyze the effect on feeding time, order of arrival and number of sods visited we used general linear mixed models. Feeding time was log-transformed to meet the assumption of normality. As fixed effects in all models we fitted boldness, dominance, body condition, body size and sex. To avoid pseudoreplication we fitted focal individual nested within focal pair and companion pair as random effects. We started with full models containing all terms. Minimal adequate models were obtained by stepwise deletion of non-significant terms ($P > 0.1$), starting with the least significant term. To compare the explanatory power of two subsequent models we used a log-likelihood ratio test which follows a χ^2 distribution, with degrees of freedom equal to the difference in the number of parameters between the two models. We used the package lme4 for generalized mixed model procedures and nlme for general mixed model procedures in R (version 2.7.2). For all other calculations we used SPSS (version 15.0).

Results

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

Novel object test In agreement with earlier findings in this species, novel object score was highly repeatable (mean ± se) 0.81 ± 0.07 (see also Fig. 5.1) and there was no sex difference in novel object score ($t_{26} = 0.35$, $P = 0.73$). There were no differences between bold ($N = 7$) and shy individuals ($N = 7$) in dominance rank ($t_{12} = 0.46$, $P = 0.65$), body size ($t_{12} = 0.09$, $P = 0.93$) and body condition ($t_{12} = 0.17$, $P = 0.87$).

Foraging experiment Shy individuals joined significantly more than bold individuals, with the proportion being twice as large (shy: 47.8%, bold: 22.5%; $\chi^2 = 5.60$, $P = 0.018$; Fig. 5.2a).

Dominance (just as body condition, body size and sex) did not affect the proportion of joining events (body condition: $\chi^2 = 2.94$, $P = 0.09$; all other $P > 0.1$; Fig. 5.3a). However, the proportion of being successful in a joining event increased with increasing dominance ($\chi^2 = 7.03$, $P = 0.008$; Fig. 5.3b). Boldness (just as body size, body condition and sex) did not affect the proportion of successful joining (all $P > 0.1$; Fig. 5.2b).

There was no significant difference in feeding time between bold and shy individuals ($\chi^2 = 3.74$, $P = 0.053$; Fig. 5.2c) and neither dominance ($\chi^2 = 3.14$, $P = 0.077$; Fig. 5.3c) nor sex ($\chi^2 = 3.71$, $P = 0.054$) significantly affected feeding time. There was also no effect of body size or body condition on the time spent feeding (all $P > 0.1$). Boldness, dominance, body condition and sex did not affect the order of arrival at the food patch (all $P > 0.1$), while larger individuals arrived earlier than smaller individuals ($\chi^2 = 4.02$, $P = 0.045$). Boldness, dominance, body condition and body size did not affect the number of different sods visited (all $P > 0.1$), while males visited more sods than females ($\chi^2 = 8.36$, $P = 0.004$).

To test for individual consistency in foraging tactic use throughout the experiment we calculated the average joining proportion for each individual for the first half of the experiment (day 1-7) and for the second half of the experiment (day 8 -14). There was a strong positive correlation between the results from the first and second half of the experiment ($r = 0.93$, $P < 0.001$) indicating that individuals were consistent in their foraging tactic use.

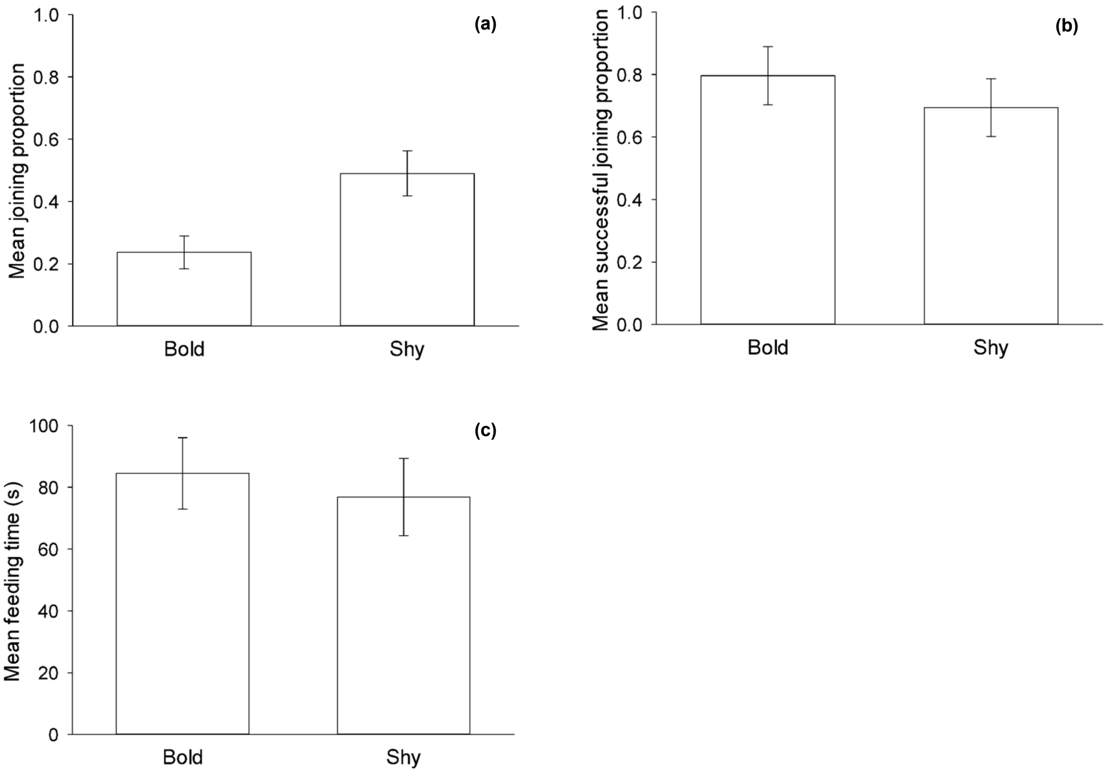

Figure 5.2 The effect of difference in boldness on (a) proportion of joining, (b) proportion of successful joining events and (c) feeding time. Shown are raw means ± 95% confidence intervals. Bold individuals: $N = 7$; shy individuals: $N = 7$.

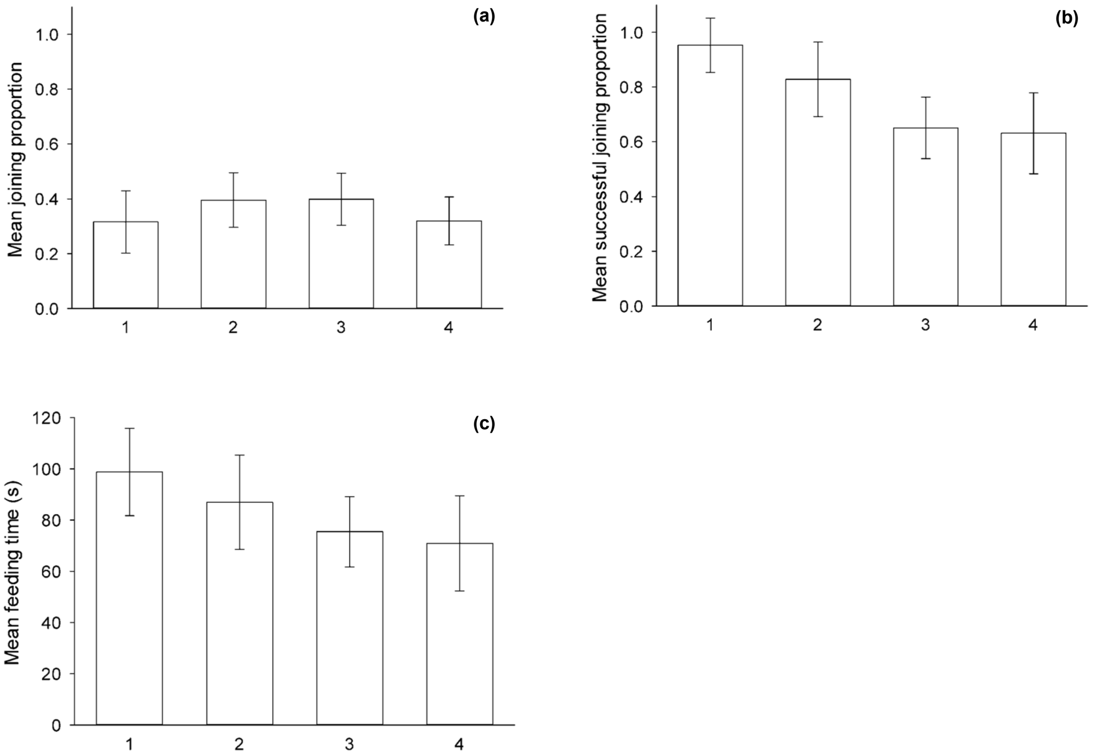

Figure 5.3 The effect of dominance on (a) proportion of joining, (b) proportion of successful joining events and (c) feeding time. Shown are raw means ± 95% confidence intervals. 1 = most dominant, 4 = most subordinate.

Discussion

Consistent with our hypothesis, we found that individuals classified as 'shy' showed a higher proportion of joining than bold individuals suggesting that personality affects scrounging behaviour. We did not find an effect of boldness on the order of arrival at the food patch or the number of different sods visited indicating that shy individuals were not more reluctant than bold individuals to approach the feeding area or to move between patches. The positive correlation between an individual's joining proportion in the first and second half of the experiment indicates that individuals were consistent in their foraging tactic use. Additionally, we already found a relationship between personality and social foraging tactic in two different contexts: in an experiment on movement order towards a food source we found that bold individuals led more often than shy individuals and that shy individuals followed more often (chapter 2). Another experiment on the use of social foraging cues revealed that shy individuals made more use of social foraging cues (chapter 4). These observations indicate that personality in barnacle geese is important in foraging tactic use under different conditions.

We propose two possible mechanisms which can explain the correlation between boldness and scrounging. Firstly, bolder individuals can be more active in exploring the environment, which is confirmed by the observation that bolder individuals are more often in the leading edge of moving groups (Beauchamp 2000; Harcourt *et al.* 2009; Schuett & Dall 2009; chapter 2). Animals occupying the front positions in a foraging group are also the first to discover new food patches. A second mechanism may be that shy individuals have a higher tendency to stay close to conspecifics. The tendency to stay close to conspecifics is termed 'sociability', and although the relation between sociability and boldness is not well understood, Côté *et al.* (2008) showed that boldness and sociability were positively correlated in common lizards (*Lacerta vivipara*). In groups of foraging sheep it has been demonstrated that shy individuals show a lower tendency to split into smaller subgroups than bold individuals (Michelena *et al.* 2008) and in guppies, *Poecilia reticulata*, and three-spined sticklebacks, *Gasterosteus aculeatus,* shy individuals have a higher shoaling tendency (Budaev 1997; Ward *et al.* 2004, Dyer *et al.* 2008). If it is true that shyer individuals stay closer to conspecifics, they may also be able to make more use of the scrounging tactic: By being closer to companions, the travel costs are reduced (Beauchamp 2008) and this might increase scrounging since patches are less likely to be empty when scroungers join.

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

If individuals are all equal and entirely flexible in their tactic use one expects that there is no difference in foraging success between individuals, since individuals can change their tactic freely if its current tactic results in a sub-optimal foraging success. However, the foraging success for individuals that are not equal (e.g., in terms of searching efficiency or competitive ability) might differ. Ranta *et al.* (1996), in their model on producer-scroungers games, included two phenotypes differing in their ability to search for food patches and to compete for food. Their model predicted that in a situation where the patch-finder gets some of the discovered food before arrival of the other competitors the intake rate of the two phenotypes would be unequal except in two cases; that is, when producers do all or a disproportionately large share of the searching, and when the scroungers are the better competitors. Both conditions were not met in our experiment. Shy individuals also frequently found their food (> 50%) and most likely did not differ in competitive abilities since there was no difference between shy and bold individuals in dominance score. Food finders in our experiment clearly got some of the food before arrival of competitors since the consumption of grass requires only a short handling time (Durant *et al.* 2003). Bold and shy individuals consistently differed in their foraging strategies in our experiment suggesting that they were unequal. We found a borderline significant difference in feeding time between bold and shy individuals suggesting that the foraging success for both types indeed could be different although this result has to be treated with care. Most models of producer – scrounger games generally assume that individuals are equal and that foraging payoffs are independent of phenotype. Although individual tactic use in producer-scrounger games is indeed partly flexible and dependent on hunger level (Lendvai *et al.* 2004), dominance (Liker & Barta 2002) and predation risk (Mathot & Giraldeau 2008) it is more likely that the tactic followed is a combination between consistency and flexibility (Beauchamp 2001). Beauchamp (2006) already showed that scrounging is related to individual foraging efficiency providing evidence for consistency in scrounging behaviour. Our observation that personality affects tactics use and the many recent examples of the presence of personality in a wide variety of species questions the general applicability of these models and stresses the need to take individual behavioural differences into account in modelling producer – scrounger games (see for example Ranta *et al.* 1996).

There are few studies which have investigated the fitness outcomes of different personality types; hence, the processes of the evolution of difference in personality traits and the maintenance of these traits in a population are largely unknown. Several mechanisms have been suggested such as frequency dependent selection and spatiotemporal variation in environmental conditions (Dall *et al.* 2004; Dingemanse *et al.* 2004; Smith & Blumstein 2008). Recently, it has been suggested that the trade-offs between life history traits could explain the evolution of personality traits (Wolf *et al.* 2007). Variation in boldness is believed to be a result of predation (Bell & Sih 2007) and it has been suggested that in absence of predation the costs of boldness are likely to disappear (Côté *et al.* 2008). In this scenario there is a trade-off between for example food intake rate and predation risk, with bold individuals enjoying a higher food intake rate but also a higher risk to be predated. A positive correlation between boldness and food intake rate has indeed been reported in several species (Biro & Stamps 2008). Our results seem to support this, since bold individuals spent more time feeding than shy individuals although this difference was at borderline significance. Similar foraging success is another possible mechanism for the maintenance of boldness differences. In a population of only bold individuals which all tend to act as producers a shy individual would probably do better than a bold individual as they rely more on the scrounging tactic. As the amount of shy individuals in the population grows the difference in success between the shy and bold individuals will probably decrease up to a certain point where both personality types perform equal. In such a scenario the producer – scrounger context might maintain differences in boldness in a population with an underlying frequency dependent selection process. In spice finches the intake rate of the scrounger tactic indeed decreased with increasing scrounging frequency whereas there was little effect on the intake rate of the producer tactic, providing experimental evidence for a negative frequency dependence of scrounger payoff on scrounger frequency (Mottley & Giraldeau 2000).

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

We found no difference between bold and shy individuals in dominance rank, which agreed with our earlier finding that in barnacle geese there is no relationship between the novel object score (i.e., boldness) and dominance (chapter 2). We found no effect of dominance on the proportion of joining, though dominant individuals had a higher proportion of successful joining than subordinate individuals (Fig. 5.3b). A higher percentage of scrounging for dominant individuals is a well described phenomenon (Liker & Barta 2002; McCormack *et al.* 2007; but see Lendvai *et al.* 2006). Studies on producer-scrounger games not always differentiate between successful and unsuccessful joining events. Our study demonstrates that it can be important to distinguish between both, especially if one wants to understand differences in foraging success. We expected that dominant individuals, as a result of a higher proportion of successful joining events, also had a higher feeding time. However, we found only a tendency for more dominant individuals to have longer feeding times. Possibly subordinate individuals had ample opportunities to search for food at different pots. In barnacle geese in the field it has been demonstrated that subordinate individuals are the first to arrive at new food patches, and that dominant individuals use this information produced by subordinates (Stahl *et al.* 2001). Our results do not agree with this finding since dominance did not affect the proportion of joining, although dominant individuals had a higher proportion of successful joining indicating that they were better competitors.

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

Acknowledgements

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Chapter 6

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 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 to the patch of individuals 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 (‘non-social 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 behaviour, but not in joining behaviour. 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 foraging decisions of group-living animals.

Submitted

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 (c.f. Bergvall *et al.* 2011, chapter 3), but show variation in personality that affects their foraging decisions. Personality describes the phenomenon that differences in behavioural and physiological traits among individuals of the same species are consistent over time and context (Gosling & John 1999; Koolhaas *et al.* 1999; Carere & Eens 2005; Groothuis & Carere 2005; Réale *et al.* 2007; Biro & Stamps 2008; Sih & Bell 2008).

There is ample evidence that variation in personality affects foraging decisions in groups. For example, in groups that collectively move towards 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* (chapter 2) and zebra finches, *Taenopygia guttata* (Beauchamp 2000; Schuett & 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 produced more food in a producer-scrounger game than shyer barnacle geese which in turn scrounged more (chapter 5). In groups of foraging sheep, bolder individuals split in smaller subgroups at smaller group sizes than shy sheep (Michelena *et al.* 2009), most likely to decrease interference competition.

These studies clearly demonstrate that personality is related to foraging decisions in groups, but causality cannot be assessed as these studies are non-experimental. When individuals are not experimentally assigned a role (e.g. leader / follower or producer / scrounger), they are able to choose their role according to intrinsic preferences. A second limitation arises due to the social nature of this type of study. In a social context, the behaviour of an individual may be affected by its own personality, the presence and behaviour (influenced by, amongst others, personality) of other individuals, and the interaction between these factors (Harcourt *et al.* 2009). Disentangling these processes is challenging, since it can be problematic to separate the individual choice from the social effect (see for example Van Oers *et al.* 2005; Magnhagen & Staffan 2005; Webster *et al.* 2007; Schuett & Dall 2009; Magnhagen & Bunnefeld 2010) and therefore requires an experimental approach.

To overcome these problems we performed a social foraging experiment, placing individuals with different boldness scores in two different standardized social environments. Individuals 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 in which 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 an identical non-social context (i.e., without a companion individual present) to study the behavioural 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 as well as companions is important in a social foraging task: in pairs, bolder individuals take the lead more often towards 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 (chapter 2). Based on chapters 2, 3, 4 and 5 we expected (1) that bolder individuals would arrive quicker in the 'leaving context' since boldness correlates positively with the propensity to go away from conspecifics; (2) that there would be no effect of boldness on arrival latency in the 'joining context'; and (3) that the arrival latency of bold individuals would not depend on the social context and that shy individuals would have a lower arrival latency in the presence of a companion next to the food patch ('joining context') compared to when there is no companion.

Methods

Experimental subjects We used captive-born wing-clipped female barnacle geese ($N = 20$), each fitted with a uniquely coded leg ring for identification. We used the first axis of a principal components 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 (± 1.0 g) 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 one group in an outdoor aviary of 12 by 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. A pond (6 by 1 m) was present in the aviary, with continuously flowing water for bathing and drinking.

