Dominance, Personality and Innovation in Black-Capped Chickadees (*Poecile atricapillus*)

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Abstract

Social dominance influences many aspects of the life of animals living in social groups, including fitness. Recent work suggests that individuals occupying different positions in a dominance hierarchy may differ in their behavioural and cognitive traits. The first objective of this thesis was to determine whether personality (i.e. consistent behavioural differences between individuals) is correlated with dominance in natural groups of black-capped chickadees (*Poecile atricapillus*) in the wild. Dominance relationships within these groups were highly asymmetrical and transitive, which is typical of linear dominance hierarchies. None of the measured personality traits (i.e. aggressiveness in hand, exploration, activity and neophilia) were significantly correlated with dominance. These results suggest that personality does not contribute to the formation of black-capped chickadee hierarchies and add to the growing body of evidence that inherent attributes of individuals are not sufficient to explain the structure of linear dominance hierarchies observed in the wild. The second objective of this thesis was to investigate how dominance and correlates of competitive ability (i.e. sex, age and body condition) are related to novel problem-solving performance, which is a proxy for innovativeness, the invention of new behavioural patterns or the modification of an existing behaviour in a novel context. Problem-solving performance was not significantly associated with sex, age or body condition, but dominants were more efficient problem-solvers than subordinates. This finding suggests that efficiency when solving a novel problem might be driven by cognitive capacity instead of the necessity induced by the social position of an individual. Overall, results of this thesis help to better understand dominance hierarchies in wild groups of animals.

Résumé

La dominance sociale influence plusieurs aspects de la vie des animaux vivant en groupes sociaux, incluant l'aptitude phénotypique. Des travaux récents suggèrent que les traits comportementaux et cognitifs des individus pourraient influencer leur position dans une hiérarchie de dominance. Le premier objectif de cette thèse était de déterminer si la personnalité (des différences comportementales constantes entre les individus) est corrélée à la dominance au sein de groupes sauvages de mésanges à tête noire (*Poecile atricapillus*). Les relations de dominance à l'intérieur de ces groupes étaient hautement asymétriques et transitives, ce qui est typique de hiérarchies de dominance linéaires. Aucun des traits de personnalité mesurés (agressivité en main, exploration, activité et néophilie) n'était significativement corrélé à la dominance. Ces résultats suggèrent que la personnalité ne contribue pas à la formation des hiérarchies chez la mésange à tête noire et s'ajoutent au nombre croissant de preuves suggérant que les attributs intrinsèques des individus ne sont pas suffisants pour expliquer la structure linéaire d'un bon nombre de hiérarchies de dominance observées dans la nature. Le second objectif de cette thèse était d'investiguer la façon dont la dominance ainsi que d'autres corrélats de la capacité compétitive (sexe, âge et condition corporelle) étaient reliés à la performance de résolution d'un nouveau problème, qui est un indicateur de l'innovation, l'invention de nouveaux comportements ou la modification de comportements existants dans un nouveau contexte. La performance lors de la résolution de problème n'était pas significativement associée avec l'âge, le sexe ou la condition corporelle des individus, mais les oiseaux dominants résolvaient le problème significativement plus efficacement que les subordonnés. Ce résultat suggère que l'efficacité lors de la résolution d'un nouveau problème pourrait être influencée par la capacité cognitive plutôt que par la nécessité induite par la position sociale d'un individu. En conclusion, les résultats de cette thèse aident à mieux comprendre les hiérarchies de dominance des groupes d'animaux dans la nature.

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Statement of contributions

Chapters 2 and 3 of this thesis are manuscripts in preparation for submission to journals. As such, some content may overlap between chapters. The pronoun “ we ” is used as manuscripts will be submitted with more than one author; however this thesis was written by myself.

Chapter 2: Measurements of personality traits for this chapter were performed in collaboration with MSc student Teri Jones. Honours students Chloé Montreuil-Spencer and Jessica Marie Cloutier, as well as UROP student Phil Angel, also participated in the coding of personality videos.

Chapter 3: The empirical work in this chapter was designed and executed in collaboration with postdoctoral fellow Maxime Cauchoix. Honours students Ethan Hermer and Jean-Michel Charbonneau participated in the collection of data related to innovation and dominance, respectively.

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CHAPTER 1

GENERAL INTRODUCTION

Social dominance is an important feature in many group-living animals (Wilson, 1975; Piper, 1997), which may strongly affect individual fitness (Arcese and Smith, 1985; Huntingford and Turner, 1987; Ellis, 1995). Dominance hierarchies are social structures established by dyadic interactions between group members, with all dyads interconnected in a network of relationships (Drews, 1993; Preuschoft and van Schaik, 2000; Chase et al., 2002; Beacham, 2003). Considering the advantages of social life, such as reduced predation risk and enhanced feeding efficiency (Krause and Ruxton, 2002; Davies et al., 2012), dominance hierarchies can reduce costs associated with intraspecific interactions and competition (Piper 1997; Preuschoft and van Schaik, 2000). Social organizations range from loosely defined structures to rigid linear hierarchies (Chase, 1980). Linear dominance hierarchies arise in small groups in particular, and are characterized by stable membership as well as asymmetry and transitivity of dominance relationships (Landau, 1951; Chase, 1980; Appleby, 1983). Asymmetry takes place when there is a clear dominance-subordination relation between dyad members, whereas transitivity arises when an individual A dominates all others, an individual B dominates all but A, and so on down to the last individual who dominates no one (A > B > C) (Chase, 1980; Appleby, 1983). Several examples of dominance hierarchies are found in Parids, with many species spending their non-breeding season wintering in flocks organized in linear dominance hierarchies (Ekman, 1989; Hogstad, 1989).

Pioneering theoretical work has focused on the formation of linear dominance hierarchies (Landau, 1951; Chase, 1980; Appleby, 1983), originally introduced as ‘peck-right order’ by Schjelderup-Ebbe (1922). These hierarchies may be generated by differences in the intrinsic attributes of animals (‘prior attributes’ hypothesis), or by the processes of social interaction among group members (‘social dynamics’ hypothesis) (Chase et al., 2002). Although the influence of physical attributes such as sex, age, and body size on dominance status is well established, a significant portion of the variance in dominance remains to be explained (e.g. Piper and Wiley, 1989). The acquisition of dominance positions may also be influenced by prior differences in individuals’ behavioural traits, such as personality (i.e. consistent behavioural differences between individuals; Gosling, 2001; Sih et al., 2004; Réale et al., 2007). Following the ‘proactive-reactive’ axis (Koolhaas et al., 1999), individuals with proactive personality type exhibit high aggressiveness, high activity, boldness, and superficial exploration, whereas ‘reactive’ individuals are characterized by low aggressiveness, low activity, shyness and thorough exploration (Koolhaas et al., 1999). Proactivity has been positively linked with life-history traits, for instance fast growth rate and high food intake (Biro and Stamps, 2008). Proactive individuals are thus suggested to exhibit a fast lifestyle (Réale et al., 2010). For instance, by facilitating access to and monopolization of resources, proactive personality traits (e.g. high levels of aggressiveness) may have coevolved with high metabolic rates (Réale et al., 2010). Because proactivity may positively correlate with competitive ability, we would expect positive relationships between proactive traits and dominance rank. Indeed, some studies have reported a correlation between dominance outcomes from pairwise confrontations of isolated dyads in captivity and personality traits such as boldness (Dahlbom et al., 2011), aggressiveness (Riebli et al., 2011), and exploratory behaviour (Verbeek et al., 1996; Beauchamp, 2000; Fox et al., 2009; Favati et al., 2014).

Working with dyads however excludes the potential influence of social dynamics on the relationship between dominance and behavioural traits. Because dominance hierarchies may not simply result from the addition of conflicts among separate pairs of individuals, relationships derived from isolated pairwise interactions may not be the proper unit of analysis to understand dominance behaviour in groups (Chase et al., 2002, 2003). Studies on social groups have reported conflicting findings on the link between social dominance and personality (see Chapter 2 for details): some found significant relationships (Verbeek et al., 1999; Dingemanse and de Goede, 2004; David et al., 2011; Cole and Quinn, 2012) and others no significant association (Boogert et al., 2006; Kurvers et al., 2009; Riebli et al., 2012; Funghi et al., 2015). Furthermore, only a few studies have investigated this relationship in natural groups in the wild (Réale et al., 2000; Dingemanse and de Goede, 2004; Cole and Quinn, 2012) and none with an avian species exhibiting a linear dominance hierarchy. This predominance of research conducted in captivity may be especially problematic if the social organization differs from the one exhibited in nature. For instance, group size in captivity is often small compared to the wild (e.g. great tits *Parus major*: group size of 5 to 8 individuals in captivity (Verbeek et al., 1999) vs. over 50 in the wild (Dingemanse and de Goede, 2004; Aplin et al., 2013a); other species: see Boogert et al., 2006; David et al., 2011; Riebli et al., 2012; Funghi et al., 2015). Moreover, most of the above-cited studies in captivity also used same-sex groups (Verbeek et al., 1999; Boogert et al., 2006; David et al., 2011; Funghi et al., 2015), although this does not reflect the groups' composition in nature. Another difference between captivity and natural conditions is that individuals cannot leave the group (e.g. Verbeek et al., 1999), and therefore captivity artificially induces a stable membership in species which do not necessarily exhibit stable group membership in the wild (e.g. great tits exhibit a fission-fusion social organization; Ekman, 1989; Aplin et al., 2012).

In the second chapter of this thesis, I investigate the relationship between animal personality and dominance measured in the wild, in natural groups of black-capped chickadees (*Poecile atricapillus*). Black-capped chickadees are small resident Paridae widespread in North America, and their winter flocks are organized into distinct linear dominance hierarchies (Smith, 1991; Ratcliffe et al., 2007). The black-capped chickadee is an ideal species to study this relationship for many reasons. For instance, dominance has been well-studied in this species (Hartzler, 1970; Glase, 1973; Smith, 1976; Desrochers et al., 1988; Mennill et al., 2004; also reviewed in Smith, 1991 and Ratcliffe et al., 2007), and its social organization is thus fairly well-known. Black-capped chickadees are distributed across diverse geographical ranges and temperate habitats, and inhabit the same area year-round, which allows conducting field studies both during the breeding and the nonbreeding season (Smith, 1991; Ratcliffe et al., 2007). They readily use feeders and dominance hierarchies are consistent whether at or away from feeders (Smith, 1976); therefore dominance data are easily obtainable. Little research has been done on personality in black-capped chickadees, with a few studies examining exploratory behaviour (Guillette et al., 2009, 2011a,b, 2015) or neophobia (An et al., 2011). Only one study investigated the link between dominance and a personality trait (i.e. neophobia) in this species, using encounters between isolated dyads in captivity (An et al., 2011). In Chapter 2, I test the ‘prior attributes’ hypothesis by investigating the relationship between dominance and four personality traits within natural groups of black-capped chickadees. I predict that dominant individuals would be more aggressive, exploratory and active, but less neophilic, than subordinates.

Social dominance may strongly affect fitness-related attributes, and its costs and benefits are not equally distributed among group members (see reviews by Ekman, 1989; Hogstad, 1989; and Ratcliffe et al., 2007). Whereas dominant individuals may benefit from higher reproductive success (Otter et al., 1998, 1999; Mennill et al., 2004; Doucet et al., 2005; Schubert et al., 2007) and enhanced survival (Smith 1984; Ekman and Askenmo, 1984; Desrochers et al., 1988) compared to subordinates, they may also experience increased costs such as fighting (Rohwer and Ewald 1981; Ficken et al., 1990) and energetic expenses (Røskaft et al., 1986; Hogstad, 1987; Bryant and Newton, 1994). An important characteristic of a dominance hierarchy is that it may determine the priority of access to limited resources. Whereas dominants can control preferential access to food owing to their greater competitive ability, subordinates often have to wait until high-ranking individuals have fed (Ficken et al., 1990; Boisvert, 1999). The use of different foraging tactics may thus be expected in relation to an individual's hierarchical position within a group.

To obtain food when foraging in groups, individuals can actively search for resources themselves ('produce') or exploit the resources discovered by others ('scrounge') (Barnard and Sibly, 1981; Giraldeau and Caraco, 2000). Dominance status has been found to affect these social foraging strategies, with higher-ranking individuals tending to produce less and scrounge more than low-ranking individuals (Barta and Giraldeau, 1998; Stahl et al., 2001; Liker and Barta, 2002; Lendvai et al., 2006; but see Beauchamp, 2006 and Jolles et al., 2013). Additionally, dominants have been shown to cache more food than individuals of inferior ranks (Lahti et al., 1998; Boisvert, 1999; Pravosudov et al., 2003), whereas subordinates carried larger body reserves than group members with higher ranks, possibly to mitigate the effects of more uncertain foraging success and increased perceived risk of starvation (Ekman and Lilliendahl, 1993; Gosler, 1996). Because of their limited access to established resources, subordinate individuals may also be forced to search for alternative solutions and thus be more likely to innovate ('necessity drives innovation' hypothesis; Laland and Reader 1999a; Reader and Laland, 2003).

Animal innovation can be described as the invention of new behaviour patterns or the modification of an existing behaviour in a novel context (Kummer and Goodall, 1985; Lefebvre et al., 1997; Reader and Laland, 2003). Innovation is commonly studied using the performance of individuals presented with novel food-motivated problems (Webster and Lefebvre, 2001; reviewed in Griffin and Guez, 2014). The 'necessity drives innovation' hypothesis predicts a negative relationship between competitive ability and innovativeness (Laland and Reader 1999a,b; Reader and Laland 2003). Poor competitors, usually juveniles, females, subordinates and individuals in poor body condition, should thus be good problem-solvers. However, empirical findings are not always consistent with predictions from this hypothesis (see Table 3.1 for detailed findings). For instance, in meerkats *Suricata suricatta*, adult male subordinates were more likely to innovate, with no effect of body condition (Thornton and Samson, 2012). In pigeons *Columba livia*, neither sex nor dominance rank was associated with problem-solving performance (Bouchard et al., 2007).

In the third chapter of this thesis, I revisit the ‘necessity drives innovation’ hypothesis by examining the relationship between problem-solving performance and correlates of competitive ability in individual black-capped chickadees presented with a novel food-motivated task in captivity. Chickadees are a good choice for this work because Paridae is a highly innovative family (Overington et al., 2009; three cases of innovations in nature reported specifically for black-capped chickadees). According to the ‘necessity drives innovation’ hypothesis, I predict that females, juveniles, individuals in poor body condition as well as subordinates should be better problem-solvers than males, adults, individuals in good condition and dominants, respectively. Dominance was measured within natural groups in the wild, which has been done only in a few empirical studies examining the link with innovative problem-solving (Gajdon et al., 2006 with keas, *Nestor notabilis*; Benson-Amram and Holekamp, 2012 with hyenas, *Crocuta crocuta*; Thornton and Samson, 2012 with meerkats; see also Cole and Quinn, 2012 using competitive ability as proxy of dominance in great tits).

Overall, my general aim in this thesis was to investigate potential behavioural and cognitive correlates of social dominance in wild animal groups. In Chapter 2 I address dominance in relation to personality, whereas in Chapter 3 I focus on innovative problem-solving.

CHAPTER **2**

PERSONALITY DOES NOT PREDICT SOCIAL DOMINANCE IN WILD GROUPS OF BLACK-CAPPED CHICKADEES, *POECILE ATRICAPILLUS*

Abstract

Dominance hierarchies characterize social groups of various species and can significantly influence individual fitness. In previous studies, individual differences in attributes, such as personality traits (i.e. consistent behavioural differences between individuals), accurately predicted the outcomes of dominance encounters in isolated dyads in captivity. However, findings from social groups of animals are less clear and suggest that these differences in attributes may not accurately predict dominance in groups, especially within linear hierarchies. Here, we investigated the relationship between four personality traits (i.e. exploration, activity, neophilia and aggressiveness in hand) and dominance in wild groups of black-capped chickadees (*Poecile atricapillus*), a resident passerine bird that winters in flocks characterized by linear dominance hierarchies. We predicted that if dominance is linked to personality within these social groups, dominant individuals should be more exploratory, active and aggressive, but less neophilic, than subordinates. Dominance relationships in our groups of black-capped chickadees were highly transitive and asymmetric, which is typical of linear hierarchies. However, none of the personality traits were significantly correlated with each other or with dominance. These results suggest that personality does not contribute to the establishment of black-capped chickadee hierarchies in the wild. We discuss the growing body of evidence suggesting that individual attributes are not sufficient to explain the linearity of many dominance hierarchies found in nature.