Boldness test We assessed the boldness level of individuals by performing novel object tests (see for details chapter 2). We habituated individuals to an experimental arena (9 x 3 m). After habituation we placed a novel object in the middle of the arena, introduced each goose for 10 min and scored the minimal distance reached between the goose and the novel object, as well as the approach latency (defined as the time elapsed before the goose came within 50 cm of the novel object). Each individual was tested twice in November or December 2008 (see chapter 2 and 5) as part of a larger group of individuals ($N = 46$). We calculated principal components (PCs) of the test variables for each test as the novel object score. Including all individuals, PC1 explained 87% and 90% of the variation for test 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 (ANOVA) 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 (0.81) (see chapter 5) indicating that individuals differed consistently in their boldness scores.

Foraging experiment We used an experimental arena consisting of two compartments: one for the focal individual and one for the companion individual (see legend Fig. 6.1 for details). In both compartments, a patch of grass (20 x 40 cm) was placed opposite of the entrance. We used commercially-bought sods of perennial ryegrass, *Lolium perenne*, an important food source for wild barnacle geese (Prins & 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 Fig. 6.1). We used a single individual (not used as a focal individual) 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 07.00–12.30 hours (15 March – 4 May 2010; summer time started 28 March 2010).

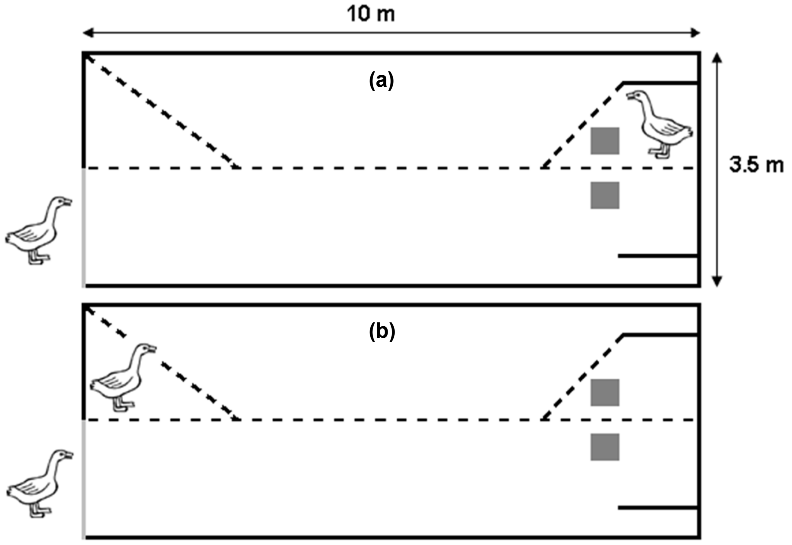

Fig 6.1 Schematic overview of the experimental arena used for the foraging experiment. The closed lines represent a wire-fence covered with white plastic (height: 80 cm). The dashed lines represent transparent wire netting. The grey squares represent grass patches. The grey lines represent a door, which 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').

Experiment 1: Joining context All individuals were first tested in the experimental arena without a companion (non-social 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 Fig. 6.1a). We repeated this procedure three times, alternating between the non-social and the social context, resulting in six 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 non-social 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 at the beginning of the arena (see Fig. 6.1b, round 8). As in experiment 1, we repeated this procedure three times.

All trials were ended one minute after the focal individual arrived at the food patch, up to a maximum of ten minutes. We measured whether the focal individual arrived at the food patch at all (yes/no), and if yes, the time elapsed until arrival at the food patch. If individuals did not arrive at the patch they were assigned an arrival latency of 601 sec. All trials were video taped and the arrival latency 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 since 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 sec) 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 (ranging from 14 to 601 sec) by the maximum arrival latency (601 sec). 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/non-social condition), the interaction between boldness score and treatment, round, body size and body condition as fixed factors. We included goose identity as a random effect in all mixed models. We report full statistical models including estimates and standard errors 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 also 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 are therefore not reported in the results.

To test if individuals of different boldness scores differed in their behavioural change between a non-social and a social context, we calculated for each individual the average difference in arrival latency between the non-social 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 Language R.

The arrival (yes/no) and arrival latencies measured in the three non-social trials in experiment 1 and 2 were compared to test whether individuals reacted differently between these trials (for example due to a habituation effect). We compared arrived (yes/no) using GLMMs with binomial errors and a logit-link function, fitting experiment (1 or 2) as fixed effect and individual 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 (Table 6.1) and no effect of round, body size and body condition (Table 6.1). Since the interaction between treatment and boldness score was close to significant ($P = 0.091$) we analyzed the effect of all fixed factors on arrival latency for both treatments separately. In the non-social context arrival latency decreased with increasing boldness score ($z = -2.385$, $P = 0.017$; Fig. 6.2a). There was no effect of round, body size or body condition (all $P > 0.2$). In the social context, however, there was no effect of boldness score on arrival latency ($z = -0.091$, $P = 0.93$; Fig. 6.3a), nor was there an effect of round, body size or body condition (all $P > 0.4$).

Experiment 2: Leaving In the leaving context the arrival latency decreased with increasing boldness score (Table 6.2). In addition larger individual had lower arrival latencies. There was no effect of round and body condition (Table 6.2). The interaction between treatment and boldness score was far from significant (Table 6.2). Both in the non-social ($z = -2.264$, $P = 0.024$; Fig. 6.2b) and social context ($z = -3.039$, $P = 0.002$; Fig. 6.3b) arrival latency decreased with increasing boldness score.

Table 6.1 Results of a GLMM analysis with the arrival latency (expressed as proportion) in the joining context as the response variable. Treatment*boldness represents the interaction between treatment (i.e., non-social/social condition) and boldness score of the focal individual. In bold are significant terms.

	Estimate	SE	z-value	Pr(>|z|)
(Intercept)	1.587	0.596	2.664	0.008
Round	-0.071	0.151	-0.469	0.639
Body size	-0.288	0.263	-1.092	0.275
Body condition	0.000	0.001	-0.182	0.855
Treatment	-3.100	0.540	**-5.742**	**0.000**
Boldness	-0.993	0.392	**-2.532**	**0.011**
Treatment*boldness	0.942	0.557	1.692	0.091

Table 6.2 Results of a GLMM analysis with the arrival latency (expressed as proportion) in the leaving context as the response variable. Treatment*boldness represents the interaction between treatment (i.e., non-social/social condition) and boldness score of the focal individual. In bold are significant terms.

	Estimate	SE	z-value	Pr(>|z|)
(Intercept)	2.338	0.737	3.173	0.002
Round	-0.204	0.164	-1.242	0.214
Body size	-1.100	0.442	**-2.486**	**0.013**
Body condition	-0.003	0.002	-1.586	0.113
Treatment	-0.977	0.590	-1.656	0.098
Boldness	-1.080	0.512	**-2.108**	**0.035**
Treatment*boldness	-0.492	0.601	-0.715	0.475

Difference between social and non-social trials There was a significant interaction between boldness and context ($P < 0.001$) on the difference in arrival latency between the social and non-social trials. In the joining context the difference in arrival latency decreased with increasing boldness score (GLM: est ± SE = -98.88 ± 37.00, $t = -2.67$, $P = 0.016$; Fig. 6.4). In the leaving context there was a trend of an effect of boldness on the difference in arrival latency between the social and non-social trials, but the effect was in the opposite direction (est ± se = 58.9 ± 28.6, $t = 2.06$, $P = 0.054$; Fig. 6.4).

Repeatability There was no significant difference in the number of arrivals between experiment 1 and 2 during the non-social context ($\chi^2 = 0.05$, $P = 0.8$), 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 arrival latency in experiment 1 and 2 during the non-social context, indicating that individual differences in arrival latency were consistent.

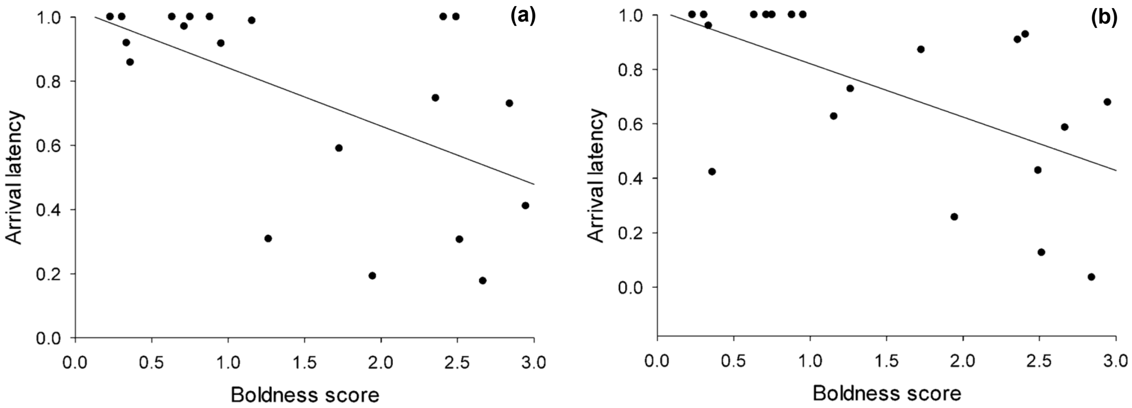

Fig 6.2 The arrival latency at the food patch (expressed as fraction of the maximum arrival latency, i.e. 601 s) decreased with increasing boldness score during the non-social context in (a) experiment 1 and (b) experiment 2. Lines are regression lines.

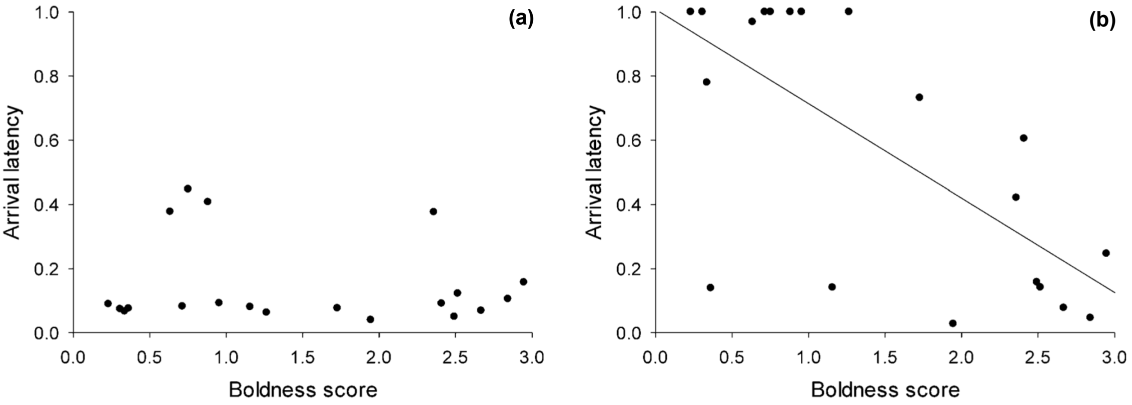

Fig 6.3 Arrival latency at the food patch (expressed as fraction of the maximum arrival latency, i.e. 601 s) during the social foraging experiments. (a) In the presence of a companion that was already present at the food patch there was no effect of boldness on the arrival latency (experiment 1); (b) In the presence of a companion that was restrained at the beginning of the arena, the arrival latency decreased with increasing boldness score (experiment 2). Line is a regression line.

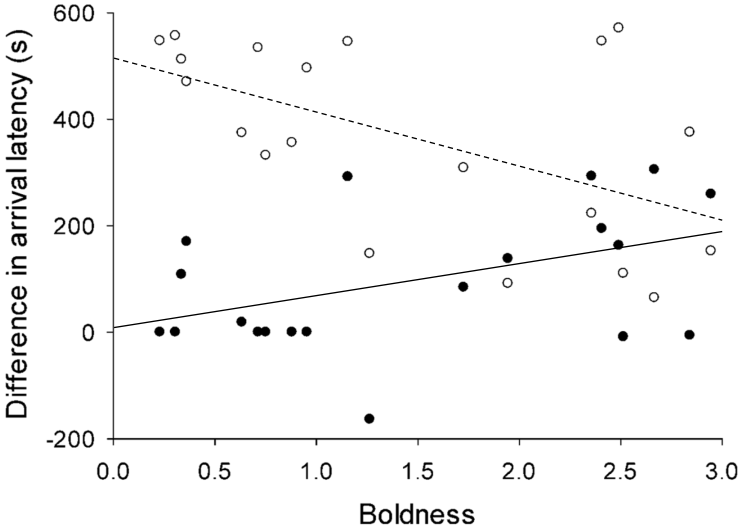

Fig 6.4 Difference in arrival latency between the non-social and social context. Open circles and dotted line represent the difference in experiment 1 (with a companion animal already present at the food patch, joining context). In the joining context the difference in arrival latency between the non-social and social context increased with decreasing boldness score. The closed circles and solid 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 non-significant (*P* = 0.054). Positive values indicate that individuals became faster in the social context as compared to the non-social context. Lines are linear regression lines.

Discussion

As predicted, 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 non-social 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 (see Introduction). Our study did not study leadership directly, since 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 in more detail. 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 itself.

For individuals living in groups, it is important to understand if and how personality traits are expressed in a social context (see Webster & Ward 2011 for a review). One of the difficulties is that individuals affect each other, so that these interaction processes are difficult to disentangle (see Introduction). 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 of 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 signalling 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 behaviour in an identical non-social context to understand how individuals (with different personality traits) actually adjust their behaviour towards the social context. Social facilitation occurs when the presence of other individuals causes the focal individual to show different behaviour or to perform behaviour at a different rate than when measured in isolation (for a review on the relation between social facilitation and personality see Webster & 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 behaviour in reaction to the presence of a companion. In the same vein, Magnhagen & Bunnefeld (2010) showed that in perch, *Perca fluviatilis*, shy individuals showed the largest change in behaviour when comparing a social and non-social context (see also Magnhagen & Staffan 2005). Similar to these studies, we found in the 'joining context' that the difference in arrival latency between the social and non-social 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 behaviour) of other individuals (see also chapter 4), whereas bolder individuals are (on the other side of the same coin) more important in affecting group behaviour, such as collective movements (see also Michelena *et al.* 2009; Magnhagen & Bunnefeld 2010; chapter 3). In experiment 2, however, there was no such pattern, indicating that a more reactive behaviour 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 & Dall 2009).

One could criticize our study because all individuals started with a trial in a non-social 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 non-social trials of experiment 1 and experiment 2 and there was no significant difference in average arrival latency (or number of trials arrived) between the non-social trials of experiment 1 and 2. Individual boldness scores were still predictive for how quickly individuals approached the food patch in the non-social trials of experiment 2, even after numerous introductions. In addition, in all our mixed models we included ‘round’ 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 non-social 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 non-social and social context, suggesting that shyer individuals are more responsive to the presence of other individuals.

Acknowledgements

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Chapter 7

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

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

Behavioral Ecology. Accepted.

Introduction

Personality in animal behaviour describes the phenomenon that differences between individuals in behavioural and physiological traits are consistent over time and context (Gosling & John 1999; Koolhaas *et al.* 1999; Carere & Eens 2005; Groothuis & Carere 2005). Different behavioural and physiological reactions have a genetic basis (van Oers *et al.* 2005a) and are often correlated. This suggests that these differences are fundamental aspects of the behavioural organization of individuals. One of the pivotal questions in animal personality is the evolution and maintenance of animal personality. Several (non-mutually exclusive) mechanisms have been suggested, such as spatiotemporal variation in environmental conditions (Sih *et al.* 2003; Dall *et al.* 2004; Dingemanse *et al.* 2004; Smith & Blumstein 2008; Réale *et al.* 2010), differences in life-history trade-offs (Wolf *et al.* 2007; Gyuris *et al.* 2010; see also Biro & Stamps 2008; Réale *et al.* 2009) and sexual selection (Schuett *et al.* 2010). A fourth mechanism is negative frequency dependent selection (Wolf *et al.* 2008). Negative frequency dependent selection operates against common phenotypes, thereby favoring the rarer phenotype in a population. The rarer phenotype for example suffers less from predation. Negative frequency dependent selection is used in many areas of evolutionary biology (Maynard Smith 1982) and is predicted to be important in generating variation in personality (Sih *et al.* 2004; Réale *et al.* 2007; Wolf *et al.* 2008; Wolf & Weissing 2010).

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

In the current experiment, individuals were classified as shy or bold based on novel object tests. Then we formed companion groups consisting of either bold or shy individuals and introduced these groups together with one focal individual (either bold or shy) in a producer scrounger game and scored the foraging tactic and foraging success of the focal individual. We measured and controlled for a potential effect of dominance. An earlier study in barnacle geese (Chapter 5) showed that shy individuals had a higher frequency of joining than bold individuals, indicating that bold individuals rely more on the producing tactic, whereas shy individuals rely more on the scrounging tactic (see also Chapter 4). Therefore, we expected in a situation with only bold companions that a shy individual would do better than a bold individual, since it could profit more from the food discoveries of its bold companions due to its increased reliance on scrounging. In a situation with only shy companions, we expected a bold individual to do better than a shy individual since there was ample opportunity to produce food, as there was a low rate of producing patches by conspecifics.

Methods

Study subjects We used captive-born wing-clipped barnacle geese, each fitted with a uniquely coded leg ring for identification ($N = 44$, 20 females, 24 males). We measured tarsus and culmen length (to the closest 0.1 mm) using calipers and wing length (1.0 mm) using a ruler. One observer carried out all measurements to minimize observer biases. Body mass was measured on a digital balance (1.0 g). We used a principal components (PC) analysis of tarsus, culmen and wing lengths to derive a measure of body size. PC1 explained 79.8% of the variation. Body condition was calculated as the residual from a regression of body mass on PC1. All geese were kept as one group in an outdoor aviary of 12 by 15 m at the Netherlands Institute of Ecology in Heteren, the Netherlands. Throughout the experiments geese were fed *ad libitum* with a mixture of grains, pellets and grass. A pond (6 by 1 m) was present in the aviary, with continuous flowing water for bathing and drinking.

Novel object test We assessed the boldness level of individuals by performing novel object tests (see for details Chapter 2). We habituated individuals to an experimental arena (9 x 3 m). After habituation we placed a novel object in the middle of the arena, introduced each goose for 10 min and scored the minimal distance reached between the goose and the novel object, as well as the approach latency (defined as the time elapsed before the goose came within 50 cm of the novel object). Each individual was tested twice in November or December 2008 (chapter 2 and 5). We calculated principal components (PCs) of the test variables for each test as the novel object score. Including all individuals, PC1 explained 87% and 90% of the variation for test 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 (ANOVA) with individual as the main effect. Repeatability was calculated following Lessells & Boag (1987) and its standard error following Becker (1984). Repeatability of novel object score was high (rep ± se = 0.81 ± 0.05, $N = 44$) indicating that individuals differed consistently in their boldness scores.