Introduction

Social dominance has key implications for fitness in group-living animals, and individuals with high dominance rank may benefit from their status in various ways. For instance in Parids wintering in dominance-structured groups, high-ranking flock members have been found to benefit from priority of access to resources, including food (Glase 1973; Hogstad, 1989; Ficken et al., 1990), breeding territories (Smith, 1976, 1994; Desrochers et al., 1988), and locations safest from predators (Ekman and Askenmo, 1984; Ekman, 1987; Hogstad, 1988, 1989; Desrochers, 1989). Dominant individuals thus exhibit enhanced survival (Smith 1984; Ekman and Askenmo, 1984; Desrochers et al., 1988) and greater reproductive success (Otter et al., 1998, 1999; Mennill et al., 2004; Doucet et al., 2005; Schubert et al., 2007) than subordinates.

Two main hypotheses have been proposed to explain the formation of dominance hierarchies: dominance ranks could be predetermined by differences in the intrinsic attributes of animals (‘prior attributes’ hypothesis), or they could be generated by the processes of social interaction among group members (‘social dynamics’ hypothesis) (Chase et al., 2002). While much work has focused on the association of hierarchical relationships with physical attributes of individuals such as body size, sex and age (see Smith, 1991 and Ratcliffe et al., 2007 for review on Paridae species), the influence of behavioural attributes on dominance is less clear. Some studies suggest that animal personality (i.e. consistent behavioural differences between individuals; Gosling, 2001; Sih et al., 2004; Réale et al., 2007), may play a role in the establishment of social status (e.g. in avian species: Verbeek et al., 1996, 1999; David et al., 2011; Favati et al., 2014; in fish species: Colléter and Brown, 2011; Dahlbom et al., 2011).

Personality has been reported for a wide range of species across the animal kingdom, including mammals, fishes, birds, reptiles, amphibians, arthropods, and molluscs (reviewed by Gosling, 2001 and Réale et al., 2007). These consistent individual differences in behaviour may affect animal life-history traits and interactions with the environment in several ways, for instance by impacting growth, fecundity, response to predators, food sources or habitat, and social or sexual interactions with conspecifics (Réale et al., 2007; Biro and Stamps, 2008). Examples of personality traits include boldness, an individual's reaction to any risky situation, but not new situations; exploration, an individual's reaction to a new situation; activity, the general level of movement of an individual; and aggressiveness, an individual's agonistic reaction towards conspecifics (Gosling, 2001; Réale et al., 2007). Aggressiveness during handling is also a trait which has been measured in different species (Overington et al., 2011; Brommer and Kluen, 2012; Réale et al., 2000). This measure is indicative of the way animals respond to handling by humans (Overington et al., 2011) and is thus not equivalent to aggressiveness towards conspecifics. Other well-studied personality traits are neophilia and neophobia. Neophilia, a positive response to novelty, can be defined as attraction towards an object simply because it is unfamiliar (Greenberg, 2003). Neophilia and neophobia (fear of novelty) are thought to be independent responses to novel stimuli, with different motivations and selective factors (Greenberg and Mettke-Hofmann, 2001; Mettke-Hofmann et al., 2002; Greenberg, 2003).

When personality traits are correlated with each other they are said to form a behavioural syndrome, which may be defined as a suite of correlated behaviours in different contexts (Sih et al., 2004; Réale et al., 2007; Wolf and Weissing, 2012).

Behavioural syndromes allow individuals to be characterized on main axes summarizing several personality traits such as the proactive-reactive axis (Koolhaas et al., 1999). Proactivity implies positive associations with boldness, aggressiveness and exploration (Koolhaas et al., 1999), as well as competitive ability and fast lifestyle (Réale et al., 2010). Indeed, studies have reported that dominant individuals tend to be more exploratory (Verbeek et al., 1996; Cole and Quinn, 2012; Favati et al., 2014), bold (Dahlbom et al., 2011), aggressive towards conspecifics (Verbeek et al., 1996; Riebli et al., 2011), proactive (David et al., 2011), and also more neophobic (Robertson, 1982; An et al., 2011) than subordinates.

Many studies of correlations between dominance and personality used dominance relationships established within isolated pairs of individuals, by conducting staged dyadic contests in captivity (Robertson, 1982; Verbeek et al., 1996; Beauchamp, 2000; Mettler and Shivik, 2007; Fox et al., 2009; An et al., 2011; Dahlbom et al., 2011; Riebli et al., 2011; Favati et al., 2014; Kozlovsky et al., 2014). The relevance of experiments on isolated pairs for understanding dominance in animals groups has been questioned (e.g. Chase et al., 2003). For instance, dominance status from pairwise contests may not reflect the social hierarchical position of an individual in the group as a whole, as this status is likely to be "dyad-specific" (i.e. depend on the identity of the two dyad members). Accordingly, rearranging dyads of zebra finches *Taeniopygia guttata* led to several changes in dominance and leadership status (Beauchamp, 2000). Furthermore, studies on the same species found different relationships between dominance and behavioural traits when testing animals under dyadic *versus* social conditions (great tits *Parus major:*

Verbeek et al., 1996, 1999; cichlid fish *Neolamprologus pulcher:* Riebli et al., 2011, 2012).

Experiments investigating social dominance and personality in group settings report conflicting results, with some having found significant correlations (Verbeek et al., 1999; Dingemanse and de Goede, 2004; David et al., 2011; Cole and Quinn, 2012), and others no significant effects (Réale et al., 2000; Boogert et al., 2006; Kurvers et al., 2009; Riebli et al., 2012; Funghi et al., 2015). Contrary to expectations from findings obtained with isolated dyads, individual differences in prior attributes may not be sufficient to explain the outcomes of dominance encounters in groups of animals, especially those forming linear hierarchies (see below) (e.g. Chase and Seitz, 2011). Moreover, with only a few noticeable exceptions (Réale et al., 2000; Dingemanse and de Goede, 2004; Cole and Quinn, 2012), all of these studies were conducted with groups created experimentally in captivity. While acknowledging that captivity allows for well-controlled experiments and that the use of captive social groups is closer to natural situations than isolated dyads, several differences still exist between captive and natural social settings (e.g. possibility of escaping from the group and the context of introduction of members in the group; Verbeek et al., 1999). There is thus a need for studies investigating the association between dominance and personality in natural groups of animals in the wild, especially with species characterized by linear hierarchies.

Linear dominance hierarchies occur predominantly in small social groups, and their two main criteria are asymmetry of dyadic relationships and transitivity of dominance relationships (Chase, 1980; Appleby, 1983; Shizuka and McDonald, 2012). Asymmetry occurs when there is a clear dominance-subordination relation between dyad members (i.e. one individual consistently wins over the other). Transitivity occurs in a hierarchy when an individual A dominates all others, an individual B dominates all but A, and so on down to the last individual who dominates no one (A > B > C; Figure 2.1) (Chase, 1980; Appleby, 1983). In contrast, if within a set of three individuals A > B > C but C > A, then the dominance is not transitive but rather said to be circular (Figure 2.1) (Chase, 1980; Appleby, 1983).

In this study, we aimed to examine the relationship between social dominance in natural animal groups and the personality traits of aggressiveness in hand, exploration, activity and neophilia. We used the black-capped chickadee (*Poecile atricapillus*), a small resident Paridae widespread in North America, as our study species. Black-capped chickadees form non-breeding flocks in fall and winter, with an average group size of eight individuals (Odum, 1942; Smith, 1991; Ratcliffe et al, 2007). These flocks are typically characterized by a stable membership and are organized into strict linear dominance hierarchies, the so-called "peck-right dominance hierarchies" (Hartzler, 1970; Smith, 1976, 1991; Ratcliffe et al., 2007). In black-capped chickadee hierarchies, males are usually dominant over females, and adults tend to dominate young birds (Desrochers et al., 1988; Smith, 1991; Odum, 1942; Ratcliffe et al., 2007); dominants also have been found to be leaner than subordinates (Schubert et al., 2007), but the impact of personality traits on dominance rank is not well understood. Following findings from previous studies in other species (see above), we predicted that dominant birds should be more aggressive, exploratory and active, but less neophilic, than subordinate individuals.

Methods

Study sites and catching procedures

This study was part of a broader project examining the potential effects of urbanization on the behaviour of birds, and therefore the field sites included different types of habitat that is treated here as a potential confounding variable. Our 16 study sites were located within the vicinity of the cities of Ottawa (ON) and Gatineau (QC), and were distributed over four habitat types along an urbanization gradient: forest (N = 5), rural park (N = 4), urban park (N = 4) and city (N = 3). Forest sites were situated in the Gatineau Park, a large protected forest area of 361 km^2, and were at least 2 km away from any house. Rural parks were natural forest patches located at least 15 km from Ottawa city centre, with the nearest house at least 200 m from our feeding platform (see below). Urban parks were situated within the city of Ottawa, less than 200 m from houses. Finally, city sites were located in the backyards of homes within the city, representing the maximum urban criterion. Forest and city sites were studied during the year 2013-2014, and rural and urban parks during the year 2014-2015. All sites were separated from each other by a distance of at least 2 km, to prevent any overlap between flocks' homes ranges (about 10 to 20 hectares; reviewed in Smith 1991). We defined a group based on the interactions observed at one feeding location per site, and site is here equivalent to group.

Birds were caught using a mist-net from November 3 to December 6, 2013 and from September 26 to December 9, 2014. They were fitted with a unique metal leg-ring, a colour ring and a unique passive integrated transponder (PIT tag). We recorded body mass (g), as well as wing, tail and tarsus lengths (mm). Body condition (Jakob et al.,

1996) was calculated for each bird by extracting the residuals from a regression of body mass against wing length (measure of body size) and the time of day birds were caught (e.g. Cole et al., 2011; Cole and Quinn, 2012) to take into account the well-known daily cycle of body mass in wintering passerines (Blem, 1976; Lehikoinen, 1987). Birds were aged as adult or juvenile using shape and colour of rectrices (Meigs et al., 1983; Pyle, 1997). Although black-capped chickadees are not strongly dimorphic (Pyle, 1997), a good proportion of individuals (e.g. up to 94%; Desrochers et al., 1988) can be successfully sexed with a discriminant function using the following biometrics: body mass, wing and tail lengths (Desrochers et al., 1988; Desrochers, 1989; Mennill, pers. comm.; see also chapter 3 of this thesis), which is what we used here.

Personality assays

We measured four personality traits in the field: aggressiveness in hand, exploration of a new environment, activity and object neophilia. Aggressiveness in hand was scored during banding and measurement, and the other traits were recorded immediately after using an open-field test modified from Kluen et al. (2012). Each bird was tested individually in a standard commercial bird cage (40 cm x 60 cm x 40 cm) which had three perches positioned at the bottom, middle and uppermost levels (Figure 2.2). Birds were introduced to the cage through a front door and were released at the bottom left of the cage. The open-field assay was videotaped for subsequent analyses, with no observer around the cage during the test. The assay lasted 14 minutes and was divided in three phases, respectively measuring exploration (first 10 minutes), activity (2 minutes), and neophilia (2 minutes).

Repeatability of each personality trait in our study population has been calculated in related work. Repeatability is defined as the proportion of behavioural variation that is accounted for by differences between individuals (Bell et al., 2009). We calculated adjusted repeatability (i.e. repeatability controlling for confounding effects as random or fixed effects; Nakagawa and Schielzeth, 2010) of the traits using linear mixed-effects models (LMM; using R package 'lme4') with the personality measure as the response variable, individual identity and group as random intercepts, and Julian date, time, method of capture (i.e. net or trap), observer (if applicable) and year (if applicable) as fixed factors. We estimated variance components from the LMM with restricted maximum likelihood (REML) and we calculated repeatability estimates (*R*) following Nakagawa and Schielzeth (2010). Statistical significance of the repeatability estimates was tested by likelihood ratio testing (LRT) using a model with and without the random intercept 'individual identity' (see Bolker et al., 2009; Nakagawa and Schielzeth, 2010): aggressiveness in hand (LRT: $\chi^2 = 3.54$, N = 50 birds measured twice, three or four times; $R = 0.24$, $P = 0.060$), exploration behaviour (LRT: $\chi^2 = 6.60$, N = 20 birds measured twice; $R = 0.53$, $P = 0.010$; Jones, pers. comm.), activity (LRT: $\chi^2 = 2.61$, N = 20 birds measured twice; $R = 0.32$, $P = 0.106$; Jones, pers. comm.), and neophilia (LRT: $\chi^2 = 3.66$, N = 20 birds measured twice; $R = 0.40$, $P = 0.056$; Jones, pers. comm.). These *P*-values from the χ_1^2 distribution are conservative, because variances components are constrained to be positive and are thus on the 'boundary of the parameter space' (Self and Liang, 1987; see also Bolker et al., 2009; Zuur et al., 2009). By adjusting the *P*-values for the test by halving them (Self and Liang, 1987; Bolker et al., 2009; Zuur et al., 2009; Bates, 2010), the values of three out of four traits would be smaller than the 0.5 threshold (aggressiveness, P = 0.030; exploration, P = 0.005; and neophilia, P = 0.028) and one would be near the traditional threshold for significance (activity, P = 0.053). Coupled with the finding that our repeatability estimates (R = 0.24-0.53) are in the range of those reported for similar behaviours in other species (reviewed in Bell et al., 2009), we are confident that our measures reflect consistent individual behavioural differences.

Aggressiveness in hand

We scored each individual for its aggressiveness during banding and measurement (Overington et al., 2011; Brommer and Kluen, 2012; see also Réale et al., 2000 for docility in bighorn sheep *Ovis canadensis*). According to the criteria from Overington and collaborators (2011), the score ranged from a minimum of 0 to a maximum of 5. We gave a score of 0 for a bird that did not move at all during measurements, 1 for a bird that moved but did not resist handling, 2 for a moderately agitated individual that resisted in hand, 3 for an agitated bird that tried to escape and that used beak or claws on the bander, 4 for a very agitated individual that used claws and beak, and 5 for a very aggressive bird that resisted and tried to escape, using both claws and beak (e.g. pecking and pinching bander's fingers repeatedly) (Overington et al., 2011).

Exploration behaviour

During the first phase of the open-field assay, considered to be the "novel environment test" (Verbeek et al., 1994), we recorded the time needed to visit the four corners of the cage (in seconds) (see Figure 2.2). We considered this measure to be analogous to the classical test in an observation room using the time required to visit a certain number of artificial trees (Verbeek et al., 1994; Drent et al., 2003). The novel environment exploration period was fixed at 10 minutes (Verbeek et al., 1994; Drent et al., 2003; Kurvers et al., 2009; Kozlovsky et al., 2014). Birds that did not visit all four corners within the maximum duration of 10 minutes were given a maximum latency of 600 seconds (i.e. 10 minutes; Verbeek et al., 1994).

Activity

After the first 10 minutes, we considered that birds were habituated to the cage (Kluen et al., 2012; Kluen and Brommer, 2013; see also Verbeek et al., 1994; Drent et al., 2003; Kurvers et al., 2009; Kozlovsky et al., 2014 for an exploration period of up to 10 minutes). With the environment no longer considered as "novel", we then recorded the birds' activity level for 2 minutes. We used the number of movements through the cage, by counting hops or short flights, as an estimate of overall activity level (Overington et al., 2011; Bókony et al., 2012; Kluen et al., 2012). This behaviour was scored using the software JWatcher Video version 1.0 (see Blumstein and Daniel, 2007).

Neophilia

We quantified neophilia as the latency to approach a novel object in a familiar environment (Mettke-Hofmann et al., 2002; Greenberg, 2003; Miranda et al., 2013). During the third phase of the open-field assay, we introduced a novel object (a small pink box) and hooked it to the roof of the cage (Figure 2.2). We chose a pink-coloured object, following Kluen et al., 2012 (see also Verbeek et al., 1994; Fox et al., 2009; Herborn et al., 2010), because this colour is not often encountered in nature and is thus not likely to have been previously associated with any stimulus. We then recorded the latency of an individual to approach within one body-length of the object (in seconds). Whenever a bird did not approach the object, its latency to approach was set to the duration of the trial (Miranda et al., 2013), namely 120 seconds (i.e. 2 minutes). Following Mettke-Hofmann et al. (2002) and Miranda et al. (2013), we assumed that latency to approach was a measure of neophilia, although a certain influence of neophobia could not be completely excluded.

Dominance

To assess dominance hierarchies, we recorded dyadic interactions between banded birds at feeding platforms (30 x 30 cm) (e.g. Ratcliffe et al., 2007), from January 9 to March 26, 2014 and from February 9 to March 24, 2015. These platforms were installed during the banding period in the fall, to familiarize birds with them. Platforms were baited with sunflower seeds and recorded with a camera to videorecord dominance interactions. An individual was considered the winner of an interaction when it: (i) supplanted or chased an opponent, (ii) resisted an attack by an opponent, (iii) elicited a submissive posture in an opponent, or (iv) fed while an opponent waited to take a seed (Ficken et al., 1990; Otter et al., 1998; Ratcliffe et al., 2007).

To construct hierarchies with the recorded interactions, we calculated a David's score for each individual of a group (David, 1987; Gammell et al., 2003). Similarly to many ranking methods, this score is based on the paired comparisons paradigm (David, 1987). An important advantage of the David's score compared to other dominance ranking methods is that it takes into account repeated interactions between group members and relative strengths of opponents (Gammell et al., 2003). Moreover, it will not be disproportionally affected by minor deviations from the main dominance direction within dyads (Gammell et al., 2003). We calculated a David's score for every individual in our groups that interacted with at least two banded conspecifics (Dingemanse and de Goede, 2004; Cole and Quinn, 2012), regardless of their sex (i.e. male, female or unknown).

To calculate the David's score, we used the procedure from Gammell et al. (2003) with correction from de Vries (1998, 2006). The first step was to calculate the dyadic proportions of wins (P_{ij}) by individual i during its interactions with another individual j, which is the number of times that i defeats j (α_{ij}) divided by the total number of interactions between i and j (n_{ij}); thus $P_{ij} = \alpha_{ij}/n_{ij}$. The proportion of losses by i in interactions with j is $P_{ji} = 1 - P_{ij}$. However, using this proportion of wins P_{ij} may induce a problem owing to the possibility that some individuals of a group may interact preferentially with, or actively avoid, other individuals. This situation could lead to variation in interaction frequency between dyads and break the David's score assumption that every dyadic interaction is independent of every other dyadic interaction (de Vries, 1998; Gammell et al., 2003). To deal with this possibility, we used the dyadic dominance index (D_{ij}) in our calculation instead of observed P_{ij}, correcting for the chance occurrence of an outcome (de Vries, 1998, 2006). This dyadic dominance index D_{ij} has been found to be a better estimator of the win probability (de Vries, 2006). It is defined as $D_{ij} = P_{ij} - \{(P_{ij} - 0.5) \text{ x Prob}[P_{ij}]\}$, where Prob[$P_{ij}$] is the probability that the observed proportion will occur by chance and equals to: $1 / (n_{ij} + 1)$ (de Vries, 2006). The David's score for each member i of a group was then calculated with the formula:

$\mathrm{DS} = w + w_2 - l - l_2$,

where $w = \sum D_{ij}$, $w_2 = \sum w$ (weighted by the appropriate D_{ij} values of those individuals with which i interacted), $l = \sum P_{ji}$ and $l_2 = \sum l$ (weighted by the appropriate D_{ji} values of those individuals with which i interacted). We did not proceed with normalization of the David's score as proposed by de Vries (2006) because we had multiple flocks with different group size (N ranging from 3 to 12; mean ± s.e. = 6.9 ± 0.8). With normalization, some dominants and subordinates from flocks of different group sizes were obtaining equivalent normalized scores (i.e. equivalent scores for dominants of smaller groups and subordinates of bigger groups). The adjusted David's score, hereafter "dominance score", was calculated using the R package Steepness 2.2 (Leiva and de Vries, 2011). To assess the robustness of our findings, we repeated all analyses using individual ranks weighted by flock size (i.e. individual rank / flock size; rank assigned following the ordered linear hierarchy) as an alternative dominance measure (Lewden et al., 2012).

The degree of linearity of dominance hierarchies often has been measured using Landau's *h* (Landau, 1951) and de Vries's corrected index *h'* (de Vries, 1995). However, a major limitation of these linearity indices is that they become biased when some pairs of individuals do not interact or when group size varies (Klass and Cords, 2011; Shizuka and McDonald, 2012). The presence of unknown dyadic relationships is a common problem in empirical studies, especially when studying natural social groups of animals in the wild. In this study, we could not calculate the Landau's linearity index because unknown dyadic relationships were present and group size varied between flocks. A potential explanation for the absence of interactions between some pairs of individuals is that a dominance-subordination relationship was already established between them, and thus subordinates would keep a safe distance from the dominant to prevent agonistic outcomes (de Vries et al., 2006). This situation is likely to have occurred in our study, because we observed birds waiting for others to leave before approaching the feeding platform (i.e. 'avoiding at a distance'; de Vries et al., 2006). Unfortunately, we could not include these behaviours in our analyses because they were not recorded by videos of the feeding platforms. Therefore, we carried out quantitative analyses on the two main criteria characterizing linear dominance hierarchies: (1) asymmetry of the relationships between all pairs of individuals, and (2) transitivity of dominance relationships (Chase, 1980; Appleby, 1983; Shizuka and McDonald, 2012). First, to quantify the degree of asymmetry of interactions within dyads and how consistently one individual won against another individual, we calculated the 'directional consistency index' (DCI; van Hooff and Wensing, 1987). This index has been used in studies on a variety of species to quantify the asymmetry of wins within pairwise relationships (e.g. Côté, 2000; Vervaecke et al., 2000, 2007; Chiarati et al., 2010). The DCI is measured by dividing the total number of interactions in the most frequent direction (*H*) minus the number of interactions in the less frequent direction (*L*) by the total number of interactions in the group: DC = (H – L)/(H + L). It ranges from 0 (equal exchange) to 1 (completely unidirectional). Interactions by 'tied' dyads (see below) were not included in DCI calculation because there is by definition no 'most frequent direction' in these cases. As another descriptive measure, we counted the number of dyads expressing different types of relationships: 'one-way' (wins only for one individual), 'two-way' (interactions at least once in each direction but more wins for one individual) and 'tied' (i.e. mutual; same number of wins for both dyad members) (Vervaecke et al., 2000, 2007; Chiarati et al., 2010). Secondly, we quantified the transitivity of dominance relations among triads (i.e. sets of three individuals that all interacted with each other). We calculated the proportion of transitive triads (Figure 2.1) relative to all triads (P_t) and triangle transitivity metric (t_{tri}) using the methodology provided by Shizuka and McDonald (2012, 2014). This measure of hierarchy structure is equivalent to linearity when relationships among all pairs of individuals are known but does not become biased when dyads do not interact (Shizuka and McDonald, 2012).

Statistical analyses

We first examined the predictive value of known determinants of dominance (age, sex, body condition, body size; Smith 1991; Ratcliffe et al., 2007) in a linear mixed model (LMM) including a random intercept for group and either David's score or weighted ranks as the response variable. We then investigated the presence of correlations between pairs of personality traits using pairwise correlations with Bonferroni correction for multiple testing (Rice, 1989). Because some birds could not be sexed (29%) or aged (9%), including these variables when examining the relationship between dominance and personality traits would have caused the loss of a third of the data points. We therefore decided to first investigate the effect of potential confounding variables (sex, age, body condition, body size, date, time and habitat) on each personality trait, and to include these variables in the dominance vs. personality analyses only if significant. For this analysis we used a LMM with each personality trait as the response variable, group as a random intercept, and the potential confounding variables as fixed factors. For the analyses of dominance vs. personality, we carried out a LMM with dominance score or weighted rank as the response variable, group as a random intercept, and the following fixed factors: one of the personality traits and significant confounds among sex, age, body condition, body size, date, time, and habitat. The term 'bander' (i.e. observer) was forced in the model with aggressiveness in hand, because inter-observer reliability could not be determined. The term 'observer' was not included in models with the behavioural traits exploration, activity and neophilia, because all correlation coefficients (r), expressing inter-observer reliability (Martin and Bateson, 2007), were more than 0.95. We fitted linear mixed models using the lmer function in the lme4 package. All analyses were conducted in R version 3.2.1 (R Core Team, 2014).

Ethical note

This study was conducted under scientific and banding permits from Environment Canada (SC-42) - Canadian Wildlife Service (10854), and the protocol was subject to ethical review by the Animal Care committee of the University of Ottawa (BL-274).

Results

Dominance

Dominance hierarchies in our black-capped chickadees social groups fulfilled the criterion of linearity, with large asymmetries in dyadic relationships (i.e. interactions were directionally consistent within dyads) and transitivity of triadic relationships. The average DCI was 0.94 ± 0.016. Out of 256 known dyads, 244 were asymmetric with 216 (84.4%) exhibiting 'one-way relationships' and 28 (10.9%) showing 'two-way relationships', whereas 12 (4.7%) did not show a clear dominance-subordination relation. All triads were transitive ($P_t = T_{\mathrm{tri}} = 1$) in seven groups, whereas six other groups were significantly more transitive than expected by null models (mean $P_t = 0.94$, mean $t_{tri} = 0.77$, $P < 0.05$); data were insufficient to calculate triangle transitivity in three flocks.

A dominance score was calculated for 101 individuals from 16 groups. Sex had a strong significant influence on dominance (David's score: LMM $F_{1,61} = 36.28$, $P < 0.0001$; weighted ranks: LMM $F_{1,61} = 55.95$, $P < 0.0001$), with males dominating females in more than 95% of the cases. Within males, there was a marginally non-significant tendency for larger individuals to have higher dominance scores (LMM $F_{1,36} = 4.08$, $P = 0.051$), but this trend was not visible using weighted ranks (LMM $F_{1,36} = 2.14$, $P = 0.152$). Dominance was not significantly affected by age (David's score: LMM $F_{1,61} = 0.672$, $P = 0.416$; weighted ranks: LMM $F_{1,61} = 1.49$, $P = 0.227$) or body condition (David's score: LMM $F_{1,61} = 0.668$, $P = 0.417$; weighted ranks: LMM $F_{1,61} = 0.003$, $P = 0.955$).

Characterization of personality traits

There was no evidence for a behavioural syndrome in our data, with no significant correlation between any of the personality traits (Table 2.1). Moreover, none of the personality traits were significantly associated with sex, age, body condition, wing length, date, time, or habitat (Table 2.2).

Dominance and personality traits

Our results showed no significant relationship between dominance and any of the personality traits: aggressiveness in hand (David's score: LMM $F_{1,94} = 0.543$, $P = 0.463$; Figure 2.3a; weighted ranks: LMM $F_{1,94} = 0.272$, $P = 0.603$), exploration (David's score: LMM $F_{1,76} = 0.001$, $P = 0.971$; Figure 2.3b; weighted ranks: LMM $F_{1,76} = 0.998$, $P =$

0.321), activity (David's score: LMM $F_{1,80} = 0.164$, $P = 0.686$; Figure 2.3c; weighted ranks: LMM $F_{1,80} = 0.208$, $P = 0.650$), and neophilia (David's score: LMM $F_{1,79} = 0.801$, $P = 0.374$; Figure 2.3d; weighted ranks: LMM $F_{1,79} = 1.52$, $P = 0.221$). The forced term 'bander', for aggressiveness in hand, was not significant (*P*-values > 0.5).

Discussion

The main aim of this study was to investigate the relationship between behavioural traits and dominance measured in wild flocks of black-capped chickadees, a bird species showing strictly linear dominance hierarchies. We indeed found that hierarchies in our study groups were linear, with transitive and asymmetric dominance relationships. However, our results did not reveal any significant correlations between pairs of personality traits, or between personality and dominance measures.

Dominance relationships within our groups of black-capped chickadees were highly transitive and asymmetrical (i.e. directionally consistent), and our flocks were thus characterized by the same linearity of hierarchies repeatedly demonstrated in this species (Hartzler, 1970; Glase, 1973; Smith, 1976; Desrochers et al., 1988). Our results showed no significant effect of age, body condition or body size on dominance measures. However, there was a significant effect of sex on dominance, with males dominating over females. This finding is also consistent with those of other studies on black-capped chickadees and Parids in general (Odum, 1942; Smith 1991; Ratcliffe et al., 2007).

We found no significant correlations between pairs of behavioural traits, and thus no evidence of a behavioural syndrome in our data. The extent to which personality traits may form or not form behavioural syndromes is still unclear (see Réale et al., 2007). In birds, for example, some studies reported evidence for syndromes (in house sparrows *Passer domesticus*: Evans et al., 2010; Bókony et al., 2012; in zebra finches: David et al., 2011) whereas others did not (in parrot species: Mettke-Hofmann et al., 2002; in barnacle geese *Branta leucopsis*: Kurvers et al., 2009). Within close relatives of the black-capped chickadee, the same inconsistencies have been reported. While studies on great tits showed positive correlations between exploratory behaviour and aggressiveness (Verbeek et al., 1996) or boldness (van Oers et al., 2004), other studies on mountain chickadees *Poecile gambeli* and blue tits *Cyanistes caeruleus* found no correlation between exploratory tendency and object neophobia (Fox et al., 2009 and Herborn et al., 2010, respectively). Together with discrepancies in trait correlations between populations of the same species (e.g. in three-spined sticklebacks *Gasterosteus aculeatus*: Bell, 2005; Bell and Sih, 2007; Dingemanse et al., 2007), these results collectively suggest that behavioural syndromes may be population- or context-dependent, for instance owing to different selective factors.

Our results showed no significant relationship between dominance in natural groups of black-capped chickadees and personality traits, namely aggressiveness in hand, exploration of a new environment, activity and object neophilia. Despite our use of two different measures of dominance (David's score and weighted ranks) to reduce the probability that the results would be influenced by our choice of measure, we cannot rule out the possibility that these dominance measures contain some uncertainty or bias. Some studies have reported that personality traits can predict social dominance, although most such studies used status derived from contests between dyads in captivity (Verbeek et al., 1996; Fox et al., 2009; An et al., 2011; Dahlbom et al 2011; Riebli et al., 2011; Favati et al., 2014). However, it appears that differences in personality and attributes in general do not have the same ability to predict the outcomes of dominance encounters for animals within social groups. For instance in great tits, opposite relationships between exploratory behaviour and dominance were found in different social contexts, namely staged pairwise confrontations *versus* groups (Verbeek et al., 1996, 1999). Similarly, Riebli and collaborators (2011, 2012) found different trends between aggressive behavioural types of cichlid fish and the likelihood of obtaining a dominant position when tested in staged dyadic encounters or in group settings. Moreover, Chase and collaborators (2003) reported that several aspects of dominance relationships were different depending on whether dyads were observed in isolation or within a group. The stability of relationships over time, the replication of relationships in successive meetings, and the extent of the loser effect (i.e. individuals losing earlier contests having increased probability of losing later ones; Chase et al., 1994; Hsu and Wolf, 1999) found in isolated pairs either disappeared or were significantly reduced when examining pairs within social contexts (Chase et al., 2003). This observation may explain why, by looking at individuals within their social groups rather than only dyads, we did not find an influence of personality traits on dominance, as has been reported in studies based on staged pairwise encounters.