We ranked all individuals based on the average of the two novel object tests and selected the 14 boldest and 14 shyest individuals for the social foraging experiment (see below). All other individuals were housed in another compartment. Since the novel object tests took place (November – December 2008) approximately one year prior to the social foraging experiment (December 2009), we repeated the novel object tests one year after the social foraging experiment (November – December 2010) to confirm that boldness levels were consistent, which they were (repeatability score over all four tests: 0.61 ± 0.07, $N = 44$).

For the final analysis we used as boldness score for the focal individuals the average of all four novel object tests, which is probably the most adequate reflection of the boldness level during the social foraging experiment.

Dominance Prior to the social foraging experiment, we scored agonistic interactions within the flock of the 28 selected individuals (7 - 11 December 2009). We identified the participants of each interaction, and scored the behaviour each used. We considered an interaction as being won by an individual when the opponent turned and walked or ran away (Stahl *et al.* 2001a). In total we scored 617 interactions (mean number per individual: 44; range: 10 - 110 interactions). We constructed a dominance matrix (using Matman 1.1, Noldus Information Technology, Wageningen) since this takes into account the identity of each opponent and all the interactions and is built in such a way that the number of contests won by individuals lower in rank are minimized. The Kendall's coefficient of linearity ($K = 0.32$, $\chi^2 = 101.9$, $P < 0.001$), Landau's index h ($h = 0.33$) and the corrected index of linearity h' ($h' = 0.37$, $P < 0.001$), allowed the use of a linear order to rank individuals. In barnacle geese dominance positively affected the proportion of successful joining (that is the chance that a joining attempt is successful) and dominance had a non-significant tendency to affect feeding time in an earlier producer-scrounger experiment (chapter 5). To avoid a possible confounding effect of dominance on tactic use and feeding time (see also Stahl *et al.* 2001a) we used the dominance rank to assign individuals to either the companion group, or the focal group during the social foraging experiment (see below).

Social foraging experiment The experimental arena consisted of an arena of 5.5 x 11 m. The floor was covered with anti-root cloth and we placed 99 flowerpots (height: 20 cm, diameter opening: 22 cm) equidistantly at 55 cm on the anti-root cloth. Flowerpots were empty, or contained a 5 x 5 cm sod of perennial ryegrass (*Lolium perenne)*, cut to a height of 1 cm. This grass is an important food source of wild barnacle geese (Prins & Ydenberg 1985). We fastened the sod into the ground using a long nail stuck through the sod and pot. To habituate the individuals to the experimental conditions we supplied half of the pots with grass and introduced all geese as one group in the experimental arena. Thereafter, we gradually decreased the group size and the number of pots filled. Prior to the start of the experiment all individuals had been introduced six times in the experimental arena. During experimental trials we filled 9 randomly chosen pots with a sod of grass ("food"). Sods were replaced after each trial if grazed upon.

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

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

All trials were video taped and we scored the behaviour of the focal individual from the recordings. Additionally, we scored the behaviour of all companions to be able to quantify a possible difference between individuals in both companion groups. Feeding events were identified either as ‘finding’ or ‘joining’, as we could not score the investment in tactic use directly (i.e., producing or scrounging, see also Coolen *et al.* 2001). In a ‘finding event’ an individual discovered a filled pot at which no other individual was present and fed from it. In a ‘joining event’ an individual attempted to start feeding at a filled pot where another individual was foraging at the arrival of the focal individual. We distinguished between ‘successful joining’ (individual actually fed from the pot) and ‘unsuccessful joining’ (individual was not successful in feeding from the pot). The number of ‘unsuccessful joining’ was extremely low for the focal individuals ($N = 3$ over all trials) reflecting that focal individuals were indeed dominant over companions. We calculated the joining proportion for each individual for each trial as the total number of joining events divided by the sum of the total number of finding events plus the total number of joining events. In addition we scored the total feeding time (s). Feeding time was defined as the total time a focal individual had its head in a filled pot.

Statistical analysis To test the effect of focal personality type and personality type of companions on focal tactic use we used linear mixed effect models. For count data (i.e., number of findings and joinings) we used generalized linear mixed effect models (GLMMs) with Poisson distributions and a log-link function; for proportion data (i.e., joining proportion) we used GLMMs with binomial errors and a logit-link function. To analyze the effect on feeding time we used general linear mixed models. Feeding time was log-transformed to meet the assumption of normality. As fixed effects in all models we fitted boldness of the focal individual (continuous), boldness of the companion (bold or shy), body condition, body size, sex and the interaction between boldness of the focal individual and boldness of the companion. A significant interaction would indicate that boldness of the focal individual had a different effect in the shy companion groups as compared to the bold companion groups, which could provide evidence for negative frequency dependent performance. We used similar statistical models to test the effect of the behaviour of companion animals (i.e., number of findings and joinings) on focal tactic use (i.e., number of findings and joinings) and focal feeding time. To avoid pseudoreplication we fitted focal individual as random effect in all models. We report full statistical models including estimates and standard errors of all fixed factors. Significance levels of individual factors for generalized mixed models were derived from the z-values and associated *P*-values.

Significance levels of individual factors for general mixed models were derived by a Monte Carlo Markov Chain with 10.000 simulations using the package Language R. We used the package lme4 (Bates & Sarkar 2007) for generalized mixed model procedures and nlme (Pinheiro *et al.* 2011) for general mixed model procedures in R (version 2.11.1, R Development Core Team 2008). For all other calculations we used SPSS (version 15.0).

Results

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

Focal individuals Focal individuals had a higher joining proportion in the presence of bold companions than in the presence of shy companions (z = -2.077, *P* = 0.038, Table 7.1, Fig. 7.1a), with the proportion being nearly twice as high (mean in bold group: 41.3%, in shy group: 21.9%). There was a tendency for shyer individuals to have a higher joining proportion (z = -1.75, *P* = 0.080, Fig. 7.2). Body size, body condition, sex and the interaction between boldness of the focal individual and the companion group did not affect the proportion of joining (Table 7.1).

Table 7.1 Results of a Generalized LMM analysis with the proportion of joining of the focal individual as response variable. Focal*companions represents the interaction between boldness score of the focal individual and boldness score of the companion group. In bold are significant terms.

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

Table 7.2 Results of a General LMM analysis with feeding time of the focal individual as response variable. Focal*companions represents the interaction between boldness score of the focal individual and boldness score of the companion group. In bold are significant terms. *P*-values were derived using a Monte Carlo Markov Chain with 10.000 simulations.

	Estimate	meanHP	HPD95lower	HPD95upper	pMCMC	Pr(>|t|)
(Intercept)	2.025	2.024	0.787	3.224	0.003	0.012
Boldness focal	0.048	0.048	-0.495	0.576	0.852	0.885
Sex	1.850	1.853	0.108	3.636	0.040	0.109
Body size	0.111	0.109	-0.693	1.006	0.787	0.842
Body condition	0.001	0.001	-0.001	0.003	0.408	0.524
Boldness companions	-0.586	-0.572	-1.025	-0.122	**0.018**	**0.010**
Focal*companions	-0.256	-0.255	-0.695	0.194	0.265	0.233

Focal individuals had a higher feeding time in the bold companion groups (mean: 64.7 s) than in the shy companion groups (mean: 53.5 s) (Table 7.2, Fig. 7.1b). Boldness of the focal individual did not affect its feeding time (Table 7.2), nor was there a significant interaction between boldness of the focal individual and boldness of the companion group (Table 7.2, Fig. 7.3), indicating that there was no evidence that the rare type did better than the common type. There was no effect of body size, body condition or sex on feeding time (Table 7.2). A post hoc power analysis of a linear regression using feeding time focal individual as dependent and boldness score of the focal individual as independent variable, split per boldness type of the companion group (see also Fig 7.3), revealed that the power was low (0.06 and 0.05 respectively), therefore we have to treat these data with care.

Focal individuals had more joining events in bold companion groups (mean: 1.34 events) than in shy companion groups (mean: 0.73 events) (z = -3.40, *P* = 0.001). There was no effect of the boldness of the focal individual (z = -1.32, *P* = 0.19), nor was the interaction between boldness of the focal individual and boldness of the companion group significant (z = -1.15, *P* = 0.25). Males joined more than females (z = 2.02, *P* = 0.044) but there was no effect of body size or body condition (all *P* > 0.1).

There was no effect of the boldness of the companion groups or the boldness of the focal individuals on the number of finding events of the focal individuals, nor was the interaction between boldness of the focal individual and boldness of the companion group significant (all *P* > 0.2). Males found more than females (z = 2.27, *P* =0.023) but there was no effect of body size (*P* = 0.92).

The number of finding events of companion animals positively affected the number of joining events of the focal individual (z = 4.53, *P* < 0.001), as well as its feeding time (*P* = 0.001) but not its number of finding events (z = 0.77, *P* = 0.44). The number of joining events of the companions did not affect the number of finding events, joining events or the feeding time of the focal individual (all *P* > 0.1).

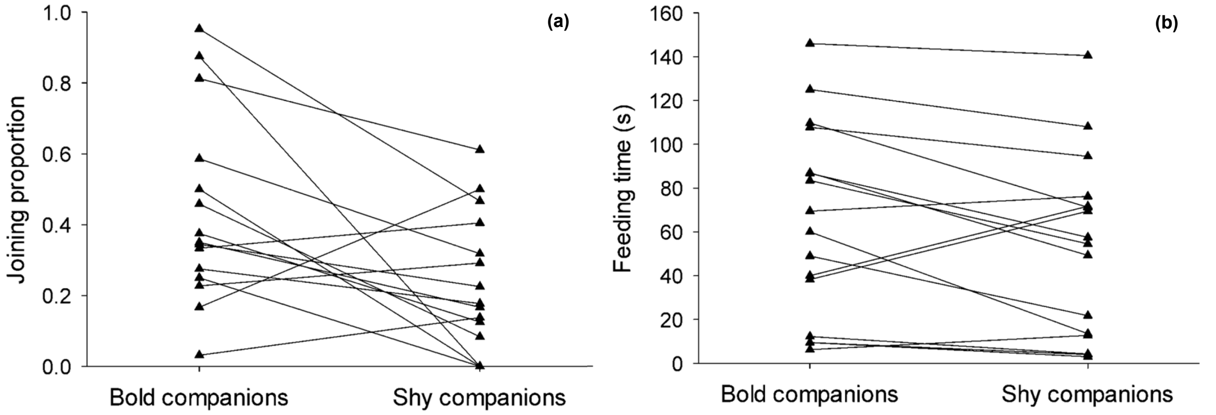

Figure 7.1 Focal individuals had (a) a higher proportion of joining and (b) a higher feeding time when foraging in a group with bold companions than when foraging in a group with shy companions. Each line indicates a different focal individual (*N* = 16).

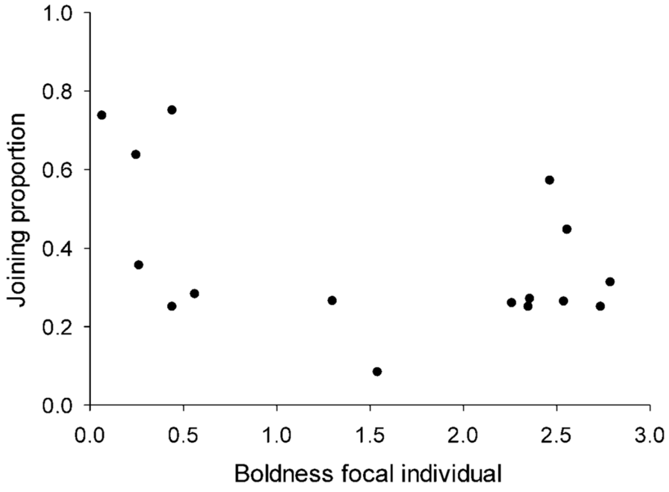

Figure 7.2 There was a tendency for bolder individuals to have a lower joining proportion (*P* = 0.080).

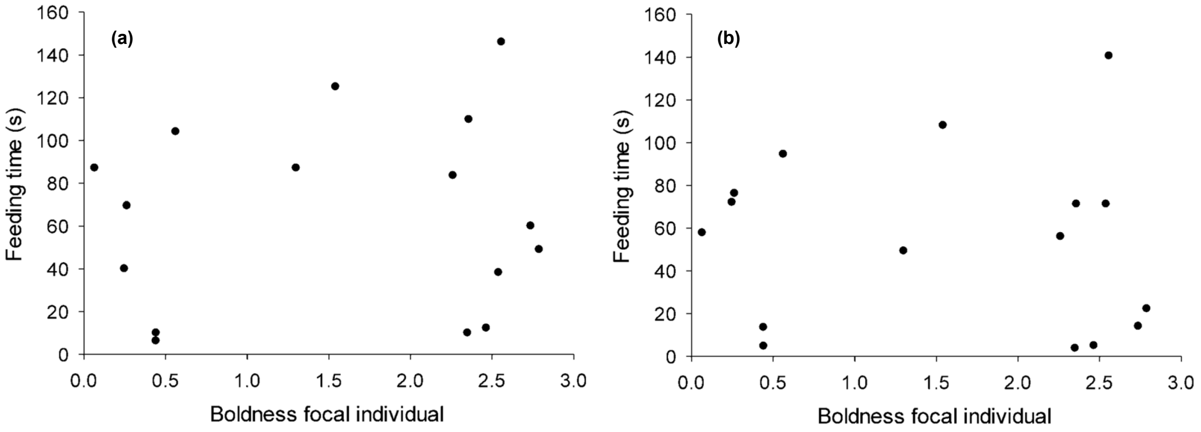

Figure 7.3 Boldness level of the focal individual did not affect its feeding time in the presence of (a) bold companions or (b) shy companions. There was no significant interaction between boldness of the focal individual and boldness of the companion group.

Discussion

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

In many species a positive correlation between boldness and food intake rates has been reported (see for a review Biro & Stamps 2008). Although we did not find a significant effect of boldness of the focal individual on feeding time, we did demonstrate that individuals profit from the presence of bold individuals since they increased their feeding time in bold companion groups as compared to shy companion groups. To the best of our knowledge, this is the first demonstration that individuals have higher foraging success in the presence of bolder individuals. The mechanism of increased feeding time is most likely due to the increased opportunity to join food discoveries as illustrated by the higher number of joining events (and joining proportion) of focal individuals in the bold companion groups and the positive effect of the number of findings of the companions on the number of joining events of the focal individual. The number of finding events of the focal individuals, by contrast, was not affected by the personality type or the number of findings events of the companions. Our demonstration that associating with bold individuals offers foraging benefits, for bold and shy individuals, can help explain why there is a preference for individuals, regardless of personality or hunger state, to join groups consisting of bold individuals rather than groups of shy individuals, as illustrated in three-spined sticklebacks, *Gasterosteus aculeatus* (Harcourt *et al.* 2010).

In focal individuals there was a weak tendency for shyer individuals to have a higher joining proportion ($P = 0.080$), confirming an earlier found patterns in this species (chapter 5). Several other studies suggest that personality traits determine producer-scrounger roles or social information use (Marchetti & Drent 2000; Dyer *et al.* 2008; chapter 5, but see Webster *et al.* 2007; Harcourt *et al.* 2010; for a review see Webster & Ward 2011). Since shyer individuals were expected to use the scrounging tactic more often, they were expected to profit more from the presence of bold (producing) individuals, than bolder individuals. However, this was not found since focal individuals, independent of their own boldness score, profited from the presence of bold companions (see Fig. 7.1). This is not totally unsurprising since all individuals do use the scrounging tactic to some extent and therefore increase their feeding success when there are more opportunities to scrounge. As a result we did not find evidence for negative frequency dependent feeding success as outlined in the introduction, though the power of the test was low. Since we only tested the feeding performance under one food condition we cannot yet generalize our conclusions. Numerous factors are known to affect scrounging frequency, including the cost of producing (Giraldeau *et al.* 1994; Beauchamp & Giraldeau 1997), patch richness (Giraldeau & Livoreil 1998; Coolen *et al.* 2001; Coolen 2002; Beauchamp 2008), group size (Barnard & Sibly 1981; Vickery *et al.* 1981; Coolen 2002) and predation risk (Mathot & Giraldeau 2010). All these factors shape the foraging payoffs and it is possible that certain parameter combinations allow negative frequency dependent feeding performance. A modeling exercise varying these parameters could elucidate this. Up to date there have been few studies that manipulated group composition based on personality types to study the effect of group composition on individual fitness (but see Sih & Watters 2005; Dyer *et al.* 2008). Clearly more experimental work is necessary in order to understand the ecological implications of personality types in group living animals and to answer the question if negative frequency dependence is an important factor for the maintenance of animal personality.

Although bold companion individuals seemed to have higher feeding rates and more finding events, there was no effect of the boldness score of the focal individual on its feeding time. This leads to the question to what extent individuals can express their personality when they are in groups of different personality types. It is known that in this (chapter 2) and other species (Magnhagen & Staffan 2005; van Oers *et al.* 2005b; Magnhagen & Bunnefeld 2009; Harcourt *et al.* 2009; Schuett & Dall 2009) individuals are affected in their behaviour by the personality of companions (see also Webster & Ward 2011 for a review). In pairs of barnacle geese the arrival time at a food patch depends on the personality type of the companion, with individuals arriving quicker in the presence of bold companions (chapter 2). Therefore we can speculate that perhaps focal individuals were highly affected by the personality type of their companions in their feeding time. In addition, differences in boldness might relate to differences in plasticity. There is a recent interest in differences in plasticity (or responsiveness) as a mechanism to explain variation in animal personality (Wolf *et al.* 2011). Morand-Ferron *et al.* (2011) tested the same individuals under different food conditions in a producer-scrounger game and found significant individual differences in plasticity. These individual differences where consistent over a period of six months. Our study was not designed to specifically test for potential differences in behavioural plasticity but the observation that both bold and shy focal individuals increased their scrounging frequency in bold companion groups suggest that there is not a direct link between boldness level and level of plasticity. A related issue is to what extent the focal individuals changed their time investment in producing and scrounging tactic between both companion groups. Though focal individuals joined more in bold companions groups this does not necessarily mean that they also invested more time in searching for joining opportunities since we did not directly measure time investments (see Coolen *et al.* 2001). We predict that focal individuals in the bold companion groups increased their investment in searching for joining opportunities since an increase in the number of producers or producing events should increase the scrounging frequency (Vickery *et al.* 1991).