Previous experiments carried out in social settings also have yielded conflicting results. For the most part, no significant association was found between dominance and various behavioural traits: docility and boldness in bighorn sheep (Réale et al., 2000); neophobia in starlings *Sturnus vulgaris* (Boogert et al., 2006); exploration, activity and novel object response in barnacle geese (Kurvers et al., 2009); aggressive propensity in cichlid fish (Riebli et al., 2012); and exploration, neophobia, fear and sociability in common waxbill *Estrilda astrild* (Funghi et al., 2015). A few studies found a significant correlation between dominance and personality: activity, neophobia, exploratory tendencies and risk-taking behaviour in zebra finches (David et al., 2011), and exploratory behaviour in great tits (Verbeek et al., 1999; Dingemanse and de Goede, 2004; Cole and Quinn, 2012). It is interesting that these last three studies used the great tit, a close relative of the black-capped chickadee, because while both species belong to the Paridae family, they express quite different social organizations. Whereas black-capped chickadees live in stable tight social units and form highly linear dominance hierarchies (Hartzler, 1970; Ekman, 1989; Smith, 1976, 1991; Ratcliffe et al., 2007; also the present study), great tits live in a more loosely organized system of fission-fusion flocks (Ekman, 1989; Aplin et al., 2012). Among other characteristics, these flocks express unstable membership and site-dependent social dominance (Ekman, 1989). Similarly, the social structure of zebra finches studied by David et al. (2011) is not likely to be linear; this species is highly gregarious and lives in large congregations in the wild, during both breeding and non-breeding periods (Zann, 1996). It thus appears that the type of social organization, whether "loose" or "strictly linear" hierarchies, could influence the link between behavioural traits and dominance. Accordingly, findings from a study on mountain chickadees (Fox et al., 2009; however using dyadic contests), a species also characterized by linear hierarchies (Ekman, 1989), are similar to our results on black-capped chickadees. Although the social status derived from pairwise encounters was significantly associated with exploration score, this status was not correlated with any of the other personality measures: exploration time, activity in the novel room and novel object approach (Fox et al., 2009), respectively similar to our measures of exploration, activity and object neophilia.

Overall, there is increasing evidence that differences in intrinsic individual characteristics (physical and behavioural) are not the only force generating linear hierarchies, and that social dynamics may be crucial for their formation (e.g. Chase et al., 2002; Correa et al., 2013). Indeed, theoretical and modelling work found that individual attributes were not sufficient to account for hierarchy linearity observed in groups of animals (Landau, 1951; Chase, 1974, 1980; Beacham, 2003). Furthermore, Verbeek et al. (1999) showed in a study on the formation of great tits dominance hierarchies that stable organization resulted from a gradual process and was only established after a first dynamic phase of several days characterized by a peak in the frequency of interactions between individuals as well as many dominance shifts. Formation of hierarchies was thus not instantaneous, based only on individuals' attributes, but also required social dynamics within the flocks. Chase and collaborators (2002) similarly found in cichlid fish that, although variation in attributes played a significant role in an individual's position within a hierarchy, social interaction was necessary to generate high proportions of groups with linear hierarchies. It thus appears that 'prior attributes' and 'social dynamics' are not mutually exclusive and may both contribute simultaneously to the establishment of linear hierarchies (Chase et al., 2002; Valderrabano-Ibarra et al 2007; David et al., 2011).

In a new process-based approach, Chase and Seitz (2011) proposed that dominance hierarchies may also be self-structuring, and that linear structures could emerge from different behavioural processes or sequences of interaction. For instance, the different types of sequences for the formation of the first two dominance relationships within a triad (e.g. double dominance or double subordination) have different implications for the formation of linear hierarchies depending on their probability of leading to transitive relationships (Chase and Seitz, 2011, see also Shizuka and McDonald, 2015). However, individual-based and process-based approaches (sensu Chase and Seitz, 2011) are not mutually exclusive when studying dominance hierarchies. Indeed, Dey and Quinn (2014) reported that pukeko (*Porphyrio melanotus melanotus*) dominance networks were influenced both by prior attributes (sex and status ornamental signal) and self-organizational processes (structural dependence between ties, with ties representing dominance interactions). New approaches using network methods and behavioural processes (Chase and Seitz, 2011; Dey and Quinn, 2014) are an exciting avenue for future research.

In summary, the current study is to our knowledge the first to address the potential relationship between social dominance and personality in wild avian groups exhibiting a linear dominance hierarchy. We found no significant relationships between dominance and four personality traits, suggesting that personality does not contribute significantly to the establishment of black-capped chickadee hierarchies in the wild. This finding adds to the increasing body of evidence showing that individual differences in attributes are not sufficient for explaining the structure of linear dominance hierarchies. We agree with the concern expressed by Chase et al. (2003) more than a decade ago, on the relevance of experiments using isolated dyads to understand dominance behaviour in groups of animals. Therefore, future studies should examine the effect of personality on the structure of dominance hierarchies within groups of freely-interacting animals, with a special call for studies on natural groups in the wild. Finally, it may be interesting to determine whether different patterns of association between dominance and personality arise under diverse types of social organization.

Table 2.1 – Correlations between pairs of personality traits.

Behaviours pairs	Pearson *r*	*DF*	*P*
Exploration – Neophilia	0.05	76	0.646
Exploration – Activity	–0.19	75	0.090
Exploration – Aggressiveness in hand	–0.02	76	0.834
Neophilia – Activity	–0.06	78	0.596
Neophilia – Aggressiveness in hand	–0.20	79	0.068
Activity – Aggressiveness in hand	–0.02	80	0.865

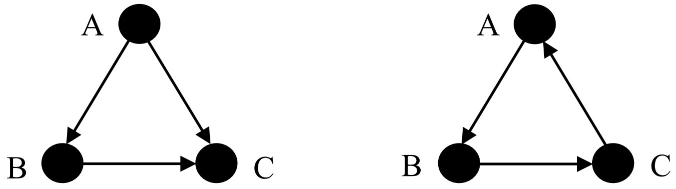
P-value of each correlation before Bonferroni correction is presented.

Table 2.2 – Predictors of (a) aggressiveness in hand; (b) exploration; (c) activity; and (d) neophilia from four linear mixed models including random intercept ‘group’.

Fixed terms	Estimate	± SE	*T*	*DF*	*P*
(a) Aggressiveness in hand					
Sex	0.085	± 0.472	0.180	49.28	0.858
Age	0.091	± 0.276	0.330	43.38	0.743
Body condition	–0.025	± 0.218	–0.114	46.44	0.910
Wing length	0.044	± 0.096	0.457	49.19	0.650
Date	0.003	± 0.008	0.375	50.35	0.709
Time	0.083	± 0.109	0.764	51.96	0.448
Habitat					
Forest	1.768	± 1.183	1.494	11.55	0.162
Rural Park	2.466	± 1.156	2.133	11.40	0.055
Urban Park	1.814	± 1.253	1.447	14.80	0.169
(b) Exploration					
Sex	39.848	± 98.206	0.406	42.52	0.687
Age	5.140	± 60.187	0.085	42.22	0.932
Body condition	16.225	± 45.372	0.358	42.79	0.722
Wing length	–7.537	± 19.638	–0.384	42.46	0.703
Date	2.408	± 1.379	1.746	9.46	0.113
Time	16.334	± 20.659	0.791	40.61	0.434
Habitat					
Rural Park	36.758	± 85.027	0.432	6.32	0.680
Urban Park	115.88	± 108.04	1.073	18.47	0.297
(c) Activity					
Sex	5.558	± 8.354	0.665	45	0.509
Age	–6.145	± 4.915	–1.250	45	0.218
Body condition	2.752	± 3.896	0.706	45	0.484
Wing length	–1.335	± 1.683	–0.793	45	0.432
Date	–0.139	± 0.111	–1.253	45	0.217
Time	1.373	± 1.711	0.803	45	0.426
Habitat					
Rural Park	–9.859	± 6.809	–1.448	45	0.155
Urban Park	–10.025	± 8.568	–1.170	45	0.248

(d) Neophilia					
Sex	0.545	± 18.954	0.029	44	0.977
Age	14.021	± 11.718	1.197	44	0.238
Body condition	–3.150	± 8.736	–0.361	44	0.720
Wing length	–2.289	± 3.816	–0.600	44	0.552
Date	0.145	± 0.260	0.556	44	0.581
Time	0.557	± 4.006	0.139	44	0.890
Habitat					
Rural Park	–1.740	± 15.866	–0.110	44	0.913
Urban Park	2.600	± 20.519	0.127	44	0.900

Reference categories with estimates set to 0 are sex: female; age: adult; habitat: (a) city and (b)-(d) forest.



Transitive

Cyclic

Figure 2.1 – Configuration of transitive and cyclic (intransitive) triads among individuals A, B and C.

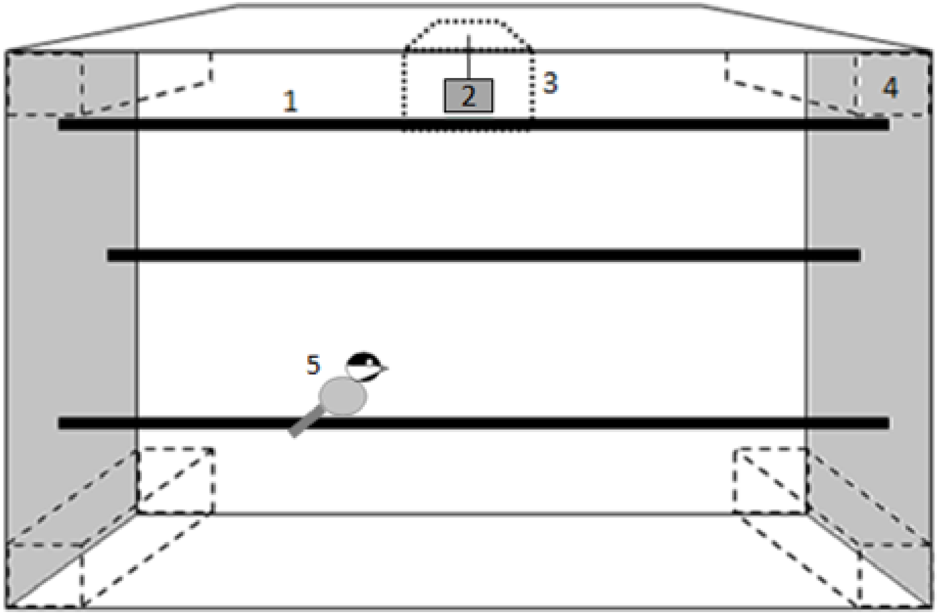


Figure 2.2 – Schematic presentation of the open-field test used for personality assays, modified from Kluen et al (2012). The numbers in the cage indicate: (1) perch, (2) novel object (pink box), (3) zone for approaches to the novel object, (4) corners for exploration measurement and (5) black-capped chickadee.

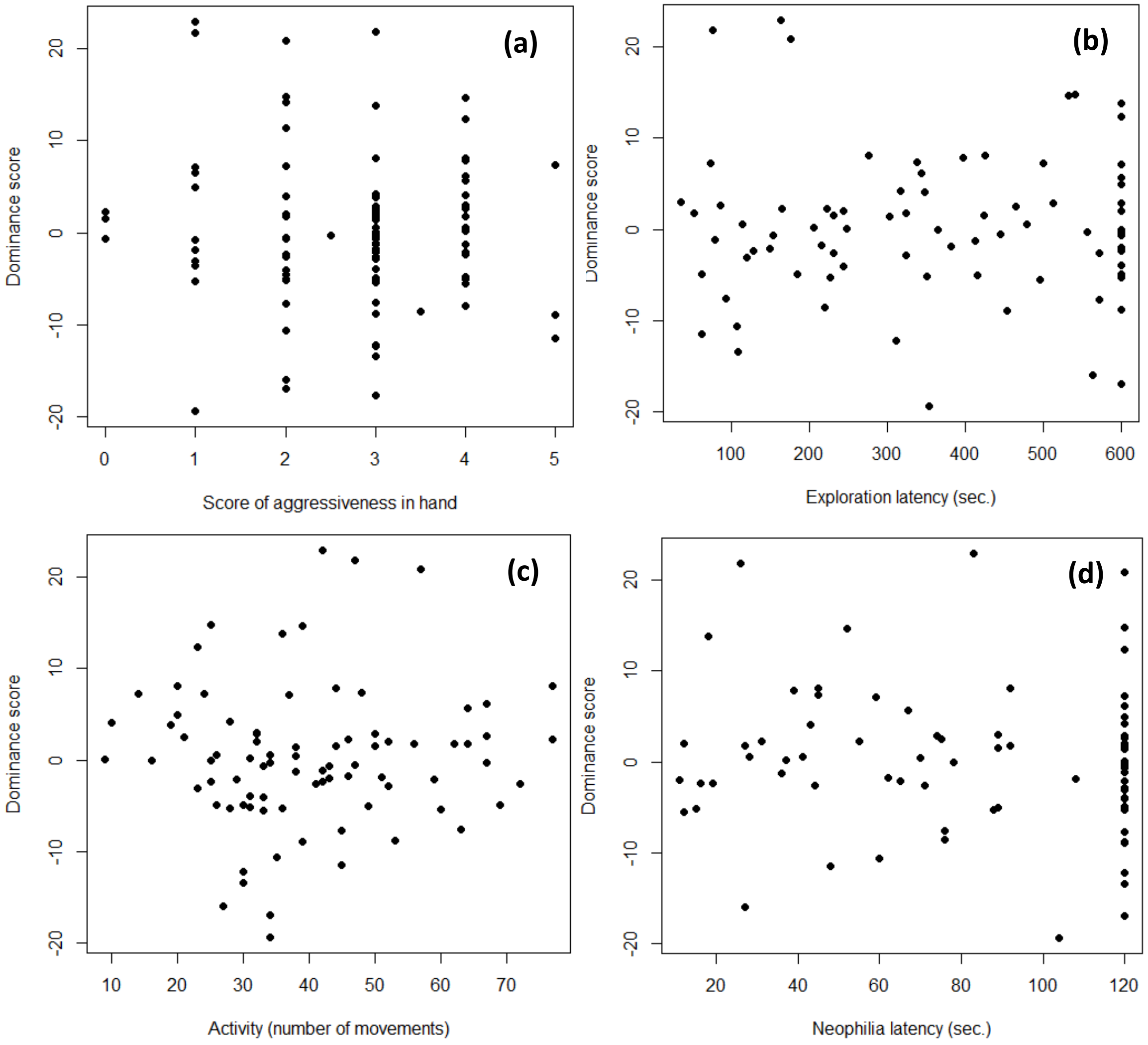


Figure 2.3 – Dominance score (i.e. David's score) in relation to (a) score of aggressiveness in hand, (b) exploration latency (seconds), (c) activity (number of movements), and (d) neophilia latency (seconds). See text for additional information.

CHAPTER 3

REVISITING THE ‘NECESSITY DRIVES INNOVATION’ HYPOTHESIS: PROBLEM-SOLVING EFFICIENCY IN THE BLACK-CAPPED CHICKADEE (*POECILE ATRICAPILLUS*)

Abstract

Innovation, the invention of new behavioural patterns or the modification of an existing behaviour in a novel context, is an important aspect of behavioural flexibility in animals. The ‘necessity drives innovation’ hypothesis predicts a negative relationship between competitive ability and innovativeness, because monopolization of limited resources by good competitors should force poor competitors to search for alternative solutions. In the current study, we presented individual black-capped chickadees (*Poecile atricapillus*) with a novel lever-pulling task in captivity and recorded both total latency to solve this problem (first contact to solution) and problem-solving efficiency (latency to solve excluding interruptions in the solving process). The two problem-solving latencies were not significantly correlated with each other, nor with sex, age, or body condition. Total latency to solve the problem was not significantly related to dominance score, whereas dominant individuals were significantly more efficient problem-solvers than subordinates (i.e. shorter problem-solving latency excluding interruptions). We suggest that different traits may drive the likelihood vs. efficiency of solving a novel problem, highlighting the importance of carefully choosing a metric that is relevant to the process studied. Necessity could increase the likelihood of solving new problems, whereas cognitive capacity could increase problem-solving efficiency. Moreover, if problem-solving efficiency and social dominance are both influenced by cognitive skills, this may explain the observed positive relationship between these two traits. Overall, our results do not support the ‘necessity drives innovation’ hypothesis.

Introduction

Animal innovation can be defined as the invention of new behaviour patterns or the modification of an existing behaviour in a novel context (Kummer and Goodall, 1985; Lefebvre et al., 1997; Reader and Laland, 2003). Well-known examples of animal innovation often occurred in the context of extraction, preparation and processing of food (Reader and Laland, 2003; Overington et al., 2009). These examples include washing of potatoes by Japanese macaques (*Macaca fuscata*: Kawai, 1965), opening of milk bottles by British titmice (*Parus* spp.: Fisher and Hinde, 1949; Hinde and Fisher, 1951), lobtail feeding in humpback whales (*Megaptera novaeangliae*; Weinrich et al., 1992), drinking from tails in ring-tailed lemurs (*Lemur catta*; Hosey et al., 1997), and predation of great tits (*Parus major*) on hibernating pipistrelle bats (*Pipistrellus pipistrellus*: Estók et al., 2010). Innovation may have key implications for ecology and evolution; for instance, innovative bird taxa display higher species richness and better ability to establish themselves in novel environments (Nicolakakis et al., 2003; Lefebvre et al. 2004; Sol et al., 2005a,b).

Because innovations are rare, a commonly-used method to study them is to examine the performance of individuals presented with a novel food-motivated problem (Webster and Lefebvre, 2001; reviewed in Griffin and Guez, 2014). It is generally recognized that individuals differ in their problem-solving performance and propensity to innovate (reviewed by Reader, 2003 and Griffin and Guez, 2014). The initial development of a novel behaviour is thus usually expressed in a few innovators, and this new behaviour may afterwards spread in the population by social transmission (Reader, 2003; Reader and Laland, 2003). Individual differences in innovation propensity are important as they may impact fitness, and have been linked with reproductive success (Keagy et al., 2009; Cole et al., 2012; Cauchard et al., 2013). As reported by Reader (2003), individual characteristics such as age, sex, competitive ability and social rank may influence the likelihood of innovation.

The 'necessity drives innovation' hypothesis states that innovation occurs predominantly when established behaviours are unsuccessful, which drives individuals to search for alternative behaviour patterns (Laland and Reader 1999a; Reader and Laland, 2003). This hypothesis thus predicts that, by monopolizing access to limiting resources, good competitors should force poor competitors to innovate, resulting in a negative relationship between competitive ability and innovativeness (Laland and Reader 1999a,b; Reader and Laland 2003). Therefore, poor competitors, for example subordinates, juveniles, smaller individuals or individuals in poor body condition, should be more likely to innovate and should exhibit higher problem-solving performance than good competitors, e.g. dominants, adults and large individuals (Reader and Laland, 2003). For example, Reader and Laland (2001) found that the incidence of innovation was higher in low-ranking chimpanzees (*Pan troglodytes*), and a study on guppies (*Poecilia reticulata*) reported that females and smaller individuals were more likely to innovate than males and larger individuals (Laland and Reader, 1999a). Similarly, juvenile great and blue tits (*Parus major* and *Cyanistes caeruleus*, respectively) were more likely to solve a foraging problem than adults (Morand-Ferron et al., 2011).

Relationships reported in other studies are not all consistent with the 'necessity drives innovation' hypothesis (Table 3.1). Cole and Quinn (2012) found that although dominant great tits performed poorly in a problem-solving task, which supports this hypothesis, there was no effect of sex even though females in this species are invariably subordinate to males. In their review of work on wild primates, Reader and Laland (2001) also revealed, contrary to expectations, that adults exhibit more innovations than juveniles and that female chimpanzees are not more innovative than males. Research on captive families of callitrichid monkeys (Kendal et al., 2005) reported as well a positive relationship between age and problem-solving success. Other studies reported no effect of social dominance (kea *Nestor notabilis*, Gajdon et al., 2006; spotted hyenas *Crocuta crocuta*, Benson-Amram and Holekamp, 2012) or body condition (great tit, Cole et al., 2011; Carib grackle *Quiscalus lugubris,* Overington et al., 2011; meerkat *Suricata suricatta*, Thornton and Samson, 2012) on the propensity to innovate. Overall, although variation in novel problem-solving is sometimes accounted for by state-dependent factors, such as sex, size or competitive ability (Reader and Laland, 2003), studies to date provide conflicting evidence for the 'necessity drives innovation' hypothesis. Moreover, most of previous studies only compared 'innovators' to 'non-innovators" (Gajdon et al., 2006; Cole et al., 2011; Overington et al., 2011; Benson-Amram and Holekamp, 2012; Cole and Quinn, 2012; Thornton and Samson, 2012), thereby removing fine-scale variation such as difference among innovators in efficiency to solve the novel problem.

In the current study, we presented individual black-capped chickadees (*Poecile atricapillus*) with a novel problem-solving task, and recorded latency to solve this problem. We then examined the relationship between problem-solving performance and sex, age, body condition, as well as dominance score of the individuals. According to the 'necessity drives innovation' hypothesis, we predicted that females, juveniles, individuals in poor condition as well as subordinates should be more efficient problem-solvers than males, adults, individuals in good condition and dominants, respectively.

Methods

Study species

Black-capped chickadees are common small resident Paridae of North America. They live in an alternating social system, forming monogamous, territorial breeding pairs during the spring and summer, and non-breeding flocks in fall and winter (Smith, 1991). Winter flocks are organized into distinct, linear pecking orders, or dominance hierarchies (Smith, 1991; Ratcliffe et al., 2007). Males are dominant over females (Smith, 1991; Ratcliffe et al., 2007), adults tend to dominate over juveniles (Smith, 1991; Ratcliffe et al., 2007), and dominants tend to be leaner than subordinates (Schubert et al., 2007; Ratcliffe et al., 2007). In addition to being a great choice to study dominance (see Chapter 2; Smith, 1991; Ratcliffe et al., 2007), the black-capped chickadee is a good model species to study innovation because Paridae is a highly innovative family (Overington et al., 2009).

Study sites and housing

This study was part of a broader project, and therefore our field sites included two types of habitat, urban and rural. Three urban sites were located in the backyards of homes within the city of Ottawa (ON), and six rural sites were located in Gatineau Park (QC), a protected forest area of 361 km^2, for a total of nine sites. The sites were separated from each other by a distance of at least 2 kilometers to prevent any overlap between flocks' home ranges (which average about 10 to 20 hectares; reviewed in Smith 1991). We defined a group (i.e. flock) based on the interactions observed at one feeding location per site, and site is here equivalent to group.

Birds were caught using a mist-net and fitted with a unique metal leg-ring, a colour ring and a unique passive integrated transponder (PIT tag). From January 16 to March 5, 2014, individuals were kept in captivity for one week for problem-solving tests. They were housed singly in wire cages (40 cm x 60 cm x 40 cm) and were visually, but not acoustically, isolated from each other. Each cage contained three perches, a small rattan nest in which the bird could hide and rest, bowls containing fresh water, unshelled and shelled sunflower seeds, as well as a petri dish with mealworms. Ad libitum food was provided except during the test (45 minutes) and the preceding fasting period (15 minutes). The individuals were kept under a natural light regime (12L:12D) using automated timers, with 30 minutes of gradual transition for dusk and dawn.

At the end of the week in captivity, on the day before release, a blood sample was collected and used for DNA sex identification (Griffiths et al., 1998). Blood samples (up to 60 μL) were obtained by puncturing the left brachial vein with a needle and collecting the blood with heparinized capillary tubes. We used red blood cells to determine sex. Birds were also sexed with a discriminant analysis based on body mass, wing length and tail length (Desrochers et al., 1988; Desrochers, 1989; Mennill, pers. comm.; 60% of the individuals could be sexed this way in the present study). Out of 29 individuals with sex results from both the discriminant function and DNA sexing analyses, 28 (96.6%) were sexed accurately. The remaining individual was only sexed unsuccessfully one out of three times with the discriminant function, and was coded as "unidentified" the other two times. We thus concluded that the discriminant function was sufficiently conservative and can be used to sex birds in our population. Birds were aged as adult or juvenile (hatched-year) based on plumage, more specifically, the shape and colour of rectrices (Meigs et al., 1983; Pyle, 1997). Body condition was calculated for each bird by extracting the residual from a regression of body mass against body size (Jakob et al., 1996). We used wing length as a body size measure (e.g. Cole et al., 2011; Cole and Quinn, 2012; Aplin et al., 2013b), and did not include time of day in the model as all birds were weighed within the same one-hour period. Body condition was measured four days after the problem-solving trial; birds were not weighed on testing days to avoid interference from handling stress. Body condition at capture was missing for three individuals; an additional analysis on this restricted dataset returned qualitatively equivalent results (not shown).

Problem-solving assay

The problem-solving test was carried two days after capture and transfer to captivity. The trial lasted 45 minutes, following a food-deprivation period of 15 minutes. The novel problem-solving task consisted of a lever-pulling device. Lever-pulling is a problem-solving task commonly used to study innovation in passerine birds, such as house sparrows (*Passer domesticus*) (Bókony et al., 2014), blue tits (Morand-Ferron and Quinn, 2011; Morand-Ferron et al., 2011) and great tits (Cole et al., 2011; Morand-Ferron and Quinn, 2011; Morand-Ferron et al., 2011; Cole and Quinn, 2012). The test apparatus consisted of a transparent plastic rectangular box, containing a platform supported by a lever (Figure 3.1). To access the two mealworms placed on the platform, the individual had to pull the lever, causing the platform and mealworms to fall in a feeding dish. A 'free' mealworm was placed in the feeding dish below the container when initiating the trial (Cole et al., 2011; Aplin et al., 2013b) to ensure that all individuals had sufficient motivation (i.e. the individuals that did not eat the ‘free’ mealworm were removed from the analyses).

As the lever-pulling device had not been placed into the cage prior to the test, the birds were not familiar with it. We thus began recording problem-solving latency after the initial physical contact of the bird with the device, thereby controlling for potential differences in motivation and/or neophobia (Overington et al., 2011). The complete latency between first contact with the task and solution is hereafter referred as “total latency to solve”. We also recorded latency to solve excluding interruptions in the solving process (Morand-Ferron et al., 2011). To do so, we summed all times when the bird was within one body length from the task, from the first contact until solution.. This latency to solve excluding interruptions therefore comprises only working bouts instead of the complete duration between first contact with the device and solution. The problem-solving assay was video-recorded for subsequent analysis, with no observer present in the testing room during trials to minimize any external disturbances.

Dominance score

Dominance hierarchies within flocks were assessed by tabulating pairwise interactions between banded birds at feeding platforms (30 x 30 cm) in the field(see Ratcliffe et al., 2007), from January 9 to March 26, 2014. The platforms had been installed in the previous fall during banding to familiarize birds with them. Platforms were baited with sunflower seeds and a camera was left on site to videorecord all observations so as to avoid any potential interference from the presence of an observer. Four types of interactions were noted from videofiles. An individual was considered to be the winner of an interaction when it: (i) supplanted or chased an opponent, (ii) resisted an attack by an opponent, (iii) elicited a submissive posture in an opponent, or (iv) fed while an opponent waited to take a seed (Ficken et al., 1990; Otter et al., 1998; Ratcliffe et al., 2007). Using the recorded interactions, we then calculated a David's score for each individual of a group (David, 1987), using the procedure from Gammell et al. (2003) with corrections from de Vries (1998, 2006) (see Chapter 2 for details). The David's score, hereafter "dominance score", was calculated using the R package Steepness 2.2 (Leiva and de Vries, 2011).

Statistical analyses

As outlined above, the position of an individual in a dominance hierarchy may correlate with other variables including sex, age and body condition (for chickadees, see reviews by Smith, 1991 and Ratcliffe et al., 2007). Therefore, we decided to proceed with two distinct series of linear mixed models. The fixed factors were respectively sex, age and body condition for the first ones, and dominance score for the second set of models. Group was included as a random intercept in all models, and the response variable was either total latency to solve (first contact to solution) or latency to solve excluding interruptions (both in seconds, log-transformed to improve normality). We also needed to control for habitat type (urban and rural) and Julian date of capture for captivity, because these variables may correlate with problem-solving performance (e.g. habitat: Liker and Bókony, 2009; date: Cole et al., 2011). However, owing to unexpected events during the course of the experiment, most urban birds were tested at later dates and relative effects of habitat and date could thus not be teased apart. Because of our small sample size (N = 24), we decided to initially include these two variables in the models as potential confounding variables, and remove them if non-significant. We fitted linear mixed models (LMM) using the lmer function in the lme4 package. All analyses were conducted in R version 3.2.1 (R Core Team, 2014).

Ethical note

The protocol for this study was subject to ethical review by the Animal Care committee of the University of Ottawa (BL-274). This study was conducted under scientific and banding permits from Environment Canada (SC-42) - Canadian Wildlife Service (10854). During captivity, all individuals were closely monitored for any changes in health or behaviour. No more than one week following the date of capture and transfer to captivity, the birds were released at least three hours before sunset at their respective site of capture, where supplemental food was provided by feeders filled with sunflower seeds.

Results

Almost all birds (25/27) ate the ‘free’ mealworm in the dish of the test apparatus. The two individuals that did not eat this mealworm were excluded from analyses because they were likely not motivated by the food reward. Data from another individual were excluded as we discovered a minor injury to one foot at the time of the problem-solving trial. All birds (N = 24) solved the problem successfully within the 45 minutes allocated to the trial, with mean times to solve (± standard deviation): mean total latency to solve = 375.92 sec. ± 236.95, and mean latency to solve excluding interruptions = 21.75 sec. ± 20.44. Mean number of interruptions (± standard deviation) was 2.83 ± 2.04. Total latency to solve the problem and latency to solve excluding interruptions were not significantly correlated (Pearson’s r = -0.099; N = 24; *P* = 0.64; Figure 3.2). Neither problem-solving latency was significantly affected by habitat (total latency: LMM $F_{1,6.29} = 0.069$, $P = 0.80$; latency excluding interruptions: LMM $F_{1,16} = 0.45$, $P = 0.51$) or date (total latency: LMM $F_{1,13.52} = 0.89$, $P = 0.36$; latency excluding interruptions: LMM $F_{1,16} = 1.46$, $P = 0.24$); both procedural variables were consequently removed from the final models. These models showed no significant effect of sex, age or body condition on problem-solving latencies (Table 3.2).

Out of 13 individuals for which we had both problem-solving and dominance data, only one was from the urban habitat. We thus excluded this individual from the analysis, keeping only birds from the forest habitat (N = 12) in the second model. Again, there was no effect of date on either problem-solving latency (total latency: LMM $F_{1,8.76} = 0.97$, $P = 0.35$; latency excluding interruptions: LMM $F_{1,9} = 1.00$, $P = 0.34$) and this variable was thus removed from final models. There was no significant relationship between dominance score and total problem-solving latency (LMM estimate ± SE = 0.00059 ± 0.0096; $F_{1,8.87} = 0.004$, $P = 0.95$; Figure 3.3a). However, we found a significant negative relationship between dominance and problem-solving latency excluding interruptions (LMM estimate ± SE = -0.021 ± 0.0094; $F_{1,10} = 5.24$, $P = 0.045$; Figure 3.3b).

Discussion

The main aim of this study was to revisit the ‘necessity drives innovation’ hypothesis, by examining fine-grained individual differences in novel problem-solving efficiency, rather than success or failure as often used in the literature. In our study, two different measures of problem-solving performance did not correlate significantly with each other, and neither was predicted by sex, age, or body condition. There was no relationship between dominance and total latency to solve the problem, but individuals with higher dominance scores had significantly shorter latencies to solve excluding interruptions (i.e. were more efficient problem-solvers).

Problem-solving performance was not significantly related to sex, age, or body condition. A limitation of our study is small sample size, and for the age factor in particular, the unbalanced number of juveniles (N = 18) vs. adults (N = 4). Some caution is thus needed when interpreting these results. For instance, the small sample size might have prevented us to detect an effect of sex, age, or body condition, on problem-solving performance. Although our results do not support predictions from the ‘necessity drives innovation’ hypothesis, they are not inconsistent with the literature. Indeed, most studies on problem-solving success found no significant relation with body condition (Cole et al., 2011; Overington et al., 2011; Thornton and Samson, 2012), sex (Seibt and Wickler, 2006; Cole et al., 2011; Morand-Ferron et al., 2011; Benson-Amram and Holekamp, 2012), or age (Keagy et al., 2009; Biondi et al., 2010; Morand-Ferron et al., 2011; Benson-Amram and Holekamp, 2012; also reviewed in Griffin and Guez, 2014). Moreover, latency to solve in pigeons *Columba livia* was not significantly associated with sex (Boucahrd et al., 2007), and neither sex nor age significantly influenced the ability of chimpanzees to retrieve food rewards from novel foraging puzzles (Hopper et al., 2014). Together with our results, these findings suggest that neither likelihood nor efficiency of novel problem-solving depend on state factors.