Our results suggest that it is better to join bold individuals than shy individuals to increase feeding time. This confirms earlier observations that bolder individuals approach food sources quicker (Beauchamp 2000; Dyer *et al.* 2008; Harcourt *et al.* 2009; Schuett & Dall 2009; chapter 2), thereby offering potential foraging benefits for their companions. Dyer *et al.* (2008) suggest that it can also be beneficial for individuals to join shy individuals since the increased vigilance behaviour of shy individuals can have anti-predator benefits. This would suggest that in risky areas it is more beneficial to join shy individuals, whereas in low risk areas it is better to join bold individuals. This hypothesis awaits empirical scrutiny. An intriguing question is whether barnacle geese are able to discriminate between different boldness types. Drent & Swierstra (1977) showed that groups of artificial geese models can attract wild barnacle geese, and that groups containing a higher percentage of geese models with their head down ('grazing') were more attractive than groups containing a higher percentage of geese models with their head up ('vigilant'). If boldness corresponds to differences in vigilance behaviour, then this could be a potential mechanism how searching individuals can use the boldness of other individuals in patch choice decisions. Next to boldness, other factors might play a role in the decision to join or leave a foraging flock in a natural environment. Stahl *et al.* (2001b) 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 since they have a lower dominance status than paired geese (Stahl *et al.* 2001a) and will therefore suffer more from resource depletion. Rowcliffe *et al.* (2004) showed that the most successful foragers in barnacle geese flocks were largely unaffected by resource depletion over time, whereas the least successful foragers experienced severe depletion. Thus most likely in a natural situation dominance interacts with family status causing unpaired subordinate birds to leave foraging groups quicker and search for new food opportunities. In our experiment family status was not important since there were no pair bonds, and no parent-offspring relationships. Furthermore, dominance was controlled for by assuring that all focal individuals were dominant over all companion group members.

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

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Chapter 8

Scroungers are shy and producers are either: The co evolution of boldness and alternative foraging tactics

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Animals foraging in groups may use either the producing or the scrounging tactic to obtain food items. Most models of producer – scrounger games generally assume that individuals are competitively equal such that pay-offs are independent of phenotype. However, personality, most notably boldness, is known to affect the use of foraging strategy. Here we use a genetic algorithm to determine how the use of producer and scrounger tactics interacts with the evolution of boldness. Agents varied in boldness and scrounging probability and the genetic algorithm searched for the optimal combination of boldness and scrounging probability under different ecological parameters. Our simulations show that over a wide range of ecological conditions bold individuals evolve to play both producer and scrounger, whereas shy individuals remain confined to scrounging. An increase in patch density increased boldness, whereas patch richness did not affect boldness. We argue that this difference is due to the spatial dynamics: patch density, in contrast to patch richness, is a spatial component and therefore directly affects the optimal spatial positioning of individuals foraging in groups and as a result their boldness. For each parameter combination the genetic algorithm selected a single optimum level of boldness for all individuals demonstrating the absence of any negative frequency dependence of personality types in a producer – scrounger game. Our results show that differences in ecological conditions in a social foraging game may generate variation in boldness between populations.

Submitted

Introduction

Animals may either collect personal information about their environment, or they may observe other individuals to collect social information (Danchin *et al.* 2004). One of the best studied systems related to social information gathering is known as the producer – scrounger game (Barnard & Sibly 1981), in which individuals either search for food themselves (producing, = personal information) or make use of information about food made available by other group members (scrounging, = social information) (Hamblin *et al.* 2010). Most models of producer – scrounger games generally assume a symmetric game, a situation where phenotypic differences among individuals have no incidence on the payoffs they obtain from using one or the other foraging alternative. However, some phenotypic differences such as social dominance, energetic reserves or competitive ability will likely affect the payoffs obtained via one or the other foraging alternative (Barta & Giraldeau 1998; Liker & Barta 2002; Lendvai *et al.* 2004, 2006; McCormack *et al.* 2007; King *et al.* 2009).

"Personality" in animal behaviour is used to describe differences between individuals in some behavioural and or physiological traits that remain consistent over time and context (Gosling & John 1999; Koolhaas *et al.* 1999; Carere & Eens 2005; Groothuis & Carere 2005). Different behavioural and physiological reactions have a genetic basis (van Oers *et al.* 2005) and are often correlated, suggesting that these differences are fundamental aspects of the behavioural organization of individuals. These animal personalities are documented at an increasingly quick pace (Réale *et al.* 2007; Biro & Stamps 2008; Sih & Bell 2008). More recently, experimental evidence shows that tactic choice in producer – scrounger games is related to personality differences; bolder barnacle geese (*Branta leucopsis*) use the producing tactic more often than shyer geese (chapter 5). This is in agreement with several studies which show that, in groups, bolder / more explorative individuals approach food ('produce') more readily than shyer individuals (e.g., Beauchamp 2000; Dyer *et al.* 2008; Harcourt *et al.* 2009; Schuett & Dall 2009; chapter 2), whereas shyer / less explorative individuals are more often observed following others (Dyer *et al.* 2008; Harcourt *et al.* 2009; chapter 2, see also chapter 4).

Although the association between bold producing and shy scrounging makes intuitive sense, there is no a priori reason to believe that it should be universal and applicable to all circumstances. For instance, could some foraging conditions call for dissociation between this personality trait and social foraging tactics? Do some foraging conditions call for monomorphic populations of intermediate boldness that allows for maximum flexibility in the use of producer and scrounger tactics? Here we incorporated personality differences in a producer – scrounger simulation model to explore the conditions under which personality and social foraging traits should co evolve. As a measure of the personality trait boldness, we varied the tendency of individuals to move away from other conspecifics and explore the environment. Bolder individuals were more likely to move away from other individuals than shyer individuals. We allowed individual agents to vary both in boldness as well as in scrounging probability in a spatially explicit producer-scrounger model. We used a genetic algorithm (Sumida *et al.* 1990) to find the optimal combination of boldness and foraging tactic while varying patch density, patch richness and predation pressure. Genetic algorithms mimic the action of natural selection to model population change over time (Barta *et al.* 1997;

Hamblin & Hurd 2007; Ruxton & Beauchamp 2008), selecting the most successful individuals (i.e. those with the highest foraging rates) to reproduce in the next generation.

The Model

The foraging simulation Individuals searched for 200 time units for N_P patches containing N_S indivisible food items randomly distributed on a 500 by 500 grid in a population size N_I. At each time unit individuals could either be feeding or not. When individuals were feeding they would continue feeding in that patch, consuming one food item per time unit until the patch depleted. When individuals were not feeding, their action consisted of two steps. In the first step, they chose whether or not to move towards other flock members and in the second step they searched for food opportunities. Choosing to move towards flock members was selected according to the probability P_M, the likelihood that an individual moves back to its conspecifics, calculated as:

$$\mathrm{P_M} = \exp - (\beta \cdot \mathrm{b} \cdot (\frac{1}{d_m}))$$

b is boldness (ranging from 0 to 1), β is a scaling parameter that affects the rate of moving back to conspecifics and d_m is the median distance between the focal individual and its conspecifics. The probability of moving back to conspecifics increased with decreasing boldness score, implying that shyer individuals showed a higher tendency to move back to conspecifics as compared to bolder individuals. This is in agreement with the observation that shyer individuals show a lower tendency to split in smaller subgroups (Michelena *et al.* 2008) and have a higher shoaling tendency (Budaev 1997; Ward *et al.* 2004; Dyer *et al.* 2008). P_M increased with increasing median distance d_m, ensuring the maintenance of group cohesion.

If an individual decided to move towards the other flock members, its direction of movement was calculated as follows: a new direction was chosen by averaging the directions from the focal individual to each conspecific, weighted by the distance to each conspecific so that closer conspecifics weighted the new direction more heavily, according to the weighting function:

$$\mathrm{w}(d_i) = \mathrm{W} \,.\, \mathrm{e}^{(-\mathrm{d}_i^2)/(2.W^2)}$$

where w is the calculated weight as a function of distance, W is a weighting constant and d_i is the Euclidean distance to a conspecific i. To handle edge cases where every conspecific was too far away to affect the direction of the focal individual, a new direction of movement would be calculated by adding a random component drawn from a Gaussian distribution that was added to the previous direction (a correlated random walk).

When searching for food an individual could either (1) search for food itself (producing) or (2) search for food discoveries of other individuals (scrounging) (see section ‘The genetic algorithm’ for an individual’s probability of scrounging). (1) When producing, an individual investigated its close vicinity for food (as defined by a radius R_V), and if food was encountered, it started feeding in the next time unit. If no food was found, it took a step randomly. Random movement was calculated by selecting from a uniform distribution over the set of new directions within 45 degrees on either side of the current direction. (2) When scrounging, an individual scanned the environment for producers exploiting a patch. The probability of detecting feeding producers P_F declined with distance d_i to the forager: $P_F = \exp(-(d_i/H^2))$. H determines the scrounging horizon; small values indicate that scroungers could only identify producers close by. If it identified a feeding producer it moved in its direction during the next time step with twice its normal step length. If the individual arrived in the next time step, it started feeding. If it did not arrive it continued in the direction of the foraging patch, provided that the patch still contained food items, until it reached the patch. If the patch was emptied during the movement, or if the scrounger did not find a forager in its initial search it moved randomly as described previously. A scrounger could only forage from the food discoveries of other foragers.

In all cases (moving to conspecifics or random movement), the length of the step S_I was a decreasing function of boldness: $S_I = b * S_{MAX}$. S_{MAX} is the maximal step length. To avoid a potential value of zero, a small random Gaussian component was added to every individual's step length. An increasing step length with increasing boldness reflects a higher exploration tendency for bold individuals, a well-described phenomenon since bold individuals are more often found in the leading edge of moving groups (Beauchamp 2000; Harcourt *et al.* 2009; Schuett & Dall 2009; chapter 2).

The predation probability P_P represents the chance that an individual will be predated each round (from 0 to 90%); each round a random uniform number was compared to the probability, and if it was lower, predation was applied to the population. To implement predation, the centroid (geometric center) of the population was first calculated as the average of each member's position. Each member of the population then received a distance score from the centroid, c_i and an individual was chosen to be predated proportionally to its distance score (with individual probability:

$$\mathrm{P_i} = \mathrm{c_i} / \sum\nolimits_N^j (c_j)$$

The maximum predation limit P_L was set to 5% of the population size.

The genetic algorithm An individual's strategy was encoded in a 2-locus real-valued chromosome, with locus 1 coding for the probability of scrounging and locus 2 coding for the value of boldness. Both loci ranged from 0 to 1, and all individuals in a given population size N_I started the genetic algorithm with a randomly generated chromosome value. At the end of each foraging simulation the number of consumed food items was computed for each individual and individuals were ranked on the basis of their fitness and the highest 60% was allowed to reproduce, all other individuals were removed from the population. Crossover probability was 0.9 implying that the probability of a selected chromosome to remain unchanged in the next generation (apart from any changes due to mutation) is 0.1. The mutation rate was 0.1; if a locus was selected for mutation, it would be shifted from the old value by drawing a uniform random number between {-0.1, 0.1} and adding that to the old value. We varied patch density, patch richness and predation pressure (see Table 8.1 for parameter ranges). All simulations were done in Python.

Measuring the evolution of personality and scrounging For each parameter combination (see Table 8.1) we ran $T_G = 100$ generations (hereafter called a run) with five replicates per parameter combination for a total of 3850 runs. We analyzed the mean scrounging and boldness values, averaged over the last 10 generations of each run to reduce the effects of stochasticity. For each run of the genetic algorithm, we searched for a polymorphism in scrounging and boldness using model-based cluster analysis on the final scrounging and boldness values for each member of the population using the Mclust package in R (Fraley & Raftery 2002, 2006); Mclust provides the optimal model according to BIC (Bayesian Information Criterion) for expectation maximization in Gaussian mixture models. If a clear polymorphism of boldness and scrounging values was present (e.g., bold producers and shy scroungers), the cluster analysis would be expected to select a model with two clusters.

Table 8.1 Parameters of the simulation and behavioural variables.

Symbol	Meaning	Value or range
N_P	Number of patches	5,10,20,30,40,50,60
N_S	Number of indivisible food items in each patch	5,10,20,30,..,100
T	The length of the tournament	250
T_G	The number of generations for each run of the genetic algorithm	100
R_P	Spatial radius of a food patch	10
R_V	Radius of patch detection for producers	20
N_I	Population size	50
P_L	Predation limit	0.05
H	Scrounging horizon	10
B	Rate of moving back to conspecifics	25
W	Parameter of weighting function	50
P_P	Predation probability	0,0.2,0.4,0.6,0.8
S_{MAX}	Maximal step length	50
P_S	Scrounging probability	0.0-1.0
B	Boldness	0.0-1.0
P_F	Probability of detecting producers	0.0-1.0
P_M	Probability of moving back to conspecifics	0.0-1.0
S_I	Step length	0.0-50.0

Table 8.2 Optimal number of components selected in a cluster analysis of each run of the genetic algorithm.

Model components	1	2	3	4	5	6	7	8	9
Number of runs	116	394	507	534	548	448	509	398	396

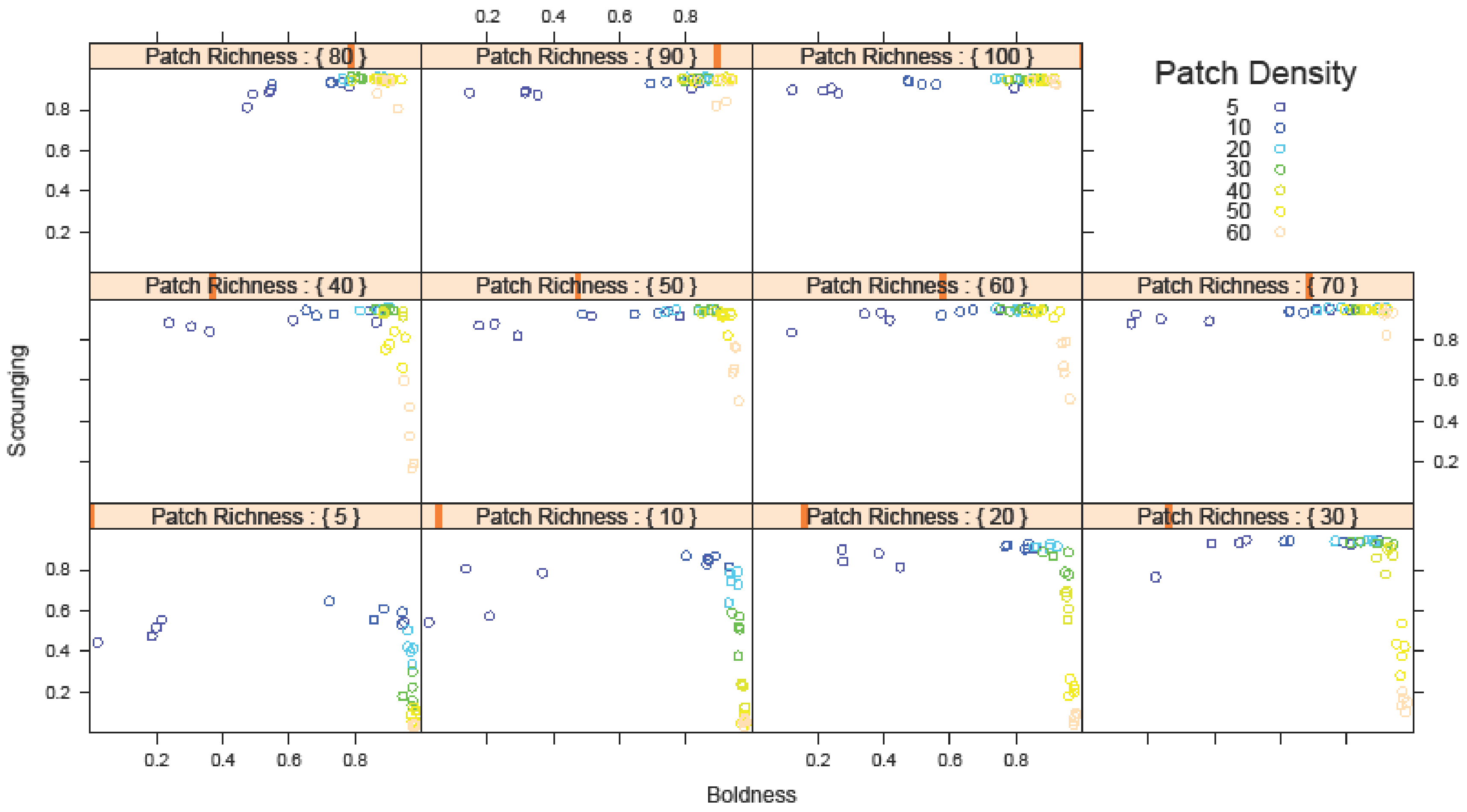
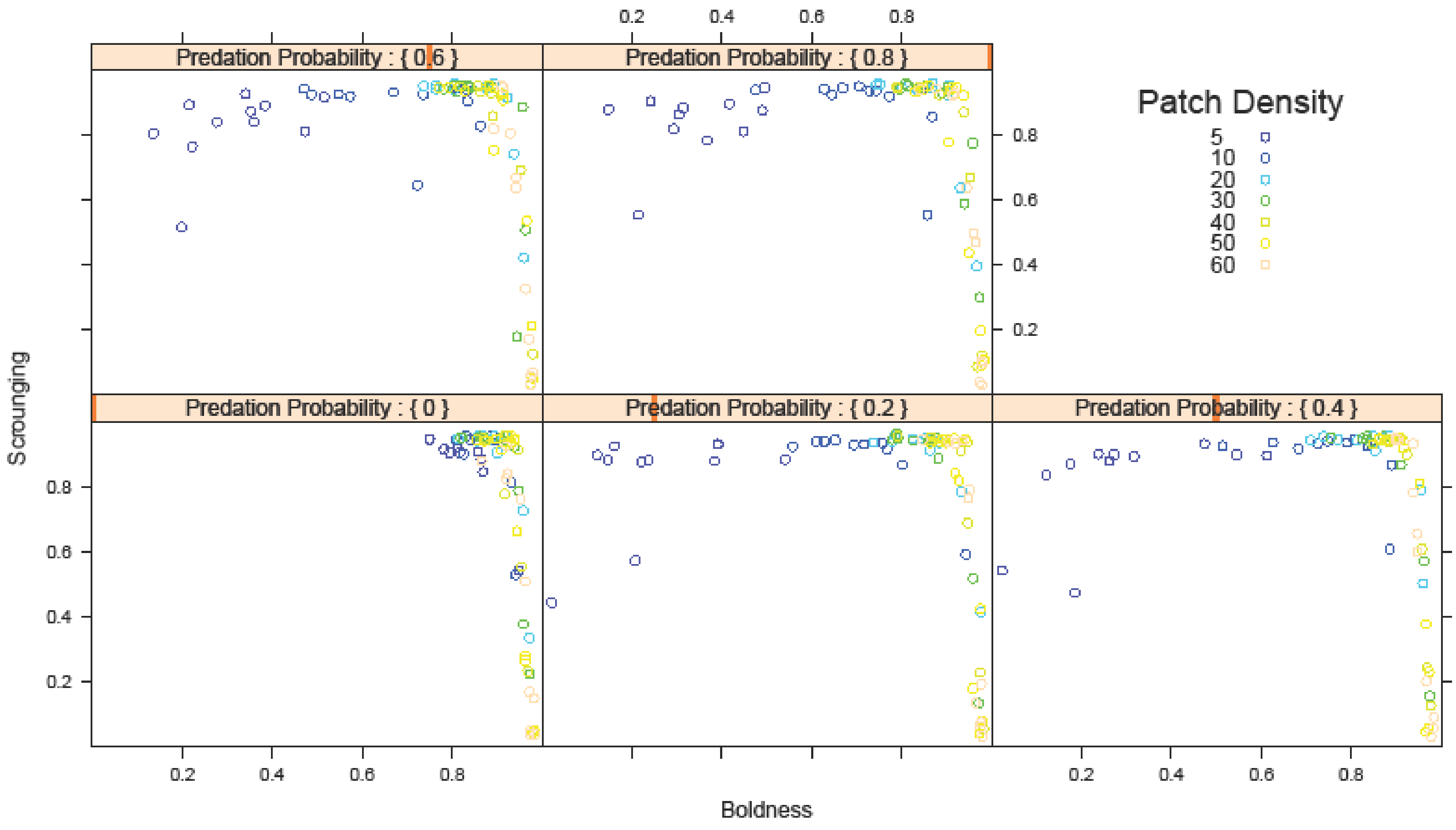


Figure 8.1 The effect of patch density and patch richness on boldness and scrounging values. An increase in patch density led to an increase in boldness and a reduction in scrounging, but the latter only under conditions of low / intermediate patch richness. An increase in patch richness resulted in increased scrounging, but there was no effect on boldness levels.

Figure 8.2 The effect of predation pressure and patch density on boldness and scrounging values. An increase in predation resulted in a reduction in boldness, but there was no effect on scrounging proportion.



Results

Boldness and scrounging became associated in the course of our runs: the shyest individuals ending up with high scrounging proportions, whereas the boldest individuals had low scrounging proportion (Fig. 8.1 and 8.2). High scrounging was observed over nearly the full range of boldness levels, except at the very extremes of boldness. Low scrounging was only observed at high values of boldness (Fig 8.1 and 8.2).

An increase in patch density led to an increase in boldness: under conditions of low patch density shy individuals were selected, but boldness increased rapidly with increasing patch density (Fig. 8.1). This pattern was consistent and appeared over the entire range of patch richness values (Fig. 8.1) and predation pressure, although the effect in the absence of predation was weaker (Fig. 8.2). An increase in patch density also led to a reduction in scrounging. This effect disappeared at high patch richness (Fig. 8.1). An increase in patch richness resulted in an increased scrounging, both for bold and shy individuals (Fig. 8.1). There was, however, no effect of patch richness on boldness (Fig. 8.1).

In the absence of predation, only bold individuals emerged (Fig. 8.2). When predation was present, shy individuals were selected and so boldness declined. There was no effect of predation on scrounging proportion (Fig. 8.2).

There was no evidence for a dichotomy in boldness. Model-based cluster analysis produced no evidence of preference for a model with 2 clusters (Table 8.2), and inspection of the data revealed that this was due to low variance in both scrounging and boldness across runs (mean $\sigma_{\mathrm{scr}} = 0.049$, mean $\sigma_{\mathrm{bold}} = 0.038$); the results of cluster analysis are bound to be unstable when overall variance is so restricted. Every run converged to a single value of boldness (max $\sigma_{\mathrm{bold}} = 0.067$), and only 54 runs failed to converge to a single value of scrounging ($\sigma_{\mathrm{scr}} > 0.1$). Inspection of these runs confirmed the results of the statistical analysis in finding that no dimorphism in either boldness or scrounging existed.

Discussion

The outcomes of our simulations showed a broad range of both boldness score as well as scrounging probability. Interestingly, high rates of scrounging were observed over nearly the full spectrum of boldness values, whereas high rates of producing were only observed at high boldness values. This conforms to earlier experimental evidence that shy barnacle geese scrounge more than bold individuals (chapter 5) and that boldness did not affect scrounging, but did affect producing, with bolder individuals producing a patch faster (chapter 6). At the same time these outcomes illustrate that the relationship between social foraging and boldness is not a simple linear relationship. Variation in patch density, patch richness and predation pressure all shaped the relationship between scrounging and boldness.

Our simulations showed that differences in patch density, patch richness and predation pressure result in a broad range of different optimal combinations of boldness and scrounging across runs. Differences in selection pressures (either in space or time) in a social foraging game may generate different optimal boldness levels, suggesting that spatio-temporal dynamics (i.e., fluctuating environments) may cause variation in boldness levels between populations (see also Dall *et al.* 2004; Dingemanse *et al.* 2004, 2009; Bell & Sih 2007; Smith & Blumstein 2008). Populations evolved towards a monomorphism where a single optimal level of boldness characterized all the individuals in the population. We found no evidence for a stable co-existence of different personality types within one population submitted to a given assortment of environmental conditions. Playing the producer – scrounger game seems thus to be insufficient to allow the evolution and maintenance of different personality types by means of for example negative frequency dependent selection as suggested by recent theoretical work (Wolf *et al.* 2008; McNamara *et al.* 2009; Wolf & Weissing 2010).

Predation pressure did not affect scrounging probability. This is in line with Coolen & Giraldeau (2003) and Ha & Ha (2003) who show that predation danger did not affect the stable equilibrium frequency of scrounging (but see Barta *et al.* 2004). Although predation danger did not affect the stable equilibrium frequency of scrounging (group response), individual manipulation of predation danger (individual response) did affect scrounging: individual zebra finches, *Taeniopygia guttata*, increased their scrounging frequency when treated with wing-load manipulations that increased their vulnerability (Mathot & Giraldeau 2010). How predation risk shapes scrounging pay offs and frequency is highly affected by the (in)compatibility between scrounging tactic and anti-predatory vigilance. If the scrounging tactic is compatible with anti-predatory vigilance increased predation risk should lead to more scrounging. In our simulations scrounging tactic and scanning for predators were not compatible, following Coolen & Giraldeau (2003) who show that scrounging tactic and anti-predatory vigilance are not compatible in nutmeg manikins (but see Ranta et al 1998; Mathot & Giraldeau 2010)

As predicted by Stamps (1991) we found that increasing the risk of predation resulted in reduced boldness and hence shyer individuals. In our model the risk of being preyed upon increased with increasing distance from the flock centre. Because bolder individuals moved further out of the centre of the group, they suffered an increased predation pressure. Differences in boldness are suggested at least in part to be the consequence of differences in predation pressure (Bell & Sih 2007). Côté *et al.* (2008) went as far as suggesting that the costs of being bold likely disappear in the absence of predation. In that case there is a trade-off between food intake rate and predation risk, with bold individuals enjoying a higher food intake rate but also a higher risk of being predated. A positive correlation between boldness and food intake rate has indeed been reported in several species (for review see Biro & Stamps 2008) and there is now also evidence accumulating that bolder individuals suffer a higher predation risk (Dugatkin 1992; Bremner-Harrison *et al.* 2004; Bell & Sih 2007; Carter *et al.* 2010), due to an increased tendency to expose themselves to risky situations. It is, however, noteworthy that boldness may also be favored by increased predation pressure, if bolder individuals engage more in predator inspection events and predator inspection deters predators as is suggested by a study in bighorn sheep ewes (Réale & Festa-Bianchet 2004).

An increase in patch density led to a reduction in scrounging level, but only at low values of patch richness (see Fig. 8.1). This prediction conforms to Beauchamp's (2008) results and is a consequence of the spatial explicitness of our model. The first models of producer – scrounger games (Barnard & Sibly 1981; Vickery *et al.* 1991; Caraco & Giraldeau 1991) assumed scroungers would instantaneously join food discoveries of other individuals and so obtain equal shares of any remaining food items independently of their initial spatial position. Under these conditions, scrounging frequency was independent of patch density.

Beauchamp (2008) created a spatially explicit model of producers and scroungers, thereby introducing traveling time to scrounged food patches (hence a decrease in the share of food items scroungers received with increasing distance). Beauchamp & Giraldeau (1997) demonstrated the importance of traveling time by showing that producing nutmeg mannikins, *Lonchura punctulata*, were more likely to leave a patch as scroungers arrived when search time was short. Our results confirm Beauchamp's (2008) prediction that increasing patch density should reduce scrounging, because scrounging becomes less profitable when it is easy to find food (Clark & Mangel 1984). Koops & Giraldeau (1996), however, showed that increasing patch density resulted in an increase in the proportional use of scrounging. This increase in scrounging was, however, marginal and the patches were spatially miniscule. An experiment varying patch density on a larger spatial scale would be valuable for testing our predictions. That an increase in patch density led to a reduction in scrounging level only under conditions of low patch richness makes sense. Under conditions of high patch richness, the profitability of scrounging increases rapidly, making producing relatively less profitable. Interestingly, an increase in patch density not only led to a reduction in scrounging level, but also favored an increase in boldness. When patches are poor the bolder individuals turn to producing such that at a high density of poor patches more producing emerges. Producer success depends on the producers' ability to distance themselves from conspecifics (Barta *et al.* 1997; Flynn & Giraldeau 2001). In our simulation a tendency to increase one's distance from conspecifics is achieved by increasing boldness, meaning that shy individuals forage at close proximity of each other, whereas bolder individuals are more spaced out.

We think that these spatial dynamics are the single most important reason for the various effects we found on boldness. At low patch density the tendency to scrounge increases and the success of scrounging requires remaining close to potential producers (Barta *et al.* 1997; Flynn & Giraldeau 2001). So, our simulations predict that shy individuals do best at low patch densities. Our simulation results also suggest that gregariousness, the tendency to remain close to each other, breaks down at high patch density, because selection favors bold producers (that is spaced out solitary foraging). Several models predict that group foraging is more likely to occur only when food patches are scarce and rich (Waltz 1982; Clark & Mangel 1986; Barta & Giraldeau 2001) exactly the situation where our simulation predicts the most scrounging and closest proximity (i.e., shyest individuals). Interestingly, in our simulation boldness declined with increasing patch scarcity when patches were rich, but scrounging levels remained similar. This suggests that although scrounging levels are similar, the optimal spatial positioning of individuals in a foraging group depends on the number of patches. Most likely, when there are very few patches finding a patch is a rare event such that one needs to remain close to as many other group mates as possible if scrounging is to be profitable at all. However, when there are many patches, finding a patch is commoner so scrounging success is less dependent on the number of individuals kept close by.

Increasing patch richness resulted in an increase in scrounging frequency. This was a very consistent pattern across the complete range of boldness values. This is in agreement with both empirical and theoretical results for producer – scrounger games (Giraldeau & Livoreil 1998; Coolen *et al.* 2001; Coolen 2002; Beauchamp 2008): with an increase in patch richness the finder's share decreases (or seen from a scrounger perspective: the joiner's share increases), resulting in an increase in scrounging pay-offs. Patch richness, in contrast to patch density, did not affect boldness. We think that this is due to the spatial dynamics of the producer – scrounger game: patch richness is not a spatial component, whereas patch density is primarily a spatial component. Because patch richness is not a spatial component it does not affect the optimal spatial positioning of individuals in a foraging flock and this is, we think, the reason for the lack of effect of patch richness on boldness. Interestingly, Michelena *et al.* (2008) showed that the spatial distribution of bold and shy Scottish blackface sheep, *Ovis aries*, differed with bold sheep splitting into subgroups at smaller group sizes than shy sheep. The differences in spatial distribution could be simulated by a model that included simple rules on sensitivity to crowding and social attraction (Michelena *et al.* 2010). Although our model is different as it runs over an evolutionary time scale both theirs and our model show the importance of differences in social attraction rules on the spatial dynamics of individuals foraging in groups. Clearly, how personality affects social attraction rules between group living individuals and how this in turns affects collective processes is an exciting avenue for further research.

To conclude, we have shown that boldness and social foraging are linked. Bold individuals are able to play both producer and scrounger, whereas shy individuals are confined to the scrounging tactic. In general an individual’s scrounging probability increased with decreasing boldness. An increase in patch density resulted in the evolution of bolder individuals, whereas patch richness did not affect boldness levels. The genetic algorithm selected a single optimum level of boldness for each parameter combination, thereby showing no evidence for a negative frequency dependent selection of personality types in a producer – scrounger game.

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Chapter 9

Synthesis: an outlook on personality in group-living species

The current understanding of the role of animal personality in group-living individuals, both from a proximate as well as from an ultimate perspective is relatively poor. This thesis aimed at studying the importance of animal personality on various aspects of group-living. In the last chapter of this thesis, I synthesize the most important findings. I discuss several aspects of group-living in relation to personality, namely collective movements, social information and the link between collective movements and social information. Finally, I will discuss the maintenance of variation and end with a general discussion about the relationship between personality and group-living. In each section I will discuss the current state of knowledge, state the contribution of this thesis to the current knowledge, identify research gaps and suggest fruitful avenues for future research.

Collective movements

The movement of animal groups is ultimately the consequence of the behaviour of individuals and one of the intriguing questions is which individuals contribute most to collective movements (Prins 1996; Conradt & Roper 2009). The importance of individual differences on collective movements is illustrated by studies where information was provided to only a few individuals within a group. Both in fish and humans, a small minority of informed individuals were able to guide a group to a target destination (Reebs *et al.* 2000; Dyer *et al.* 2009), showing that individual differences can have profound consequences on collective movements. In this thesis I investigated the role of animal personality on collective movements. More specifically, I studied whether variation in personality corresponded to variation in leadership and subsequently to collective movements. Leadership is the initiation of new directions of locomotion by one or more individuals, which are then followed by other group members (Krause *et al.* 2000). I will first describe recent studies investigating the link between personality and leadership, then highlight my contribution to the role of personality in relation to leadership and conclude with a general discussion about the relationship between personality and leadership.

Recently, several studies investigated whether behavioural variation also contributes to elements of leadership: In pairs of 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 pairs of 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). In groups of four guppies, *Poecilia reticulata*, bold individuals entered a novel feeder more often than shy individuals (Dyer *et al.* 2008). Lastly, in groups of 8-12 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 chapter 2 I studied whether individual variation in boldness was important in leadership behaviour in pairs of barnacle geese moving to a feeding site. Prior to this I quantified the personality trait boldness of geese by using novel object tests. The reaction of individual barnacle geese towards a novel object was highly consistent over a period of one year. Boldness was important in the subsequent leadership trials: bolder individuals were more often leading the pair, and arrived quicker and more often at the food patch. Interestingly, an individual's arrival at the food patch was affected not only by its own boldness score, but also by the novel object score of the companion individual, indicating that movement patterns of individuals living in groups is 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. This demonstrates that leadership is a collective process, and that next to leaders, also *followers* play a vital role. In chapter 3 I introduced naïve individuals, differing in boldness score in a labyrinth together with either one or three informed individuals, which had knowledge on travelling directions. In groups of 2 individuals, I found that the probability of exploring the labyrinth before the informed individual chose a direction increased with increasing boldness score. However, in groups of three informed individuals, boldness of the naïve individual was not important anymore.

These results fit the general observation that bolder/more explorative individuals are generally found at the forefront of collective movements and highlight the importance of personality on collective movements and leadership in small groups. However, empirical evidence is still scarce and in the remainder of this section I address some important issues regarding the relationship between personality and leadership.

(1) Most studies relating personality and leadership were done in relatively small groups, most often pairs (e.g., Beauchamp 2000; Schuett & Dall 2009; Harcourt *et al.* 2009; chapter 2). All these studies find clear effects of a certain personality trait on the willingness to lead the pair, but in nature groups of individuals are often much larger than two individuals, and in order to understand the importance of personality on leadership behaviour it is necessary to study larger group. In fact, the only study which used larger groups (of 8-12 individuals) was the only study that did not find an effect of boldness on leadership (Leblond & Reebs 2006). The experiment in chapter 3 also showed that the effect of boldness disappeared in groups of four individuals, although it has to be noted that the four players in the experiment were not alike in terms of information so it is not a direct of the effect of personality on leadership since agents also differed in information. Nonetheless, this chapter stresses the need to study these effects in larger groups.

(2) The importance of behavioural variation on following behaviour has received far less attention, although leaders are only able to act as leaders as long as there are *followers*, stressing the importance of followers in collective movements (King 2010). In three-spined sticklebacks more explorative individuals followed an informed conspecific through a maze

to a larger extent than shy individuals (Nomakuchi *et al.* 2009). On the contrary, in barnacle geese there was no evidence for an effect of boldness on following behaviour through a novel labyrinth (chapter 3). Thus, although there seems to be strong evidence that 'leaders' can be characterized as being bold, it is less certain which behavioural characteristics, if any, are typical of followers, and future research could investigate this in more detail. Future research could make use of recent technological advancements such as the introduction of robotic animals (Halloy *et al.* 2007; Faria *et al.* 2010) to test the effect of personality on following and leading in a more standardized way. Robotic animals can for example be used to force individuals in a certain role (leading or following) to avoid the problem of observational studies in which individuals can choose their own role according to intrinsic preferences (see also chapter 6).

(3) The environment in which a personality trait is studied is often of crucial importance, and it is highly likely that the environment determines to a large extent the outcome of a study investigating personality and leadership. To illustrate, I want to draw a parallel with novel object tests in which the choice of the novel object is critical. If the novel object is very challenging for the study species, then most animals will be too afraid to approach, and it is unlikely that there is an effect of personality. If, however, the object is not challenging at all, then there will also be no effect of personality, since most animals will approach it readily. Only when using an "intermediate" challenge, personality traits are expected to become evident. The same is important when studying the effect of personality on leadership (or any other behaviour). If leadership is studied in a very familiar and non-challenging environment it is expected that variation in boldness is less important than at an intermediate level of challenge. Most studies finding an effect of personality on leadership used a novel environment (Dyer *et al.* 2009, Schuett & Dall 2009; chapter 2 and 3), whereas Leblond & Reebs (2006), whom did not find an effect of boldness on leadership, used a familiar fish tank. One could study the importance of the environment on the relationship between personality and leadership by studying the same group of individuals under different challenges (slowly building up the challenging environment). If the environment is indeed important, then it is critical to study the challenges that individuals face in a natural situation. Are these challenges actually comparable to an "intermediate" level? Studying this over gradients of fear in a natural setting (Brown 1999) could also elucidate this topic and one could even use the giving up density (Brown 1999) of individuals to quantify personality in a natural environment.