Dominance score was not significantly correlated with total latency to solve, but was significantly negatively related to problem-solving latency excluding interruptions, which represents problem-solving efficiency. Owing to our small sample size, we cannot rule out the possibility that these results may be an artefact of using a potentially non-representative sample. Both results are opposite to the a priori prediction that subordinates, through necessity induced by their low social position, should be better problem-solvers. Taken together with evidence from the literature, the influence of competitive ability and social rank on the likelihood of problem-solving seems quite weak (see Table 3.1; also reviewed in Griffin and Guez, 2014). For instance, previous studies reported that subordinate individuals were more likely to innovate than dominant ones (Reader and Laland, 2001; Cole and Quinn, 2012; Thornton and Samson, 2012), whereas other studies did not find an effect of social status on success (Kothbauer-Hellmann, 1990; Gajdon et al., 2006; Benson-Amram and Holekamp, 2012; Benson-Amram et al., 2013). Interestingly, all of these studies examined the outcome of problem-solving as either solving or not solving the task. In contrast, Bouchard and collaborators (2007) measured latency to solve the novel task and found no association with dominance rank, which is consistent with what we found using the same measure (i.e. total latency). In groups of starlings *Sturnus vulgaris,* social ranks significantly predicted which birds were the first to solve novel extractive foraging tasks, with dominants exhibiting a higher innovative propensity (Boogert et al., 2008). Moreover, Hopper et al. (2014) used the proportion of possible parts of the apparatus removed as a measure of problem-solving success (total of eight rewards in different holes), and found a positive correlation with dominance in chimpanzees. These findings are more similar to what we found with problem-solving efficiency, with a better performance of dominants compared to subordinates. Coupled with the non-significant correlation between our two measurements for problem-solving latency, it therefore appears that solving success (solving or not), total latency to solve and efficiency when solving (i.e. latency excluding interruptions) could reflect different processes involved in innovative behaviour.

A hypothesis that remains to be tested is that necessity could influence the likelihood to engage in novel problem-solving and to successfully solve a novel problem, perhaps owing to greater perseverance or exploration, but not problem-solving efficiency. There is consistent evidence for an important role of persistence in the likelihood of problem-solving (reviewed in Griffin and Guez, 2014). For instance, in wild meerkats, persistence was critical in novel food extraction tasks (Thornton and Samson, 2012). In comparison to other group members, innovators essentially always persisted longer when interacting with the apparatus, and the successful individual within a group was the member that spent most time manipulating the task (Thornton and Samson, 2012). Juveniles were more likely to interact with the tasks than adults, but rarely solved them (Thornton and Samson, 2012). Spotted hyenas that were successful at solving novel food-motivated problems also exhibited more persistence and diversity in their exploratory behaviours (Benson-Amram and Holekamp, 2012; Benson-Amram et al., 2013). In captive Carib grackles, innovators had higher exploration scores than non-innovators and, when they contacted the correct part of the problem-solving device, they continued to do so until they solved the problem (Overington et al., 2011). Morand-Ferron and collaborators (2011) found that juvenile tits were more likely to solve a novel problem than adults in the field, but that this age effect disappeared when controlling for total duration of problem-solving attempts. Juveniles thus seemed to be more innovative because they persevered longer, and not because of increased efficiency (Morand-Ferron et al., 2011; see also Biondi et al., 2010 with caracaras *Milvago chimango*).

An alternative to the 'necessity' hypothesis is the hypothesis of 'capacity', which predicts a positive influence of cognitive skills on innovation (e.g. Bókony et al., 2014). Positive correlations between innovation rate and relative brain size in both birds and primates at the interspecific level (Lefebvre et al., 1997; Reader and Laland, 2002) support this prediction of an influence of cognitive capacity on innovative propensity. At the intraspecific level, performance of male spotted bowerbirds (*Ptilonorhynchus maculatus*) in a problem-solving task loaded positively, along with performance in other cognitive tests, onto a principal component representing general cognitive ability (Isden et al., 2013). Moreover, by measuring variables such as corticosterone (a stress hormone), glutathione (a key antioxidant) and coccidian parasites, Bókony and collaborators (2014) recently pointed out that individuals in better physiological state exhibited higher problem-solving performance, which was measured as latency to solve the task. Thus, superior physiological condition may ensure a greater cognitive capacity and problem-solving performance. Coming back to our results, dominant individuals could potentially exhibit higher cognitive capacity due to priority access to resources such as high quality food (e.g. priority access in Parids: Glase 1973; Hogstad, 1989; Ficken et al., 1990).

Social dominance may therefore affect cognitive performance, or vice versa. Acquisition of dominance status has been found to affect maze learning ability in laboratory mice, with two paired individuals expressing differences in learning only after the establishment of aggressive rank relationships between them (Barnard and Luo, 2002). Benefiting from a higher cognitive capacity could also allow individuals to obtain a better position in a dominance hierarchy. Intrinsic differences ('prior attributes'; Chase et al., 2002) in individuals' cognitive skills may partly determine their "social success" and dominance status ('social intelligence' hypothesis; Jolly, 1966; Humphrey, 1976; Byrne and Whiten, 1988; Seyfarth and Cheney, 2002). Indeed, complexities of group living and contingencies of interactions in social groups may require important cognitive faculties (Jolly, 1966; Humphrey, 1976; Byrne and Whiten, 1988). Greater cognitive skills could thus help some individuals achieve higher hierarchical ranks. Although additional empirical work would be required to firmly assess the direction of the relationship and infer causality, there is undoubtedly increasing evidence for a positive association between cognitive ability and social dominance. For instance, in captive groups of starlings, individuals occupying the highest competitive ranks were both better learners (Boogert et al., 2006, 2008) and the firsts to solve novel food-motivated tasks (Boogert et al., 2008). Additional support is provided by laboratory work on mountain chickadees (*Poecile gambeli*) demonstrating that subordinate individuals had less efficient cache retrieval ability, inferior spatial memory performance and lower rates of hippocampal cell proliferation compared to dominants (Pravosudov et al., 2003; Pravosudov and Omanska, 2005). If cognitive capacity affects both dominance and problem-solving efficiency, this may explain the positive association found here between these two traits.

In conclusion, we found no significant relationship between the two measured problem-solving latencies as well as between these latencies and sex, age, or body condition. There was also no significant correlation between total latency to solve and dominance score, but dominant individuals were significantly more efficient problem-solvers (shorter latency to solve excluding interruptions) than subordinates. Overall, our results do not support the ‘necessity drives innovation’ hypothesis, and suggest that problem-solving efficiency may be essentially independent of state-dependent factors. We suggest that necessity may act on the probability of encountering, engaging in, and/or successfully solving a novel problem, for instance by increasing exploratory behaviours and persistence when trying to solve the problem. However, efficiency when solving a novel problem may be driven by different forces, such as cognitive capacity. Testing the effect of necessity and capacity on both the likelihood of success and the efficiency at novel problem-solving would be an interesting avenue for future studies.

Table 3.1 – Review of innovative problem-solving findings in relation to sex, age, body condition and dominance. Studies reporting significant results supporting predictions from the 'necessity drives innovation' hypothesis, no significant relationships, and significant results contrary to predictions are listed. General predictions are that females, juveniles, individuals in poor body condition and subordinates should be more likely to innovate. Numbers refer to the studies cited below and letters to the vertebrate group (bird, mammal or fish). Brackets (i.e. [ ]) point out results significant only in some contexts or a non-significant trend. Studies are listed in chronological order.

	Significant support	No significant relationship	Significant opposite
Sex	2c; [17b]	6a; 7a; 11a; 12a; 14b; 18b	3b; 5a; 16b
Age	[11a]; [12a]	9a ; 10a; 14b; 18b	3b; 4b; 5a; 16b; 17b
Body condition	–	11a; 13a; 16b	–
Dominance or Competitive ability	3b; 15a; 16b	1a; 5a; 7a; 14b; 17b	8a; 18b

a: bird; b: mammal; c: fish; [ ]: only in some contexts or non-significant trend

1-Kothbauer-Hellmann, 1990; 2-Laland and Reader, 1999a; 3-Reader and Laland, 2001; 4-Kendal et al.,2005; 5-Gajdon et al., 2006; 6-Seibt and Wickler, 2006; 7-Bouchard et al., 2007; 8-Boogert et al., 2008; 9- Keagy et al 2009; 10-Biondi et al., 2010; 11-Cole et al., 2011; 12-Morand-Ferron et al., 2011; 13-Overington et al., 2011; 14-Benson-Amram and Holekamp, 2012; 15-Cole and Quinn, 2012; 16-Thornton and Samson, 2012; 17-Benson-Amram et al., 2013; 18-Hopper et al 2014

Table 3.2 – Results of linear mixed models including one of the two novel problem-solving latencies (seconds, log-transformed) as response variable, and group as a random intercept. Sex, age and body condition were included as fixed factors.

Fixed effect	Estimate	± SE	*DF*	*F*	*P*
Total problem-solving latency					
Sex	0.060	± 0.120	13.683	0.25	0.625
Age	-0.217	± 0.154	14.260	2.00	0.179
Body condition	0.029	± 0.085	14.038	0.11	0.743
Problem-solving latency excluding interruptions					
Sex	-0.195	± 0.184	16.965	1.12	0.305
Age	-0.156	± 0.233	17.352	0.45	0.511
Body condition	0.202	± 0.130	17.260	2.42	0.138

Reference categories are female (sex) and adult (age), with estimates set to 0.

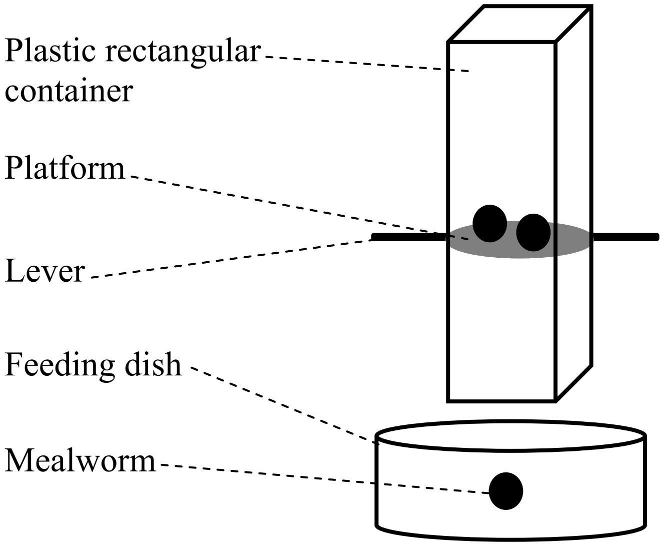


Figure 3.1 Problem-solving apparatus. The lever-pulling device consisted of a transparent plastic rectangular container, containing a platform supported by a lever, above a feeding dish. Two mealworms were inserted on the platform as food rewards, and a freely accessible mealworm was placed in the dish to assess feeding motivation.

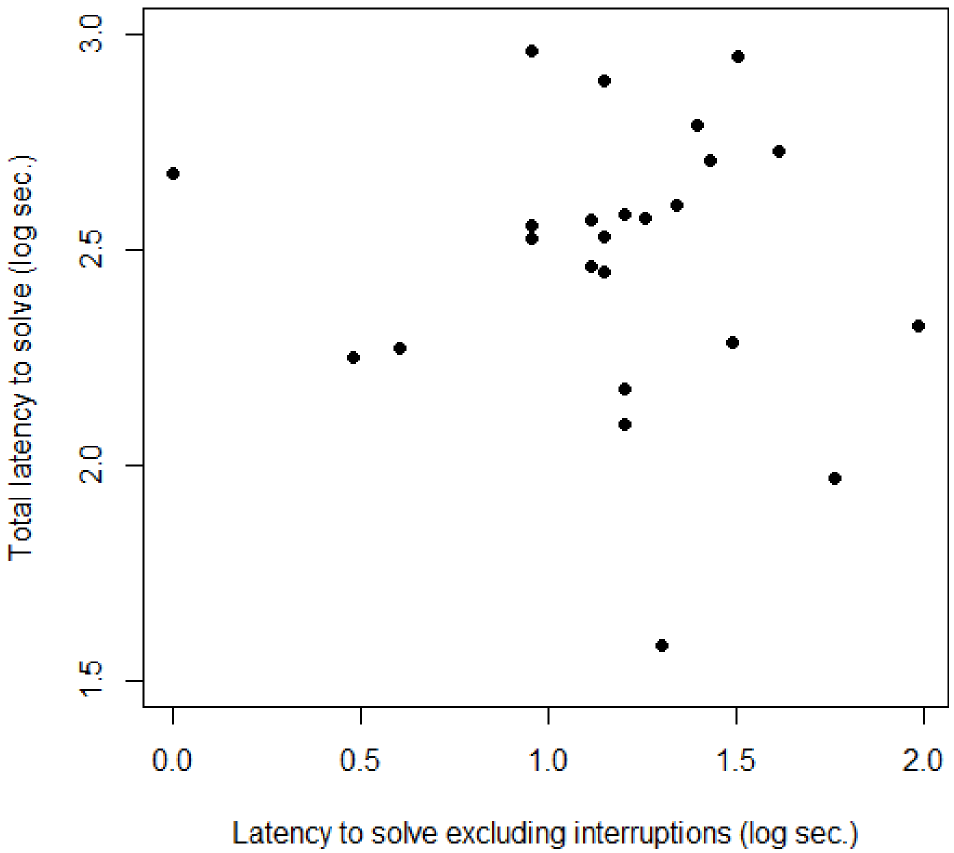


Figure 3.2 – Total latency to solve (seconds, log-transformed) against latency to solve excluding interruptions (seconds, log-transformed).

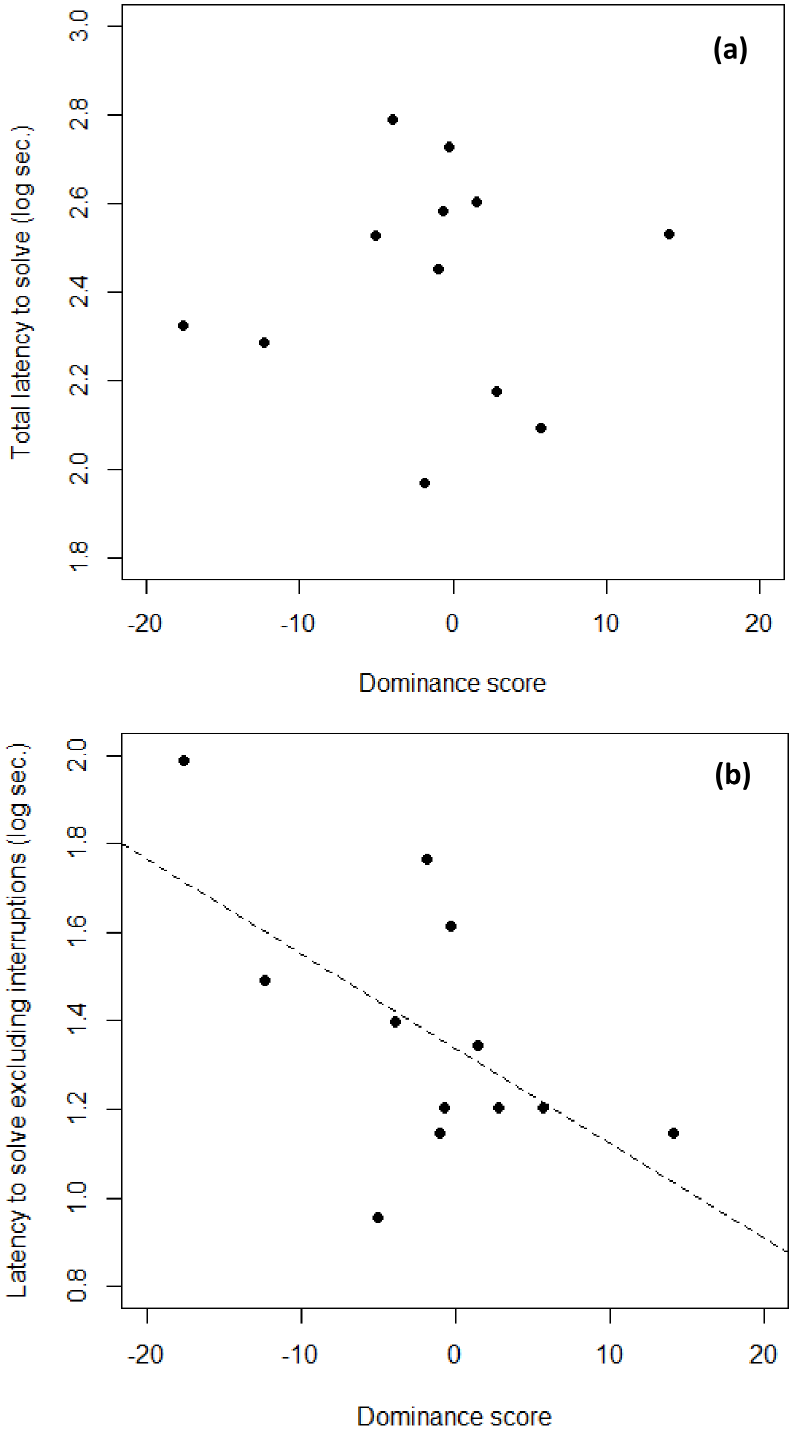


Figure 3.3 – Relationships between (a) total latency to solve (seconds, log-transformed), (b) latency to solve excluding interruptions (seconds, log-transformed), and social dominance score (David's score) of individual birds. Only birds from the forest habitat were included in the model.