(4) Most studies on animal personality are conducted in captivity and translation to natural situations is still a relatively rare thing (but see Herborn *et al.* 2010). It is possible that in experiments unnatural challenges are presented which rarely happen in natural situations (see also previous remark). Currently, there is no understanding if personality is important in leadership of individuals in a natural environment. Studying collective movements from an individual perspective in the field is challenging, especially since it is difficult to track individuals with enough precision to resolve intra-group spatial relations in moving animals (Nagy *et al.* 2010). On the up side, technological developments in tracking technology proceed fast and a recent study demonstrated elegantly that it is possible to track homing pigeons at such a fine scale that it was possible to study the spatial position of individuals in a

flying flock of pigeons (Nagy *et al.* 2010). Using high-resolution lightweight GPS devices made it possible to not only get data on intra-group spatial relations, but also to study how changes of flight direction (leaders) were copied by other individuals (followers), showing that leadership was not equally distributed among flock members, but was hierarchical with a tendency for better navigating individuals to be higher in the hierarchy. These technological advancements open up the exciting opportunity to study the effect of personality on leadership in groups of animals in their natural environment.

(5) If individuals in a group differ in their preferred movement direction, but do not want to split then the group has to arrive at a consensus decision (Prins 1996). Consensus decision-making can have many different forms with on the one end equally shared decision-making and on the other end unshared decision-making (Conradt & Roper 2009). In equally shared consensus decision-making all individuals contribute equally to the decision outcome (‘democracy’). In unshared consensus decision, one member makes the decision on behalf of the entire group (‘dictatorship’). Mostly a mix of both forms is found with some individuals contributing more than others (partially shared decision-making, Conradt & Roper 2009). In chapter 3 I demonstrated that bold individuals, at least in pairs, wait less for the information of the informed individual but rather start exploring themselves, suggesting that bolder individuals contribute more to consensus decision-making. One could test if certain personality types (e.g., bold individuals) indeed contribute more to consensus decision-making by providing conflicting information to different personality types and place them together to test how they resolve conflict. In addition it would be interesting to see if individuals that live in systems that are characterized by equally shared decision-making show a similar amount of variation in personality as compared to individuals that live in systems which are characterized by unshared consensus decision-making. My prediction would be that there is less variation in animal personality in systems of shared-decision making since everybody contributes equally to the decision-making process.

(6) Consistent individual differences in resting metabolic rate have been proposed as a general framework to explain consistent individual variation in a wide variety of behaviours (Biro & Stamps 2008, 2010). Individual differences in resting metabolic rate might give rise to differences in growth and fecundity and as such to differences in several behaviours: individuals with high energetic demands should be more active, aggressive and bold in contexts related to food acquisition than individuals with lower energetic requirements. These differences in energetic requirements also offer a possible explanation for the association between leadership and boldness. Rands *et al.* (2003) showed in a modeling study that differences in energy requirements can lead to differences in leading and following behaviour in a pair of individuals with the individual with the highest energetic needs acting as leader and the other as follower. Examples in many species, including fish (Krause 1993), caterpillars (McClure *et al.* 2011) and zebras (Fischhoff *et al.* 2007) indeed show that individuals with higher energetic requirements are more often observed in the leading edge of moving groups. Therefore, the association between boldness and leadership might arise as a result of increased energy requirements of bolder individuals. This hypothesis awaits empirical scrutiny.

To conclude this part, there appears to be a relationship between personality and leadership at least in small groups in captivity, but this relationship is poorly understood and there is much scope for further research. Future studies focusing on personality and leadership could investigate (1) larger groups, (2) the importance of followers, (3) variable environments, (4) the natural situation, (5) consensus decision-making and (6) energy requirements.

Social information

Individuals might use two forms of information, either personal information, usually retrieved on a trial and error basis by interacting with the physical environment, or they might use information made available by other individuals, referred to as social information (Danchin *et al.* 2004; Dall *et al.* 2005). But what actually is information? A narrow definition of information is everything that reduces uncertainty (Danchin *et al.* 2004), but for evolutionary ecologists to understand the use of information and its consequences this definition is not very insightful (Dall *et al.* 2005; Seppänen *et al.* 2007). More insightful is to talk about the value of information. For information to be valuable an individual should have a higher fitness return by observing this information and hence change the functioning of an individual in an evolutionary relevant manner (Stephens 1989; Dall *et al.* 2005; Danchin *et al.* 2005; Seppänen *et al.* 2007). Thus the difference in fitness between a decision with and without the information renders the value of that particular bit of information (Seppänen *et al.* 2007). It is important to distinguish here between the proximate and ultimate cause. Though the ultimate cause (i.e., the outcome of all decisions of an individual) is ultimately the operational level of selection, individuals take most decisions based on proximate reasons (e.g. to still hunger or to reduce fear). And to test the value of social information it is therefore necessary to study also the proximate causes of social information use. In this thesis, I mainly focused on the proximate causes of social information. To illustrate the proximate value of social information, imagine a bird searching for food alone, or with a partner. In the latter case it can make use of social information by joining the food discoveries of the other bird. By comparing the food intake rate between both situations it becomes possible to quantify the value of social information expressed in grams of food. With this framework of the value of information in mind it is possible to study information in an evolutionary meaningful way and ask specific questions about information and which factors affect the value of information. It becomes for example obvious that the value of information is dependent on the distance in space and time (Seppänen *et al.* 2007). E.g., joining a food discovery of a conspecific is more profitable when you are at a close spatial distance when food patches are exhaustible (Ruxton *et al.* 1995).

Despite the long tradition of studies on social information (Galef & Giraldeau 2001; Valone & Templeton 2002; Danchin *et al.* 2004; Valone 2007) the relationship between personality and social information use, and the more specific question if variation in personality results in a different value of social information is poorly studied. That the value of social information might be different for 2 individuals in a group has already been illustrated in the introduction. (In short: if individual a observes individual b foraging and is dominant over b it can profit from this information. Individual c, however, is subordinate to b so if individual c observes b foraging then that information has no value for c). Thus although the value of social information might be different between individuals, most studies assume that the value of social information is equal to all individuals and focus on the conditions under which an animal is expected to use social information (Galef & Giraldeau 2001; Danchin *et al.* 2004; Kendal *et al.* 2005; Valone 2007), rather than studying which individuals use social information. In this thesis I studied the relationship between social information use and personality in several different contexts to test if variation in personality reflects differences in the use of social information.

In chapter 6 I studied how boldness affected the approach latency towards a food patch in the presence or absence of a demonstrator at the food patch. In a situation without a demonstrator bolder individuals arrived faster at the food patch than shyer individuals. In the presence of a demonstrator at the food patch, there was no effect of boldness on approach latency. As a consequence the difference in approach latency increased with decreasing boldness score. When this is translated into the value of social information, and the presence of a companion is regarded as social information signalling that the food patch is a safe place, then it can be argued that the value of social information increased with decreasing boldness score. In chapter 3 naïve barnacle geese were introduced in a labyrinth with either 1 or 3 informed demonstrators, which were trained to walk to the exit of the arena. In pairs, shyer individuals followed the demonstrators more often than bolder individuals, suggesting that shyer individuals used more social information. In chapter 5 I performed a producer–scrounger experiment. Individuals were introduced in a foraging arena and could either produce food (i.e., personal information) or join food discoveries of other individuals (i.e., social information). Shy individuals had a higher frequency of joining (/social information use) than bold individuals. The most direct test of social information use is described in chapter 4: an individual was allowed to watch two pairs of demonstrators which revealed the location of a food resource. After an observation period, the observing individual was allowed to join one of the pairs, thereby revealing whether it used the social information. In agreement with previous chapters, the use of social information decreased with increasing boldness.

So in several different contexts variation in boldness was correlated with social information use, with shyer individuals making more use of social information. The question arises why differences in boldness relate to variation in social information use and to answer this I turn back to the value of social information and I will argue that the value of social information is higher for shy individuals than for bold individuals, because it is costlier for shy individuals to collect personal information (see also Fig. 9.1). Models of social information predict that when the cost of collecting personal information increases, the reliance on socially acquired information increases. Webster & Laland (2008) showed that minnows, *Phoxinus phoxinus*, increase the use of social cues when selecting a prey patch in the presence of a predator, most likely as a result of an increased cost of collecting personal information. If the cost of collecting personal information is indeed higher for shyer individuals then this might explain their increased reliance on social information. Bolder / more explorative individuals (as is already implicitly present in the definition) explore their environment (that is collect personal information) faster than shyer individuals and it seems reasonable to assume that shyer individuals experience more stress when they explore the

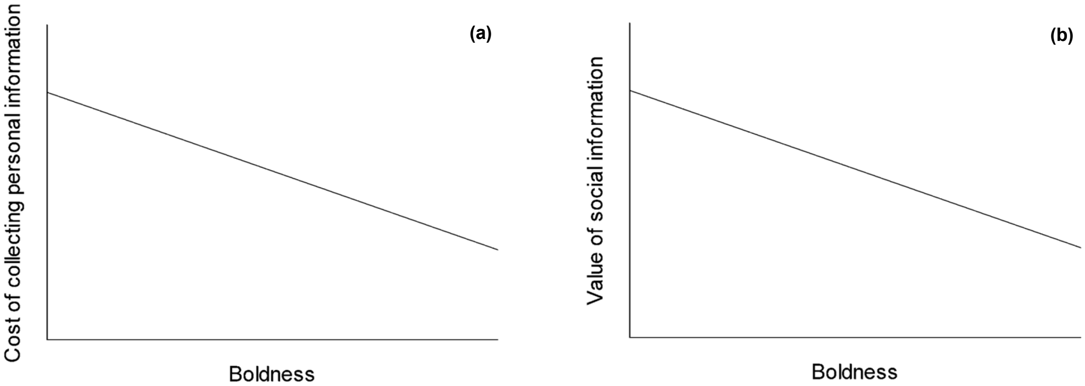

Figure 9.1 (a) With increasing boldness the cost of collecting personal information is expected to decrease. (b) As a consequence the value of social information decreases with increasing boldness.

environment as compared to bold individuals. This is for example illustrated by the observation that bolder individuals are found more often in the leading edge of moving groups (see above).

With this framework I return to the chapters of this thesis to see if it can explain my findings. In chapter 3 naïve individuals had to find their way out of a labyrinth. Individuals could either wait for the decision of their conspecific or explore themselves. Individuals thus faced a trade-off between waiting for social information, or start collecting personal information. Most likely, shyer individuals faced a higher cost of collecting personal information so they waited longer for the other individual to move. Since the informed individual had more time to choose an exit the chance of using social information increased with decreasing boldness. In chapter 5 individuals could either explore the environment itself, or join food discoveries of other individuals. If bolder individuals indeed had lower costs when exploring the environment a logical consequence is that they will rely more on the producer tactic, and shyer individuals more on the joining tactic. Applying the same logic, I now can explain chapter 4 by simply considering that bolder individuals would face lower costs when not following the social information, since they could more easily switch sides when making an incorrect decision. So a parsimonious way to explain my results is to assume that for shyer individuals it is costlier to collect personal information, therefore social information is more valuable to them. This also explains the outcome of several studies that show that shy/slow individuals are more reactive to companions than bold/fast individuals (van Oers *et al.* 2005b; Stöwe & Kotrschal 2007; Harcourt *et al.* 2009; chapter 4), suggesting that shy/slow individuals pay more attention to the behaviour of conspecifics, or termed differently collect more social information. With this in mind I will now discuss several topics which might inspire future research on the relationship between personality and social information.

(1) At the heart of my discussion is the idea that the value of social information is higher for shyer individuals than for bolder individuals. To date, no direct test of this has been performed, so studies which quantify the value of social information for individuals differing in personality are needed. One could for example measure the intake rates of individuals alone, and in a social context, to test whether variation in personality corresponds to a variation in the value of social information (measured as the difference in intake rate between

a non social and social context, see also chapter 6). Another experiment which could test this hypothesis is to provide individuals with personal information and subsequently confront them with conflicting social information to test if shyer individuals switch faster to social information. Foraging nine-spined sticklebacks for example are known to switch from relying on personal information to relying on social information with increasing uncertainty of the personal information and when the period since experiencing personal information is longer (Van Bergen *et al.* 2004).

(2) Social information use is a process across space and the value of social information is a decreasing function of the distance of an individual from the information (Seppänen *et al.* 2007). So the spatial dynamics of individuals within a group has direct consequences for the value of social information and as such also the trade-off between using either personal or social information. Shy individuals are known to have a higher tendency to stay close to conspecifics (‘sociability’) (Budaev 1997; Ward *et al.* 2004; Dyer *et al.* 2008; Michelena *et al.* 2008). Since shyer individuals stay closer to conspecifics, they can potentially make more use of social information. Therefore it can be difficult to evaluate whether a higher use of social information by shy individuals is merely the result of their higher tendency to stay close to others, or whether it is an active strategy (Sih & Bell 2008) and it is important to design experiments in which the proximity and the use of social information can be studied separately. For example, in chapter 4 I showed that, independent of proximity, shyer individuals used social information to a larger extent than bolder individuals, suggesting that proximity alone is not enough to explain the observed relationship between boldness and scrounging in chapter 5. Thus, variation in personality can affect the spatial dynamics in groups which in turn can affect social information use (see also chapter 8).

(3) In this thesis I mainly studied social foraging information, but social information is used in a wide variety of contexts (Galef & Giraldeau 2001; Valone & Templeton 2002; Danchin *et al.* 2004; Valone 2007, see also chapter 1). For example an individual can use social information when choosing a mate. If a potential partner is preferred by another individual, this choice can be copied (mate-choice copying, c.f. Dugatkin 1992; Jones *et al.* 2007; Mery *et al.* 2009). Whether personality is important in this copying behaviour is unknown, but if different personality types differ in the cost of collecting personal information, then it might be expected that also in these situations personality might predict the copying behaviour. Therefore, my findings can be applied and tested in a variety of contexts, but it remains to be seen if the observation that shy individuals use more social information is a general phenomena in the animal kingdom or not. It is even possible that the relationship between social information use and boldness is opposite in some situations. In avian habitat selection, individuals can use the post-breeding songs of conspecifics to decide where they are going to settle next year. Betts *et al.* (2008) showed that in black-throated blue warbler, *Dendroica caerulescens*, there is a positive correlation between post-breeding song and reproductive success. By manipulating song intensity they could even lure individuals to inferior habitats where they normally would not occur, indicating that they use the song intensity in settlement decisions. In these situations where individuals have to travel between different habitats to collect social information in order to compare different habitats it is not unlikely to expect that bolder individuals have access to more social information than shyer

individuals due to their more explorative nature. In these situations an opposite relationship between social information use and boldness could thus be expected. (Different personality types might even differ in their optimal individual settlement rules. If shyer individuals sample fewer habitats, they are expected to be satisfied faster than individuals that sample more habitats (‘the secretary problem’).). Nomakuchi *et al.* (2009) trained three-spined sticklebacks to follow a route through a maze and introduced these informed individuals together with naïve individuals differing in exploration score. They found that more explorative individuals followed the informed individual to a larger extent than less explorative individuals and thus made more use of social information. It is important to note that the naïve individuals did not explore the maze by themselves, therefore in this situation there was no trade-off between collecting either personal information or using social information (see chapter 3). There was only a choice between following the conspecific or not. The explanation for their observation is most likely that bolder individuals are less afraid to follow another individual into a novel environment and as a result bolder individuals can exploit social information under these conditions to a larger extent than shy individuals. Thus, in predicting the relationship between personality and social information use it is of critical importance to study the cost and benefits of personal versus social information.

(4) The relationship between social information use and personality is poorly understood and no study to date has tested this relationship in a natural environment. Testing social information use in a natural environment on an individual basis is not easy as the conditions in the field are often difficult to manipulate or even control (chapter 1). Correlation studies are a first step in describing patterns and this would also be a good starting point for studying personality and social information use in a natural setting. There are numerous options of which I will consider one, as this is of special interest to the species studied in this thesis (Ydenberg *et al.* 1983). Many birds, including barnacle geese, roost communally and one of the functions of this communal roost is thought to be the transfer of information. Ward & Zahavi (1973) introduced this idea as the information centre hypothesis. The information centre hypothesis suggests that individuals in a roost use conspecifics as a source of information, most often considered in terms of suitable foraging locations (see Bijleveld *et al.* 2010 for other functions of a roost). Individuals that use these roosts have three options for arriving at a suitable feeding site. They can use personal information, start searching themselves or sit-and-wait for social information by following successful foragers. The optimal strategy might differ between unequal competitors. Dominant common cranes, *Grus grus*, switched between feeding sites less often than subordinate cranes and when they did they stayed longer in the roost, possibly to track the main departing flows (Alonso *et al.* 1997), confirming the prediction that dominant individuals can exploit social information better than subordinate individuals. Thus phenotypic differences might coincide with strategy differences in these roosts. My prediction would be that shyer individuals spend more time in the roost before departing to a feeding site since it is costlier for them so collect personal information.

To conclude this part the relationship between social information use and personality is poorly understood and there is much scope for further research. Future studies could address (1) the value of information, (2) the spatial dynamics, (3) the natural situation and (4) the information centre hypothesis. In the following paragraph I discuss the links between personality, social information and leadership.

Linking personality, social information and leadership

An important aspect of animal personality is that different behaviours are correlated across contexts (Wolf *et al.* 2011). For example more explorative males of the European house cricket, *Acheta domesticus*, also produce more mating calls and emerge quicker following a predation event as compared to slower exploring males (Wilson *et al.* 2010). So behaviours may be correlated across different contexts, therefore personality is also termed behavioural syndromes (Sih *et al.* 2004a, b; see also Wolf *et al.* 2011). An important implication of this is that traits do not always evolve independently but as a package of behaviours. Thus each trait does not evolve independently to its own optimum, but may be constrained to reach this optimum due to underlying physiological, behavioural or genetic constraints associated with the behavioural syndrome (Wolf *et al.* 2011). In this thesis I found that bolder barnacle geese were more often taking the lead in collective movements (chapter 2 and 3) and used less social information (chapter 3, 4, 5 and 6) than shyer individuals, raising the question why both behaviours are correlated. Although I cannot disentangle whether selection acts on both behaviours independently or simultaneously, I can speculate about the proximate causes of this correlation. Several studies investigated the role of information in collective movements and showed that informed individuals are more often found in the leading edge of moving groups than uninformed individuals. Providing a small minority of individuals in a large crowd of humans with information about a target destination resulted in collective movements led by the informed humans (Dyer *et al.* 2008, 2009). Likewise, a minority of informed golden shiners (Reebs 2000) was able to lead groups towards a food source. Also honeybee (Beekman *et al.* 2006) and ant migrations (Langridge *et al.* 2008) are led by a minority of informed individuals (see also Couzin *et al.* 2005). As I stated in the section on social information I expect bolder individuals to collect personal information at a lower cost than shyer individuals (Fig. 9.1a) and as a consequence bolder individuals are expected to have more personal information. If in groups bold and shy individuals indeed differ in the amount of personal information, then a logical result is that the individuals with the most information (i.e., the bold individuals) will more often lead collective movements. So more personal information might result in an increased tendency to lead collective movements and as such information can be an explanation why bolder individuals are more often found in a leading role. The link between personality, social information and leadership also became evident in the final part of the previous section where I discussed the information centre hypothesis where I predicted that bolder individuals would more often use the searching tactic to collect personal information and shy individuals would more often use the sit-and-wait tactic to collect social information (‘following’). The leader-follower game that individuals play in an information centre can indeed be seen as a producer–scrounge game (Barta & Giraldeau 2001), with the following individuals scrounging the information from the leading individuals.

Maintenance of variation in animal personality

One of the pivotal questions in animal personality is the evolution and maintenance of animal personality. Several (non-mutually exclusive) processes have been suggested (see chapter 1). Negative frequency dependent selection has been proposed as one of these important processes (Sih *et al.* 2004; Réale *et al.* 2007; Wolf *et al.* 2008; Wolf & Weissing 2010). The proposed mechanism involved is social interactions during competition (and cooperation) between conspecifics (Dall *et al.* 2004; Wolf *et al.* 2008; McNamara *et al.* 2009).

Empirical evidence for a role of negative frequency dependent selection in animal personality is, however, scarce. In fruit flies, *Drosophila melanogaster*, there are two larval foraging types: rovers or sitters, depending on the allele frequency in the foraging gene. Fitzpatrick *et al.* (2007) showed that under nutrient poor conditions the rare foraging type had a higher proportion of larvae that survived to pupation, providing evidence for negative frequency dependent selection. Pruitt & Riechert (2011) showed in temperate social spiders, *Anelosimus studiosus*, which live in colonies consisting of social and asocial individuals, that females of both phenotypes experienced higher fitness (as inferred from individual egg-case masses) when they were in a colony consisting of unlike individuals.

In chapter 7 I tested the foraging performance of barnacle geese in the presence of similar and dissimilar individuals in term of boldness scores. I did not find any evidence for negative frequency dependent feeding performance of boldness in a producer-scrounger game. Both bold and shy individuals increased their feeding success when paired with bolder companions as compared to shyer companions. In chapter 8 I investigated the possibility of negative frequency dependent selection further by mimicking the evolution of boldness in a producer-scrounger game using a genetic algorithm. The genetic algorithm allowed us to test how variation in boldness evolved as a result of differences in spatial resource distribution and predation and to test if a producer-scrounger game could theoretically maintain variation in boldness. The simulations of chapter 8 showed that over a wide range of ecological conditions bold individuals evolved to play both producer and scrounger, whereas shy individuals remain confined to scrounging. Low patch density and high predation pressure favoured the evolution of shy individuals, whereas high patch density and absence of predation favoured bold individuals. Differences in selection pressures (either in space or time) in a social foraging game may thus generate different optimal boldness levels, suggesting that spatio-temporal dynamics (i.e., fluctuating environments) may cause variation in boldness levels between populations (see also Dall *et al.* 2004; Dingemanse *et al.* 2004, 2009; Bell & Sih 2007; Smith & Blumstein 2008). However, I found no evidence for a stable co-existence of different personality types within one population submitted to a given assortment of environmental conditions. Populations evolved towards a monomorphism where a single optimal level of boldness characterized all the individuals in the population. Playing the producer–scrounger game seems thus to be insufficient to allow the evolution and maintenance of different personality types by means of negative frequency dependent selection.

The evidence for negative frequency dependent selection as an explanation of the evolution and/or maintenance of variation in animal personality, though frequently suggested by modelling studies (Sih *et al.* 2004; Réale *et al.* 2007; Wolf *et al.* 2008; Wolf & Weissing

2010) is still very poor. There is much scope for both experiments and field observations. Experimentally manipulating group composition and measuring the fitness consequences is necessary to better understand the role of negative frequency dependent selection. Social insects, social spiders (Pruitt & Riechert 2011) or fish (Dyer *et al.* 2008) provide excellent study systems. In parallel, long term field data on reproductive success in relation to the 'phenotype' of the environment could elucidate the possible importance of negative frequency dependent selection in a natural context. The long-term study on reproductive success of great tits, *Parus major*, on the Veluwe, the Netherlands, offers great potential to address this in a natural context (see also Fucikova 2011).

An outlook on personality differences in group-living species

As illustrated in the previous sections there are a lot of interesting opportunities for studying consistent individual differences in group-living species of which leadership, collective movements and social information are just a few examples. I think that the surface of this exiting new research field has barely been scratched. In this section I will broaden the scope and raise some fundamental unresolved issues about the relationship between group-living and personality.

One of the fundamental questions is to what extent group-living promotes and/or constrains the development of personality differences between group members. Or termed differently, does living in groups promote individual differences? In answering this question a number of different approaches can be taken. Firstly, a meta-analysis could look at the amount of inter-individual variation as compared to the amount of intra-individual variation (repeatability) in relation to group-living. For group-living one might use the average social group size of a particular species. Given that animal species might show a great diversity in complexity a comparison across very different species groups is problematic, because different species may show different group structures with implications for the development of animal personality (Pollard & Blumstein 2011). A second problem in comparing distinct species is that the type of personality test used is most likely very different as different species require different personality tests, making it difficult to compare the repeatability outcomes across species. One possibility is to focus on either closely related species which show variation in their average group size (c.f. Pollard & Blumstein 2011) or to focus on one species that has populations that differ in the amount of group-living. In the latter approach one needs to take into account that there might be a direct cause for the observed difference in group-living between populations (for example a difference in predation risk) which also might affect the amount of variation in personality. Another approach would be to study the effect of the social environment on the ontogeny of animal personality. Phenotype is the result of the combination between genes and environment and animal personality is no exception to that. In common voles, *Microtus arvalis*, and great tits the level of anxiety is negatively correlated with the family group-size (Carere *et al.* 2005; Lantová *et al.* 2011) illustrating the importance of the social environment on the development of personality. Although a few studies looked at the effect of social environment on the level of a particular personality trait, no study to my knowledge investigated whether a difference in group-size during ontogeny affects the amount of variation in personality. One could investigate this by raising individuals in different group-sizes and study the amount of variation between individuals undergoing different treatments.

A second issue is to what extent personality differences measured in isolation are expressed in a social context. Though natural selection might still act on personality traits, even when they are not expressed in a social context, it is important to study if personality traits are important in explaining variation in behaviour in groups since this can have important implications for the functioning of animal groups. In a social context individuals may be inclined to engage in the behaviour of the majority of the group, known as conformity. A second process that can occur is social facilitation meaning that the presence of group mates affects the behaviour of another individual (c.f. chapter 6). How the expression of personality is affected by social facilitation and/or conformity and how this in turn is affected by group size are important subjects for further study to elucidate the role of animal personality in group-living species. A recent study by Webster & Ward (2011) reviewed these issues therefore I will not discuss these issues here in more detail but I suffice with referring to this excellent review.

Lastly, I want to mention the poorly explored subject of group formation and group size in relation to personality. Individuals within one population can differ strongly in their level of sociability (an individual's reaction towards conspecifics, excluding agonistic interactions) (Budaev 1997; Ward *et al.* 2004; Dyer *et al.* 2008). It is highly likely that differences in personality traits might correspond to differences in optimal group size. Also whether individuals form (dis)assortative groups based on personality traits is a largely unanswered question and social network analysis is a promising tool to study these processes (see also Krause *et al.* 2010).

Geese as a case study of group foragers

The work in this thesis highlights the important role of animal personality in group foraging. Barnacle geese are highly gregarious foragers and these groups are highly dynamic fission-fusion societies with frequent exchange of individuals between groups. Geese are constantly faced with new areas and different individuals. In these conditions it is expected that individuals use a lot of social information and several studies showed the importance of social information use in a natural setting (Drent & Swierstra 1977; Ydenberg *et al.* 1983; Stahl *et al.* 2001). The chapters in this thesis indicate that social information is indeed widely used in various contexts in this species and that animal personality plays an important role in this process. Since the major part of this thesis has been conducted in captivity, it is an open question if my results can be translated to a natural situation but the results of our experimental work suggest strongly that both social information and personality are important in the movement, habitat choice and as a result the distribution of geese and should thus be taken into consideration when predicting the distribution of geese.

Conclusion

The work in this thesis shows the importance of the role of animal personality in group-living individuals. I show that animal personality can affect various aspects of group-living including leadership, collective movements, producer-scrounger dynamics and social information use. The results in this thesis suggest that animal personality is a component that cannot be neglected when studying animals in groups and that more research is necessary to understand the proximate and ultimate causes and consequences of group-living. In this last chapter my goal was to illustrate that the role of animal personality in group-living species offers ample opportunities for exciting research and I hope that this thesis will inspire other researchers to study this exciting topic.

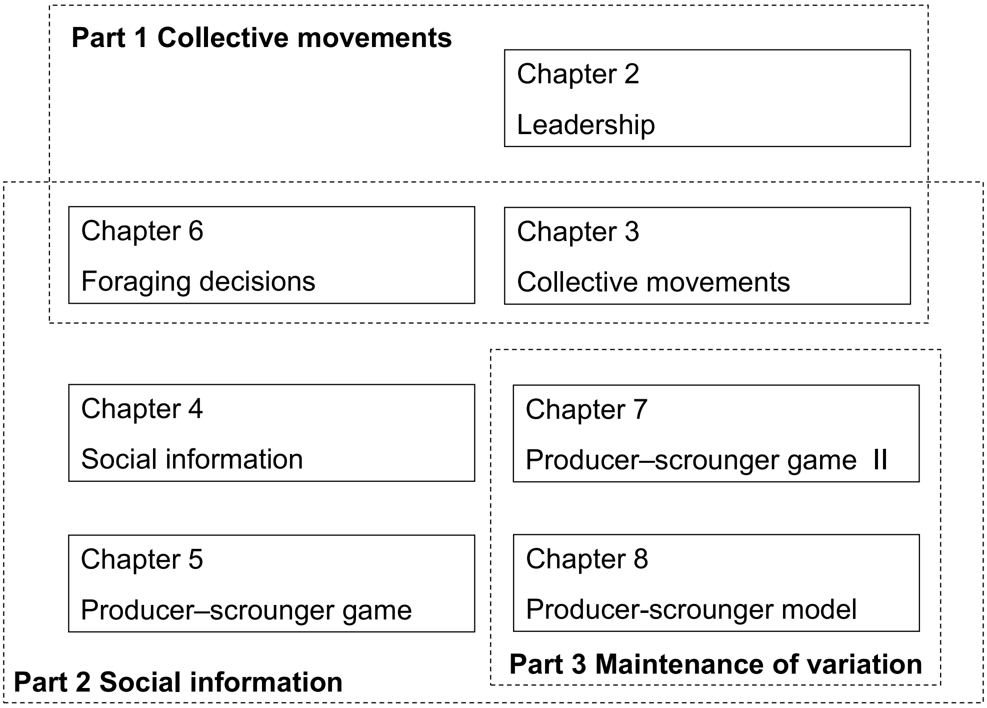

Figure 9.2 Conceptual scheme of the topics covered in the different chapters of this thesis**.**

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Summary

Many animals live in groups either year round, or during large parts of the year. Groups are a collection of individuals and much work has been done to understand how and why individuals live in groups. Recently, there has been a sharp increase in studies reporting consistent individual variation in behaviour between individuals within a population across a wide range of animal taxa, termed animal personality. Personality in animal behaviour describes the phenomenon that differences between individuals in behavioural and physiological traits are consistent over time and context. The current understanding of the role of animal personality in group-living individuals is relatively poor, both from a proximate and an ultimate perspective. In this thesis the importance of animal personality on various aspects of group-living, including collective movements, social information use and negative frequency dependent performance, was studied, using the highly gregarious barnacle goose as study species.

Animals living in groups have to decide frequently on travel directions. One of the intriguing questions is which individuals contribute most to collective movements. The role of animal personality in collective movements is a remarkably poorly understood subject. Therefore, the role of animal personality on collective movements was investigated in this thesis. In chapter 2 the role of boldness on movement order towards a food patch was tested in pairs of geese. Barnacle geese differed consistently in their reaction towards novel objects (termed boldness) and boldness was important in the foraging task: bolder individuals walked more often in front and arrived more often at the food patch than shyer individuals. The arrival of an individual at the food patch also depended on the boldness score of its companion: when paired with a bold companion an individual arrived more often than when paired with a shy companion. In chapter 3 the role of boldness on collective movements was tested. A naïve goose was introduced in a labyrinth together with either one or three informed demonstrators, which possessed information about the route through the labyrinth. In pairs, bolder individuals decided more often for themselves where to go compared with shyer individuals, whereas shyer individuals waited more often for the demonstrators to decide and followed this information. In groups of four individuals, however, there was no effect of boldness on decision making. The results of chapter 2 and 3 match the general observation that bolder individuals are more often found at the forefront of collective movements and highlight the importance of personality on collective movements and leadership in small groups. Furthermore they demonstrate that the movement of a group can be affected by the mix of personality types present in the group.

One of the advantages of living in groups is that individuals have access to information made available by other individuals, known as social information. Social information is known to affect various important aspects of an individual's ecology, including foraging, dispersal and space use. Despite a rich tradition of studies on social information the relationship between animal personality and social information is poorly studied and generally it is assumed that social information is equally valuable to each individual in a

population and consequently most studies focus on the conditions under which an animal is expected to use social information. In this thesis the relationship between social information and personality in several different contexts was studied to test if variation in personality reflected differences in the use of social information.

In chapter 4 individual geese were allowed to watch two pairs of demonstrators. One pair of demonstrators received food, whereas the other pair did not. After an observation period the individual was allowed to join one of both demonstrator pairs. Shyer geese joined the foraging pair of demonstrators more often than bolder individuals, demonstrating that they used more social information. In chapter 5 the use of social information was tested in a situation where individuals had to search for food in groups in a producer–scrounger game. Individuals could either search for food themselves (personal information, producing) or join food discoveries of other individuals (social information, scrounging). The frequency of scrounging increased with decreasing boldness score. In chapter 3 it was shown that shyer individuals followed informed demonstrators through a labyrinth more often than bold individuals. Thus in three different contexts the use of social information decreased with increasing boldness score and the question arises why differences in boldness relate to variation in social information use. It is hypothesized that the value of social information is higher for shy individuals than for bold individuals, because it is costlier for shy individuals to collect personal information since shyer individuals experience more stress when they explore the environment (i.e., collect personal information). This also provides a potential link between boldness, social information and leadership. Informed individuals are known to lead collective movements. If bolder individuals indeed have more personal information, then they are expected to lead collective movements. To test if the value of social information was indeed higher for shyer individuals the arrival latency towards a food patch was measured in the presence and absence of a conspecific (chapter 6). This enabled us to study the value of social information by comparing both conditions. In the absence of a conspecific, bolder individuals arrived faster at the food patch than shyer individuals. In the presence of a conspecific, there was no effect of boldness on approach latency. As a consequence the difference in approach latency increased with decreasing boldness score, suggesting that shyer individuals profited more from the presence of a conspecific, or termed differently the value of social information increased with decreasing boldness score.

Next to proximate mechanisms, this thesis also studied the ultimate causes of why group-living individuals are consistently different. Negative frequency dependent selection has been proposed as one of the important processes, with social interactions during competition between conspecifics as the mechanism. Empirical evidence for a role of negative frequency dependent selection in animal personality is, however, scarce. In chapter 7 the feeding performance of barnacle geese in the presence of similar and dissimilar individuals in term of boldness scores was tested in a producer-scrounger game. There was no evidence for negative frequency dependent feeding performance of boldness. Both bold and shy individuals enjoyed higher feeding success when paired with bold companions than when paired with shy companions. In chapter 8 the possibility of negative frequency dependent selection was investigated in more detail by mimicking the evolution of boldness in a producer-scrounger game using a genetic algorithm. There was no evidence for a stable co-existence of different personality types within one population submitted to a given assortment of environmental conditions. Populations evolved towards a monomorphism where a single optimal level of boldness characterized all the individuals in the population. The optimal level of boldness, however, depended on the ecological conditions of the game. Low patch density and predation pressure favoured the evolution of shy individuals, whereas high patch density and absence of predation favoured bold individuals, suggesting that differences in selection pressures (either in space or time) in a social foraging game may explain differences in boldness levels between individuals of different populations. The simulations showed that bold individuals evolved to play both producer and scrounger, whereas shy individuals remain confined to scrounging. This outcome was experimentally confirmed in chapter 6 where geese were forced in either a producing or scrounging role: bolder individuals produced at a faster rate than shyer individuals, but there was no effect of boldness on scrounging behaviour.

To conclude, this thesis shows the importance of animal personality in group-living individuals. It shows that animal personality can affect various aspects of group-living including leadership, collective movements, producer-scrounger dynamics and social information use. These results suggest that animal personality is a component that cannot be neglected when studying animals in groups and that more research is necessary to understand the proximate and ultimate causes and consequences of group-living.

Samenvatting

Veel dieren leven in groepen gedurende het hele jaar, of tijdens grote delen van het jaar. Een groep is een verzameling van individuen en er is veel onderzoek gedaan om te begrijpen hoe en waarom individuen in groepen leven. Recentelijk is er een sterke toename van studies die consistente individuele verschillen in gedrag rapporteren tussen individuen binnen een populatie. Dit wordt "persoonlijkheden" genoemd. Persoonlijkheden in het dierenrijk beschrijft het fenomeen dat individuen van dezelfde soort, leeftijd en geslacht consistent verschillen in gedrag en fysiologie in zowel tijd als context. De huidige kennis van de rol van persoonlijkheden in in groepsverband levende dieren is echter gering, zowel op het gebied van de proximate als de ultimate verklaringen. In dit proefschrift is het belang van persoonlijkheden op verschillende aspecten van groepsleven onderzocht, waaronder collectieve bewegingen, sociaal informatie gebruik en sociale beslissingen. Dit onderzoek is verricht aan de brandgans.