CHAPTER 4

GENERAL CONCLUSION

The objectives of this thesis were to investigate the behavioural and cognitive correlates of social dominance in natural groups of animals in the wild. In Chapter 2, the results showed no significant relationship between four personality traits and dominance within linear hierarchies of black-capped chickadees (*Poecile atricapillus*). This finding suggests that personality does not contribute significantly to dominance outcomes in groups of animals and adds to the growing body of evidence that intrinsic attributes of individuals are not sufficient to explain the structure of linear dominance hierarchies. Although this hypothesis was not tested here, social processes may instead be the predominant factor underpinning hierarchy formation. In Chapter 3, the results demonstrated that novel problem-solving performance was not significantly related to sex, age, or body condition of birds. Total latency to solve the problem was not significantly correlated with latency to solve excluding interruptions, which more likely reflects individuals' efficiency at solving. Total latency was not significantly linked to dominance score, but there was a significant relationship between latency excluding interruptions and dominance. Dominant individuals were significantly more efficient problem-solvers than subordinates, a finding that does not support the 'necessity drives innovation' hypothesis. An alternative hypothesis would be that greater cognitive capacity may lead to both higher problem-solving efficiency and higher dominance ranks.

Social living and the formation of dominance hierarchies are associated with an array of cognitive abilities (Jolly, 1966; Humphrey, 1976; Byrne and Whiten, 1988), such as individual recognition and transitive inference (e.g. see Chase and Seitz, 2011). Thereby, the positive relationship found in Chapter 3 between dominance and problem-solving performance could be explained by a shared influence of cognitive capacity.

Likewise, greater cognitive skills of dominant individuals could be associated with an efficient management of social processes, which have been suggested in Chapter 2 to influence the formation of linear hierarchies. Both chapters therefore complement each other for a better comprehension of the factors that influence, or that do not influence, the position of individuals within natural dominance hierarchies.

Findings from this thesis also highlight the importance of researchers carefully considering which methods and measures they are using and how this choice may affect their conclusions. In Chapter 2, we emphasized that animals should be studied within social groups to truly understand which factors influence dominance in these groups, instead of drawing conclusions based on observed encounters between isolated dyads. Furthermore, research in natural conditions, instead of captive settings, should be prioritized. In Chapter 3, we pointed out that different measures of problem-solving may reflect different underlying processes. For instance, necessity induced by poor competitive ability might increase the likelihood of solving a novel problem, whereas cognitive capacity might increase problem-solving efficiency. Methods used in this thesis can also be helpful for future work as they allow measurements of dominance and personality traits to be collected directly in the field, without the need to bring birds into captivity. These methods are interesting from an ethics point of view as they minimize the time an individual is removed from its environment. Moreover, these methods are also flexible, for instance by allowing the study of free-ranging animals in remote areas or in different ecological contexts such as breeding season, wintering season and migration.

The results of this thesis enhance our understanding of dominance hierarchies that structure wild groups of animals. Overall, these results suggest that personality traits are not contributing to the structure of linear dominance hierarchies, but that cognitive skills may influence the position of individuals within these hierarchies. It would be interesting for future studies to investigate how behavioural and cognitive processes may influence social interactions and dominance, and especially how these processes may differ between species with contrasting social organizations.

References

An, Y. S., Kriengwatana, B., Newman, A. E., MacDougall-Shackleton, E. A. & MacDougall-Shackleton, S. A. 2011. Social rank, neophobia and observational learning in black-capped chickadees. Behaviour 148, 55-69.

Aplin, L. M., Farine, D. R., Morand-Ferron, J. & Sheldon, B. C. 2012. Social networks predict patch discovery in a wild population of songbirds. Proc. R. Soc. B 279, 4199-4205.

Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cole, E. F., Cockburn, A. & Sheldon, B. C. 2013a. Individual personalities predict social behaviour in wild networks of great tits (*Parus major*). Ecol. Lett. 16, 1365-1372.

Aplin, L. M., Sheldon, B. C. & Morand-Ferron, J. 2013b. Milk bottles revisited: social learning and individual variation in the blue tit, *Cyanistes caeruleus*. Anim. Behav. 85, 1225-1232.

Appleby, M. 1983. The probability of linearity in hierarchies. Anim. Behav. 31, 600-608.

Arcese, P. & Smith, J. 1985. Phenotypic correlates and ecological consequences of dominance in song sparrows. J. Anim. Ecol. 54, 817-830.

Barnard, C. & Sibly, R. 1981. Producers and scroungers: a general model and its application to captive flocks of house sparrows. Anim. Behav. 29, 543-550.

Barnard, C. J., & Luo, N. 2002. Acquisition of dominance status affects maze learning in mice. Behav. Process. 60, 53-59.

Barta, Z. & Giraldeau, L.-A. 1998. The effect of dominance hierarchy on the use of alternative foraging tactics: A phenotype-limited producing-scrounging game. Behav. Ecol. Sociobiol. 42, 217-223.

Bates, D. M. 2010. lme4: mixed-effects modeling with R. Springer, Madison, WI.

Beacham, J. 2003. Models of dominance hierarchy formation: Effects of prior experience and intrinsic traits. Behaviour 140, 1275-1303.

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

Beauchamp, G. 2006. Phenotypic correlates of scrounging behavior in zebra finches: Role of foraging efficiency and dominance. Ethology 112, 873-878.

Bell, A. M. 2005. Behavioural differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*). J. Evol. Biol. 18, 464-473.

Bell, A. M. & Sih, A. 2007. Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). Ecol. Lett. 10, 828-834.

Bell, A. M., Hankison, S. J. & Laskowski, K. L. 2009. The repeatability of behaviour: a meta-analysis. Anim. Behav. 77, 771-783.

Benson-Amram, S. & Holekamp, K. E. 2012. Innovative problem solving by wild spotted hyenas. Proc. R. Soc. B 279, 4087-4095.

Benson-Amram, S., Weldele, M. L., & Holekamp, K. E. 2013. A comparison of innovative problem-solving abilities between wild and captive spotted hyaenas, *Crocuta crocuta*. Anim. Behav. 85, 349-356.

Biondi, L.M., Bo, M.S. & Vassallo, A.I., 2010. Inter-individual and age differences in exploration, neophobia and problem-solving ability in a Neotropical raptor. Anim. Cogn. 13, 701-710.

Biro, P. A. & Stamps, J. A. 2008. Are animal personality traits linked to life-history productivity? Trends Ecol. Evol. 23, 361-368.

Blem, C. R. 1976. Patterns of lipid storage and utilization in birds. Am. Zool. 16, 671-684.

Blumstein, D. T., & Daniel, J. C. 2007. Quantifying behavior the JWatcher way. Sinauer Associates Incorporated, Sunderland, MA.

Boisvert, M. J. 1999. Winter food-caching, feeding, and body weight in relation to social dominance in black-capped chickadees (*Poecile atricapillus*). Master thesis, University of Western Ontario.

Bókony, V., Kulcsar, A., Toth, Z. & Liker, A. 2012. Personality traits and behavioral syndromes in differently urbanized populations of house sparrows (*Passer domesticus*). PLoS One 7, e36639.

Bókony, V., Lendvai, A.Z., Vágási, C.I., Pătras, L., Pap, P.L., Németh, J., Vincze, E., Papp, S., Preiszner, B., Seress, G. & Liker, A., 2014. Necessity or capacity? Physiological state predicts problem-solving performance in house sparrows. Behav. Ecol. 25, 124-135.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H. & White, J.-S. S. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol. Evol. 24, 127-135.

Boogert, N. J., Reader, S. M. & Laland, K. N. 2006. The relation between social rank, neophobia and individual learning in starlings. Anim. Behav. 72, 1229-1239.

Boogert, N. J., Reader, S. M., Hoppitt, W., & Laland, K. N. 2008. The origin and spread of innovations in starlings. Anim. Behav. 75, 1509-1518.

Boogert, N.J., Monceau, K. & Lefebvre, L., 2010. A field test of behavioural flexibility in Zenaida doves (*Zenaida aurita*). Behav. Process. 85, 135-141.

Bouchard, J., Goodyer, W. & Lefebvre, L. 2007. Social learning and innovation are positively correlated in pigeons (*Columba livia*). Anim. Cogn. 10, 259-266.

Brommer, J. E. & Kluen, E. 2012. Exploring the genetics of nestling personality traits in a wild passerine bird: testing the phenotypic gambit. Ecol. Evol. 2, 3032-3044.

Bryant, D. & Newton, A. 1994. Metabolic costs of dominance in dippers, *Cinclus cinclus*. Anim. Behav. 48, 447-455.

Byrne, R. W. & Whiten, A. 1988. Machiavellian intelligence: social expertise and the evolution of intellect in monkeys, apes and humans. Clarendon Press, Oxford.

Cauchard, L., Boogert, N.J., Lefebvre, L., Dubois, F. & Doligez, B., 2013. Problem-solving performance is correlated with reproductive success in a wild bird population. Anim. Behav. 85, 19-26.

Chase, I. D. 1974. Models of hierarchy formation in animal societies. Behav. Sci. 19, 374-382.

Chase, I. D. 1980. Social-process and hierarchy formation in small-groups: a comparative perspective. Am. Sociol. Rev. 45, 905-924.

Chase, I. D., Bartolomeo, C. & Dugatkin, L. A. 1994. Aggressive interactions and inter-contest interval: how long do winners keep winning? Anim. Behav. 48, 393-400.

Chase, I. D., Tovey, C., Spangler-Martin, D. & Manfredonia, M. 2002. Individual differences versus social dynamics in the formation of animal dominance hierarchies. Proc. Natl. Acad. Sci. U.S.A. 99, 5744-5749.

Chase, I. D., Tovey, C. & Murch, P. 2003. Two's company, three's a crowd: differences in dominance relationships in isolated versus socially embedded pairs of fish. Behaviour 140, 1193-1217.

Chase, I. D. & Seitz, K. 2011. Self-structuring properties of dominance hierarchies: a new perspective. Adv. Genet. 75, 51-81.

Chiarati, E., Canestrari, D., Vera, R., Marcos, J. M., & Baglione, V. 2010. Linear and stable dominance hierarchies in cooperative carrion crows. Ethology 116, 346-356.

Cole, E. F., Cram, D. L. & Quinn, J. L. 2011. Individual variation in spontaneous problem-solving performance among wild great tits. Anim. Behav. 81, 491-498.

Cole, E. F. & Quinn, J. L. 2012. Personality and problem-solving performance explain competitive ability in the wild. Proc. R. Soc. B 279, 1168-1175.

Cole, E.F., Morand-Ferron, J., Hinks, A.E. & Quinn, J.L., 2012. Cognitive ability influences reproductive life history variation in the wild. Curr. Biol. 22, 1808-1812.

Colléter, M. & Brown, C. 2011. Personality traits predict hierarchy rank in male rainbowfish social groups. Anim. Behav. 81, 1231-1237.

Correa, L. A., Zapata, B., Samaniego, H. & Soto-Gamboa, M. 2013. Social structure in a family group of Guanaco (*Lama guanicoe*, Ungulate): Is female hierarchy based on 'prior attributes' or 'social dynamics'?. Behav. Process. 98, 92-97.

Côté, S. 2000. Determining social rank in ungulates: A comparison of aggressive interactions recorded at a bait site and under natural conditions. Ethology 106, 945-955.

Dahlbom, S. J., Lagman, D., Lundstedt-Enkel, K., Sundstrom, L. F. & Winberg, S. 2011. Boldness predicts social status in zebrafish (*Danio rerio*). PLoS One 6, e23565.

David, H. 1987. Ranking from unbalanced paired-comparison data. Biometrika 74, 432-436.

Davies, N. B., Krebs, J. R. & West, S. A. 2012. An introduction to behavioural ecology, 4th edn. Wiley-Blackwell, Chichester.

David, M., Auclair, Y. & Cezilly, F. 2011. Personality predicts social dominance in female zebra finches, *Taeniopygia guttata*, in a feeding context. Anim. Behav. 81, 219-224.

Desrochers, A. 1989. Sex, dominance, and microhabitat use in wintering black-capped chickadees - a field experiment. Ecology 70, 636-645.

Desrochers, A., Hannon, S. & Nordin, K. 1988. Winter survival and territory acquisition in a northern population of black-capped chickadees. Auk 105, 727-736.

Dey, C. J. & Quinn, J. S. 2014. Individual attributes and self-organizational processes affect dominance network structure in pukeko. Behav. Ecol. 25, 1402-1408.

Dingemanse, N. & de Goede, P. 2004. The relation between dominance and exploratory behavior is context-dependent in wild great tits. Behav. Ecol. 15, 1023-1030.

Dingemanse, N. J., Wright, J., Kazem, A. J. N., Thomas, D. K., Hickling, R. & Dawnay, N. 2007. Behavioural syndromes differ predictably between 12 populations of three-spined stickleback. J. Anim. Ecol. 76, 1128-1138.

Doucet, S., Mennill, D., Montgomerie, R., Boag, P. & Ratcliffe, L. 2005. Achromatic plumage reflectance predicts reproductive success in male black-capped chickadees. Behav. Ecol. 16, 218-222.

Drent, P., van Oers, K. & van Noordwijk, A. 2003. Realized heritability of personalities in the great tit (*Parus major*). Proc. R. Soc. B 270, 45-51.

Drews, C. 1993. The concept and definition of dominance in animal behavior. Behaviour 125, 283-313.

Ekman, J. 1987. Exposure and time use in willow tit flocks: the cost of subordination. Anim. Behav. 35, 445-452.

Ekman, J. 1989. Ecology of non-breeding social-systems of *Parus*. Wilson Bull. 101, 263-288.

Ekman, J. & Askenmo, C. 1984. Social rank and habitat use in willow tit groups. Anim. Behav. 32, 508-514.

Ekman, J. & Lilliendahl, K. 1993. Using priority to food access: fattening strategies in dominance-structured willow tit (*Parus montanus*) flocks. Behav. Ecol. 4, 232-238.

Ellis, L. 1995. Dominance and reproductive success among nonhuman animals: a cross-species comparison. Ethol. Sociobiol. 16, 257-333.

Estók, P., Zsebők, S. & Siemers, B.M., 2010. Great tits search for, capture, kill and eat hibernating bats. Biol. Lett. 6, 59-62.