Dieren die in groepen leven moeten vaak beslissen nemen over de te nemen route. Eén van de intrigerende vragen is welke individuen het meest bijdragen aan collectieve bewegingen. De rol van persoonlijkheden in deze collectieve bewegingen is een opmerkelijk slecht begrepen onderwerp. Daarom is de mogelijke rol van persoonlijkheden in collectieve bewegingen onderzocht in dit proefschrift. In hoofdstuk 2 is de rol van dapperheid onderzocht in groepsbeweging. Brandganzen verschilden consistent in hun reactie wanneer ze geconfronteerd werden met nieuwe objecten (genaamd "dapperheid"). Sommige ganzen benadereden nieuwe objecten altijd snel, terwijl andere ganzen ver weg van nieuwe objecten bleven. De mate van dapperheid was belangrijk in de daaropvolgende test van groepsbeweging: dappere individuen liepen vaker voor in de groep en bereikten vaker een voedselplek. Niet alleen de dapperheid van het individu zelf was van belang, ook de dapperheid van de andere gans in de groep. Ganzen die als partner een verlegen gans hadden kwamen vaker niet aan op de voedselplek dan ganzen die een dappere gans als groepsgenoot hadden. In hoofdstuk 3 is de rol van dapperheid in collectieve bewegingen verder onderzocht. Een naïeve gans werd samen met één of drie geïnformeerde ganzen in een labyrint geplaatst. Deze geïnformeerde individuen waren getraind en kenden de route door het labyrint. In tweetallen besloten de dappere ganzen vaker op eigen houtje waar ze naar toe gingen, terwijl de verlegen ganzen juist vaker op de beslissing van het geïnformeerde individu wachten en vervolgens deze informatie volgden. In groepen van vier ganzen was er echter geen effect van dapperheid op de besluitvorming. De resultaten van hoofdstuk 2 en 3 onderstrepen de algemene observatie dat dappere individuen vaker in de voorhoede van collectieve bewegingen te vinden zijn en benadrukken het belang van persoonlijkheid in collectieve bewegingen en leiderschap in kleine groepen. Verder tonen deze bevindingen aan dat de beweging van een groep kan worden beïnvloed door de mix van de persoonlijkheden in de groep.

Eén van de voordelen van het leven in groepen is dat individuen toegang hebben tot informatie van andere individuen, zogenaamde sociale informatie. Sociale informatie kan verschillende belangrijke aspecten van de ecologie van een individu beïnvloeden, zoals foerageergedrag, dispersie en ruimte gebruik. Ondanks een rijke traditie van onderzoek naar sociale informatie is er weinig bekend over de relatie tussen persoonlijkheden en sociale informatie en over het algemeen wordt aangenomen dat sociale informatie even waardevol is voor elk individu in een populatie. Dientengevolge richten de meeste studies zich op de vraag onder welke omstandigheden een dier sociale informatie gebruikt. In dit proefschrift is de relatie tussen sociaal informatie gebruik en persoonlijkheden in verschillende situaties onderzocht om te testen of variatie in persoonlijkheid een verschil weerspiegelt in het gebruik van sociale informatie.

In hoofdstuk 4 kreeg een gans de gelegenheid om twee paar ganzen te bekijken. Eén paar kreeg voedsel aangeboden, het andere paar niet. De toekijkende gans kon aan het gedrag van de beide paren zien waar het voedsel aanwezig was. Na een observatieperiode kreeg het toekijkende individu de gelegenheid om zich bij één van beide paren aan te sluiten. Verlegen ganzen bleken zich vaker aan te sluiten bij de foeragerende ganzen, waaruit blijkt dat verlegen ganzen meer sociale informatie gebruiken dan dappere ganzen. In hoofdstuk 5 is het gebruik van sociale informatie verder onderzocht in een situatie waarin ganzen naar voedsel moesten zoeken. Het voedsel was verborgen in potten. Individuen konden ofwel zelf op zoek gaan naar voedsel (persoonlijke informatie) of zich aansluiten bij voedsel ontdekkingen van andere individuen (sociale informatie). Het bleek dat dappere ganzen voornamelijk zelf op zoek gingen, terwijl de meer verlegen ganzen zich vaker aansloten bij voedsel ontdekkingen van andere ganzen. In hoofdstuk 3 werd reeds aangetoond dat verlegen individuen sneller geïnformeerde individuen volgen door een labyrint dan dappere individuen. Dus in drie verschillende situaties waren het steeds de verlegen dieren die het meest gebruik maakten van sociale informatie en de vraag dient zich aan waarom verlegen dieren meer gebruik maken van sociale informatie. Verondersteld wordt dat de waarde van sociale informatie hoger is voor verlegen individuen dan voor dappere individuen, omdat het voor verlegen individuen kostbaarder is om persoonlijke informatie te verzamelen, omdat verlegen dieren meer stress ervaren wanneer ze zelf op zoeken dienen te gaan naar voedsel en/of informatie. Dit geeft ook een mogelijke verklaring voor de relatie tussen dapperheid, sociale informatie en leiderschap. Het is bekend dat individuen met persoonlijke informatie collectieve bewegingen leiden. Als dappere individuen meer persoonlijke informatie bezitten, dan is de verwachting dat ze ook de collectieve beweging leiden. Om te testen of de waarde van sociale informatie inderdaad hoger is voor verlegen individuen is de aankomsttijd van ganzen op een voedselplek gemeten in de aan- en afwezigheid van soortgenoten (hoofdstuk 6). Door het verschil tussen beide metingen te nemen is het mogelijk om inzicht te krijgen in de waarde is van sociale informatie (m.a.w. de aanwezigheid van een soortgenoot) voor verschillende type persoonlijkheden. In de afwezigheid van een soortgenoot kwamen dappere ganzen sneller bij het voedsel aan dan verlegen individuen. In de aanwezigheid van een soortgenoot, was er geen verschil in aankomsttijd tussen dappere en verlegen ganzen. Het verschil in aankomsttijd tussen beide situaties was groter voor verlegen ganzen dan voor dappere ganzen, wat erop wijst dat verlegen individuen meer profiteerden van de aanwezigheid van een soortgenoot. Met andere woorden, dat de waarde van sociale informatie groter was voor verlegen ganzen dan voor dappere ganzen.

In dit proefschrift zijn naast de proximate mechanismen, ook de ultimate verklaringen onderzocht waarom individuen in een groep consistent van elkaar verschillen. Negatieve frequentie afhankelijke selectie is geopperd als een mogelijke verklaring voor de aanwezigheid van verschillende persoonlijkheden in groepen, maar tot op heden is hier weinig empirisch bewijs voor geleverd. In hoofdstuk 7 is daarom het foerageersucces van zowel dappere als verlegen ganzen gemeten in de aanwezigheid van individuen die ofwel gelijk waren in de mate van dapperheid, of juist heel verschillend. Ganzen hadden geen hoger foerageersucces in de aanwezigheid van groepsgenoten die heel verschillend waren in dapperheid (hetgeen de verwachting was op basis van negatieve frequentie afhankelijkheid). Zowel de dappere als de verlegen ganzen hadden een hoger foerageersucces in de aanwezigheid van dappere dieren dan in de aanwezigheid van verlegen groepsgenoten. In hoofdstuk 8 is de mogelijkheid van negatieve frequentie afhankelijke selectie verder onderzocht door het nabootsen van de evolutie van dapperheid met behulp van een genetische algoritme. In een computer simulatie gingen verlegen en dappere individuen op zoek naar voedsel door ofwel zelf te zoeken ofwel door te profiteren van voedselontdekkingen van groepsgenoten. Alleen de best presterende individuen werden geselecteerd en gingen door naar de volgende generatie. De computer simulaties leverden geen bewijs voor een stabiele co-existentie van verschillende persoonlijkheidstypen binnen één populatie. Alle individuen in de populatie evolueerden naar hetzelfde dapperheids niveau. Dit optimale niveau van dapperheid hing echter sterk af van de ecologische omstandigheden in de simulaties. Bij een lage voedseldichtheid en een hoge predatiedruk evolueerden de individuen naar verlegen individuen, terwijl een hoge voedseldichtheid en de afwezigheid van predatie zorgden voor het ontstaan van dappere individuen. Dit suggereert dat verschillen in selectie druk (zowel in ruimte als tijd) in een sociale foerageer situatie kunnen zorgen voor verschillen in het niveau van dapperheid tussen individuen van verschillende populaties. Verder bleek uit de simulaties dat verlegen individuen in de simulaties voornamelijk zich aansloten bij andere individuen en niet zelf op zoek gingen naar voedsel, terwijl dappere ganzen zowel zelf op zoek gingen, als zich aansloten bij andere individuen. Deze voorspellingen werden experimenteel bevestigd in hoofdstuk 6 waar ganzen gedwongen werden om ofwel zelf op zoek te gaan naar voedsel, ofwel om zich aan te sluiten bij een foeragerend individu. Dappere individuen waren inderdaad sneller dan verlegen individuen als ze zelf op zoek moesten naar voedsel, maar er was geen effect van dapperheid als individuen zich aansloten bij een foeragerend individu.

Tot slot, dit proefschrift laat het belang zien van persoonlijkheden in groepsdieren. Het toont aan dat persoonlijkheid verschillende aspecten van het groepsleven kan beïnvloeden, waaronder leiderschap, collectieve bewegingen en sociaal informatie gebruik. Deze resultaten suggereren dat persoonlijkheden een belangrijk onderdeel is dat niet kan worden genegeerd bij het bestuderen van groepsdieren en dat er meer onderzoek nodig is om de proximate en ultimate verklaringen van het leven in groepen te begrijpen.

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My journey as a PhD student has been a remarkable experience. Spending four years on one research project with only few other obligations is a true privilege. Many persons contributed greatly to 'my' thesis, science truly is a 'cooperative business'.

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In 2009 I had the pleasure of visiting the lab of professor Luc-Alain Giraldeau at the Department of Biology, University of Quebec at Montreal for one month. Luc-Alain, thank you for your hospitality and your enthusiasm and insights in the world of social foraging and the live concerts during the potluck evenings. Merci beaucoup. I would like to thank Steven Hamblin for building from scratch the model that is the basis of chapter 8 of this thesis. Thanks for all the long hours of coding you put into this. It would have never been possible to do this without you. Lastly I would like to thank Kimberley Mathot. Kim, thank you for your warm welcome in Montreal, the trips you arranged in and around Montreal, your contribution to the thinking phase of the model of chapter 8, and the scientific discussions we had, I enjoyed these very much.

Prior to my PhD, I received an important part of my scientific training at the Max Planck Institute for Ornithology in Radolfzell, Germany under the supervision of Anne Peters. Thank you Anne for your training and support. I feel that in many ways working under your wings for one year greatly helped me doing this PhD. Thanks to Isabel Smallegange for thinking of me when that position opened up and for being a very good (though invisible) supervisor during my MSc project at the NIOZ. The period at the Max Planck Institute was a delight also thanks to: Kaspar, Isabel, Mark, Sjouke, Carlo and Riek.

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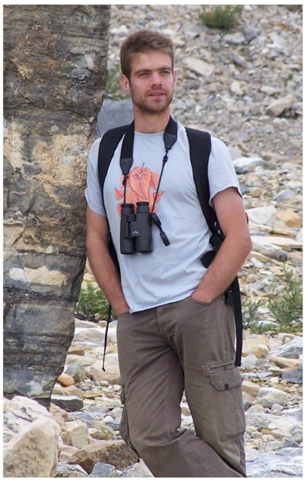
Curriculum vitae



Ralf Hubertus Johannes Maria (Ralf) Kurvers was born on the 17th of June 1981 in Geleen, the Netherlands. He obtained his gymnasium diploma in Sittard in 1999, after which he moved to Wageningen to start with the MSc Forest and Nature Conservation at Wageningen University. In his first MSc thesis, supervised by Dick van der Hoek and Ota Rauch, he visited the Czech Republic to study species-environment interactions. He spatially related species distribution to environmental conditions by mapping the distribution of plant species and analysing soil and water samples. For his second MSc thesis project he studied predator-prey dynamics at the Royal NIOZ (Netherlands Institute for Sea Research), Texel, supervised by Jaap van der Meer and Isabel Smallegange. By manipulating predator and prey density, he was able to show that interference competition takes place in a crab-bivalve system in the absence of exploitative competition. For his internship he went to Kalimantan, Indonesia, to study the natural succession of tropical peat land forest after forest fires. Here, he identified suitable tree species and field sites for tree regeneration schemes.

After completion of his MSc study at Wageningen University in 2005 he (successfully) applied for a scholarship from the Thomas More Foundation for a post graduate study of philosophy at the Radboud University in Nijmegen, the Netherlands. In this year he studied the theory and philosophy of science, with a special interest in the philosophy of nature and the philosophy of biology.

For his first professional job he moved to the Max Planck Institute of Ornithology in Radolfzell, Germany. Here he worked as a research associate under the supervision of Anne Peters and Mark Roberts on the physiology and development of avian visual sexual signals and the role of these signals in sexual selection, using a captive population of Blue tits.

In 2007 he moved back to Wageningen University to start a PhD at the Resource Ecology Group under the supervision of Herbert Prins and Ron Ydenberg in collaboration with Kees van Oers and Bart Nolet from the Netherlands Institute of Ecology (NIOO-KNAW). His PhD research focused on the ecological consequences of consistent individual variation in behaviour (‘personality’) in group-living individuals. He studied the effect of animal personality on various aspects of group-living, including social information use, collective behaviour and social networks. To study the proximate causes of animal personality he used a combination of experimental work using captive geese and fieldwork studying individuals in their natural habitat. To study the ultimate causes of personality he used theoretical modelling in collaboration with Luc-Alain Giraldeau and Steven Hamblin from the University of Quebec at Montreal, Canada.

Presently, he received a Rubicon grant from the Dutch Science Foundation (NWO) to work for 2 years with Jens Krause at the Humboldt University in Berlin. Here he will continue his work on animal personality in group-living individuals.

List of Publications

Kurvers RHJM, van Santen de Hoog SI, van Wieren SE, Ydenberg RC & Prins HHT. No evidence for negative frequency dependent feeding performance in relation to personality. Behavioral Ecology. Accepted.

Jonker RM, **Kurvers RHJM**, van de Bilt A, Faber M, Van Wieren SE, Prins HHT & Ydenberg RC. Rapid adaptive adjustment of parental care coincident with altered migratory behaviour. Evolutionary Ecology. In Press.

Kurvers RHJM, Adamczyk VMAP, van Wieren SE & Prins HHT. 2011. The effect of boldness on decision making in barnacle geese is group-size-dependent. Proceedings of the Royal Society B 278: 2018-2024.

Peters A, **Kurvers RHJM**, Roberts ML & Delhey K. 2011. No evidence for general condition-dependence of structural plumage colour in blue tits: an experiment. Journal of Evolutionary Biology 24: 976-987.

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

Kurvers RHJM, Prins HHT, van Wieren SE, van Oers K, Nolet BA & Ydenberg RC. 2010. The effect of personality on social foraging: shy barnacle geese scrounge more. Proceedings of the Royal Society B 277: 601-608.

Jonker MN, de Boer WF, **Kurvers RHJM** & Dekker JJA. 2010. Foraging and public information use in common pipistrelle bats (*Pipistrellus pipistrellus*): a field experiment. Acta Chiropterologica 12: 197-203.

Kurvers RHJM, Delhey K, Roberts ML & Peters A. 2010. No consistent female preference for more UV crown colour in the Blue Tit, *Cyanistes caeruleus*: a mate choice experiment. Ibis 152: 393 - 396 .

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. Animal Behaviour 78: 447-453.

Kurvers RHJM, Roberts ML, McWilliams SR & Peters A. 2008. Experimental manipulation of testosterone and condition during moult affects activity and vocalizations of male blue tits. Hormones and Behavior 54: 263-269.

Smallegange IM, van der Meer J. & **Kurvers RHJM.** 2006. Disentangling interference competition from exploitative competition in a crab-bivalve system using a novel experimental approach. Oikos 113: 157-167.

PE&RC PhD Education Certificate

With the educational activities listed below the PhD candidate has complied with the educational requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

Review of literature (5 ECTS)

- Social foraging information in geese: the role of familiarity, dominance and association strength on social foraging (2007)

Post-graduate courses (5 ECTS)

- The art of modelling; PE&RC (2008)
- Consumer-resource interactions; PE&RC (2010)

Laboratory training and working visits (4 ECTS)

- Producer-scrounger models; Universté du Québec à Montréal, Canada (2009)

Invited review of (unpublished) journal (2.1 ECTS)

- Journal of Mammology: formation of mixed-species groups (2009)
- Environmental Conservation: impact of grazing policy on livestock (2009)
- Behavioural Ecology and Sociobiology: producer-scrounger games (2010)
- Oikos: diet specialisation (2010)
- Wildlife Biology: geese management (2011)
- Animal Behaviour: personality and host-parasites (2011)
- Behavioral Ecology: personality and sexual selection (2011)

Deficiency, refresh, brush-up courses (10.5 ECTS)

- Network principles as applied in and via GIS; WUR (2007)
- Laboratory animal science course; WUR (2007)
- Anatomy and physiology of vertebrates; University Utrecht (2007)

Competence strengthening / skills courses (0.6 ECTS)

- Organising and supervising MSc thesis; OWU (2007)

PE&RC Annual meetings, seminars and the PE&RC weekend (4.7 ECTS)

- PE&RC Weekend (2007)
- PE&RC Day (2007-2010)
- Netherlands Annual Ecology Meeting; Lunteren, the Netherlands (2009 & 2010)

Discussion groups / local seminars / other scientific meetings (6.4 ECTS)

- Journal Club; Department of Animal Ecology, NIOO (2007-2010)
- Wageningen Evolution and Ecology Seminars (WEES) (2009-2011)

International symposia, workshops and conferences (18.1 ECTS)

- 6th Conference European Ornithological Union; Vienna, Austria (2007)
- 11th Meeting Goose Specialist Group; India, Leh (2008)
- 15th European Meeting of PhD Students in Evolutionary Biology (member of organizing committee); Schoorl, the Netherlands (2009)
- The Evolution of Society; The Royal Society, London, UK (2010)
- Workshop Annual Ecology; Simon Fraser University, Vancouver, Canada (2009)
- 16th Benelux Congress of Zoology; Wageningen, the Netherlands (2009)
- Culture Evolves; The Royal Society, London, UK (2010)
- 13th International Behavioral Ecology Congress; Perth, Australia (2010)
- Social Decision Making: Bridging Economics and Biology; Ascona (2011)

Lecturing / supervision of practical 's / tutorials (4.5 ECTS)

- Ecological Methods I; 5 days (2010)
- Animal Ecology; 10 days (2010)

Supervision of 9 MSc students; 90 days

- Personality; 3 students
- Social information use; 3 students
- Animal social networks; 3 students

The cover picture is taken by Erica Ras.

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