Evans, J., Boudreau, K. & Hyman, J. 2010. Behavioural syndromes in urban and rural populations of song sparrows. Ethology 116, 588-595.

Favati, A., Leimar, O. & Lovlie, H. 2014. Personality predicts social dominance in male domestic fowl. PLoS One 9, e103535.

Ficken, M., Weise, C. & Popp, J. 1990. Dominance rank and resource access in winter flocks of black-capped chickadees. Wilson Bull. 102, 623-633.

Fisher, J. & Hinde, R.A., 1949. The opening of milk bottles by birds. Brit. Birds 42, 347-357.

Fox, R. A., Ladage, L. D., Roth, T. C., II, & Pravosudov, V. V. 2009. Behavioural profile predicts dominance status in mountain chickadees, *Poecile gambeli*. Anim. Behav. 77, 1441-1448.

Funghi, C., Leitao, A. V., Ferreira, A. C., Mota, P. G. & Cardoso, G. C. 2015. Social dominance in a gregarious bird is related to body size but not to standard personality assays. Ethology 121, 84-93.

Gajdon, G. K., Fijn, N. & Huber, L. 2006. Limited spread of innovation in a wild parrot, the kea (*Nestor notabilis*). Anim. Cogn. 9, 173-181.

Gammell, M., de Vries, H., Jennings, D., Carlin, C. & Hayden, T. 2003. David's score: a more appropriate dominance ranking method than Clutton-Brock et al.'s index. Anim. Behav. 66, 601-605.

Giraldeau, L.-A. & Caraco, T. 2000. Social foraging theory. Princeton University Press, Princeton, NJ.

Glase, J. C. 1973. Ecology of social organization in the black-capped chickadee. Living Bird 12, 235-267.

Gosler, A. 1996. Environmental and social determinants of winter fat storage in the great tit *Parus major*. J. Anim. Ecol. 65, 1-17.

Gosling, S. 2001. From mice to men: what can we learn about personality from animal research? Psychol. Bull. 127, 45-86.

Greenberg, R. 2003. The role of neophobia and neophilia in the development of innovative behaviour of birds. In: Animal innovation (Reader, S. M. & Laland, K. N., ed). Oxford University Press, Oxford, pp. 175-196.

Greenberg, R. & Mettke-Hofmann, C. 2001. Ecological aspects of neophobia and neophilia in birds. Curr. Ornithol. 16, 119-178.

Griffin, A. S., & Guez, D. 2014. Innovation and problem solving: a review of common mechanisms. Behav. Process. 109, 121-134.

Griffiths, R., Double, M. C., Orr, K. & Dawson, R. J. D. 1998. A DNA test to sex most birds. Mol. Ecol. 7, 1071-1075.

Guillette, L. M., Reddon, A. R., Hurd, P. L. & Sturdy, C. B. 2009. Exploration of a novel space is associated with individual differences in learning speed in black-capped chickadees, *Poecile atricapillus*. Behav. Process. 82, 265-270.

Guillette, L. M. & Sturdy, C. B. 2011a. Individual differences and repeatability in vocal production: stress-induced calling exposes a songbird's personality. Naturwissenschaften 98, 977-981.

Guillette, L. M., Reddon, A. R., Hoeschele, M. & Sturdy, C. B. 2011b. Sometimes slower is better: slow-exploring birds are more sensitive to changes in a vocal discrimination task. Proc. R. Soc. B 278, 767-773.

Guillette, L. M., Hahn, A. H., Hoeschele, M., Przyslupski, A. & Sturdy, C. B. 2015. Individual differences in learning speed, performance accuracy and exploratory behaviour in black-capped chickadees. Anim. Cogn. 18, 165-178.

Hartzler, J. 1970. Winter dominance relationship in black-capped chickadees. Wilson Bull. 82, 427-&.

Herborn, K. A., Macleod, R., Miles, W. T. S., Schofield, A. N. B., Alexander, L. & Arnold, K. E. 2010. Personality in captivity reflects personality in the wild. Anim. Behav. 79, 835-843.

Hinde, R.A. & Fisher, J., 1951. Further observations on the opening of milk bottles by birds. Br. Birds 44, 393-396.

Hogstad, O. 1987. It is expensive to be dominant. Auk 104, 333-336.

Hogstad, O. 1988. Social rank and antipredator behavior of willow tits *Parus montanus* in winter flocks. Ibis 130, 45-56.

Hogstad, O. 1989. Social-organization and dominance behavior in some *Parus* species. Wilson Bull. 101, 254-262.

van Hooff, J. A. & Wensing, J. A. 1987. Dominance and its behavioral measures in a captive wolf pack. In: Man and wolf - advances, issues and problems in captive wolf research (Frank, H., ed). Junk, Dordrecht, pp. 219-252.

Hopper, L. M., Price, S. A., Freeman, H. D., Lambeth, S. P., Schapiro, S. J. & Kendal, R. L. 2014. Influence of personality, age, sex, and estrous state on chimpanzee problem-solving success. Anim. Cogn. 17, 835-847.

Hosey, G., Jacques, M. & Pitts, A. 1997. Drinking from tails: social learning of a novel behaviour in a group of ring-tailed lemurs (*Lemur catta*). Primates 38, 415-422.

Hsu, Y. & Wolf, L. L. 1999. The winner and loser effect: integrating multiple experiences. Anim. Behav. 57, 903-910.

Humphrey, N. K. 1976. The social function of intellect. In: Growing Points in Ethology. (Bateson, P. P. G. & Hinde, R. A., eds). Cambridge University Press, Cambridge, pp. 303-317.

Huntingford, F. A. & Turner, A. K. 1987. Animal conflict. Chapman and Hall, London.

Isden, J., Panayi, C., Dingle, C. & Madden, J. 2013. Performance in cognitive and problem-solving tasks in male spotted bowerbirds does not correlate with mating success. Anim. Behav. 86, 829-838.

Jakob, E.M., Marshall, S.D. & Uetz, G.W., 1996. Estimating fitness: a comparison of body condition indices. Oikos 77, 61-67.

Jolles, J. W., Ostojic, L. & Clayton, N. S. 2013. Dominance, pair bonds and boldness determine social-foraging tactics in rooks, *Corvus frugilegus*. Anim. Behav. 85, 1261-1269.

Jolly, A. 1966. Lemur social behavior and primate intelligence. Science 153, 501-506.

Kawai, M., 1965. Newly-acquired pre-cultural behavior of the natural troop of Japanese monkeys on Koshima Islet. Primates 6, 1-30.

Keagy, J., Savard, J.-F. & Borgia, G., 2009. Male satin bowerbird problem-solving ability predicts mating success. Anim. Behav. 78, 809-817.

Kendal, R.L., Coe, R.L. & Laland, K.N., 2005. Age differences in neophilia, exploration, and innovation in family groups of callitrichid monkeys. Am. J. Primatol. 66, 167-188.

Klass, K. & Cords, M. 2011. Effect of unknown relationships on linearity, steepness and rank ordering of dominance hierarchies: simulation studies based on data from wild monkeys. Behav. Process. 88, 168-176.

Kluen, E., Kuhn, S., Kempenaers, B. & Brommer, J. E. 2012. A simple cage test captures intrinsic differences in aspects of personality across individuals in a passerine bird. Anim. Behav. 84, 279-287.

Kluen, E. & Brommer, J. E. 2013. Context-specific repeatability of personality traits in a wild bird: a reaction-norm perspective. Behav. Ecol. 24, 650-658.

Koolhaas, J., Korte, S., De Boer, S., Van Der Vegt, B., Van Reenen, C., Hopster, H., De Jong, I., Ruis, M. & Blokhuis, H. 1999. Coping styles in animals: current status in behavior and stress-physiology. Neurosci. Biobehav. Rev. 23, 925-935.

Kothbauer-Hellmann, R., 1990. On the origin of a tradition: Milk bottle opening by titmice. Zool. Anz. 225, 353-361.

Kozlovsky, D., Branch, C., Freas, C. A. & Pravosudov, V. V. 2014. Elevation-related differences in novel environment exploration and social dominance in food-caching mountain chickadees. Behav. Ecol. Sociobiol. 68, 1871-1881.

Krause, J. & Ruxton, G. D. 2002. Living in groups. Oxford University Press, Oxford.

Kummer, H. & Goodall, J. 1985. Conditions of innovative behaviour in primates. Philos. Trans. R. Soc. B 308, 203-214.

Kurvers, R. H. J. M., Eijkelenkamp, B., van Oers, K., van Lith, B., van Wieren, S. E., Ydenberg, R. C. & Prins, H. H. T. 2009. Personality differences explain leadership in barnacle geese. Anim. Behav. 78, 447-453.

Lahti, K., Koivula, K., Rytkönen, S., Mustonen, T., Welling, P., Pravosudov, V. V., & Orell, M. 1998. Social influences on food caching in willow tits: a field experiment. Behav. Ecol. 9, 122-129.

Laland, K. & Reader, S. 1999a. Foraging innovation in the guppy. Anim. Behav. 57, 331-340.

Laland, K. & Reader, S. 1999b. Foraging innovation is inversely related to competitive ability in male but not in female guppies. Behav. Ecol. 10, 270-274.

Landau, H. G. 1951. On dominance relations and the structure of animal societies: I. Effect of inherent characteristics. Bull. Math. Biophys. 13, 1-19.

Lefebvre, L., Whittle, P., Lascaris, E. & Finkelstein, A. 1997. Feeding innovations and forebrain size in birds. Anim. Behav. 53, 549-560.

Lefebvre, L., Reader, S.M. & Sol, D., 2004. Brains, innovations and evolution in birds and primates. Brain Behav. Evol. 63, 233-246.

Lehikoinen, E. 1987. Seasonality of the daily weight cycle in wintering passerines and its consequences. Ornis Scand. 18, 216-226.

Leiva, D. & de Vries, H. 2011. Testing steepness of dominance hierarchies. R Package Version 2.2.

Lendvai, A. Z., Liker, A. & Barta, Z. 2006. The effects of energy reserves and dominance on the use of social-foraging strategies in the house sparrow. Anim. Behav. 72, 747-752.

Lewden, A., Petit, M. & Vezina, F. 2012. Dominant black-capped chickadees pay no maintenance energy costs for their wintering status and are not better at enduring cold than subordinate individuals. J. Comp. Physiol. B 182, 381-392.

Liker, A. & Barta, Z. 2002. The effects of dominance on social foraging tactic use in house sparrows. Behaviour 139, 1061-1076.

Liker, A. & Bókony, V., 2009. Larger groups are more successful in innovative problem solving in house sparrows. Proc. Natl. Acad. Sci. U.S.A. 106, 7893-7898.

Martin, P. & Bateson, P. 2007. Measuring behaviour: an introductory guide. Cambridge University Press, Cambridge.

Meigs, J., Smith, D. & Vanbuskirk, J. 1983. Age-determination of black-capped chickadees. J. Field Ornithol. 54, 283-286.

Mennill, D., Ramsay, S., Boag, P. & Ratcliffe, L. 2004. Patterns of extrapair mating in relation to male dominance status and female nest placement in black-capped chickadees. Behav. Ecol. 15, 757-765.

Mettke-Hofmann, C., Winkler, H. & Leisler, B. 2002. The significance of ecological factors for exploration and neophobia in parrots. Ethology 108, 249-272.

Mettler, A. E. & Shivik, J. A. 2007. Dominance and neophobia in coyote (*Canis latrans*) breeding pairs. Appl. Anim. Behav. Sci. 102, 85-94.

Miranda, A. C., Schielzeth, H., Sonntag, T. & Partecke, J. 2013. Urbanization and its effects on personality traits: a result of microevolution or phenotypic plasticity?. Global Change Biol. 19, 2634-2644.

Morand-Ferron, J. & Quinn, J.L., 2011. Larger groups of passerines are more efficient problem solvers in the wild. Proc. Natl. Acad. Sci. U.S.A. 108, 15898-15903.

Morand-Ferron, J., Cole, E. F., Rawles, J. E. C. & Quinn, J. L. 2011. Who are the innovators? A field experiment with 2 passerine species. Behav. Ecol. 22, 1241-1248.

Nakagawa, S. & Schielzeth, H. 2010. Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. Biol. Rev. 85, 935-956.

Nicolakakis, N., Sol, D. & Lefebvre, L., 2003. Behavioural flexibility predicts species richness in birds, but not extinction risk. Anim. Behav. 65, 445-452.

Odum, E. P. 1942. Annual cycle of the black-capped chickadee: 3. Auk, 499-531.

van Oers, K., Drent, P. J., de Goede, P. & van Noordwijk, A. J. 2004. Realized heritability and repeatability of risk-taking behaviour in relation to avian personalities. Proc. R. Soc. B 271, 65-73.

Otter, K., Ratcliffe, L., Michaud, D. & Boag, P. 1998. Do female black-capped chickadees prefer high-ranking males as extra-pair partners?. Behav. Ecol. Sociobiol. 43, 25-36.

Otter, K., Ramsay, S. & Ratcliffe, L. 1999. Enhanced reproductive success of female black-capped chickadees mated to high-ranking males. Auk 116, 345-354.

Overington, S.E., Morand-Ferron, J., Boogert, N.J. & Lefebvre, L., 2009. Technical innovations drive the relationship between innovativeness and residual brain size in birds. Anim. Behav. 78, 1001-1010.

Overington, S. E., Cauchard, L., Cote, K. & Lefebvre, L. 2011. Innovative foraging behaviour in birds: What characterizes an innovator? Behav. Process. 87, 274-285.

Piper, W. H. 1997. Social dominance in birds: Early findings and new horizons. Curr. Ornithol. 14, 125-187.

Piper, W. & Wiley, R. 1989. Correlates of dominance in wintering white-throated sparrows - age, sex and location. Anim. Behav. 37, 298-310.

Pravosudov, V., Mendoza, S. & Clayton, N. 2003. The relationship between dominance, corticosterone, memory, and food caching in mountain chickadees (*Poecile gambeli*). Horm. Behav. 44, 93-102.

Pravosudov, V. V. & Omanska, A. 2005. Dominance-related changes in spatial memory are associated with changes in hippocampal cell proliferation rates in mountain chickadees. J. Neurobiol. 62, 31-41.

Preuschoft, S. & van Schaik, C. P. 2000. Dominance and communication: conflict management in various social settings. In: Natural conflict resolution (Aureli, F. & de Waal, F. B. M., eds). University of California Press, Berkeley, CA, pp. 77-105.

Pyle, P. 1997. Identification to North American birds. Part I: Columbidae to Ploceidae. Slate Creek Press, Bolinas, CA.

R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna (Austria). http://www.R-project.org/.

Ratcliffe, L., Mennill, D. J. & Schubert, K. A. 2007. Social dominance and fitness in black-capped chickadees. In: Ecology and behavior of chickadees and titmice: an integrated approach (Otter, K. A., ed). Oxford University Press, Oxford, pp. 131-146.

Reader, S., 2003. Innovation and social learning: individual variation and brain evolution. Anim. Biol. 53, 147-158.

Reader, S. & Laland, K. 2001. Primate innovation: sex, age and social rank differences. Int. J. Primatol. 22, 787-805.

Reader, S.M. & Laland, K.N., 2002. Social intelligence, innovation and enhanced brain size in primates. Proc. Natl. Acad. Sci. U.S.A. 99, 4436-4441.

Reader, S. M. & Laland, K. N. 2003. Animal innovation. Oxford University Press, Oxford.

Réale, D., Gallant, B., Leblanc, M. & Festa-Bianchet, M. 2000. Consistency of temperament in bighorn ewes and correlates with behaviour and life history. Anim. Behav. 60, 589-597.

Réale, D., Reader, S. M., Sol, D., McDougall, P. T. & Dingemanse, N. J. 2007. Integrating animal temperament within ecology and evolution. Biol. Rev. 82, 291-318.

Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V. & Montiglio, P.-O. 2010. Personality and the emergence of the pace-of-life syndrome concept at the population level. Philos. Trans. R. Soc. B 365, 4051-4063.

Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution 43, 223-225.

Riebli, T., Avgan, B., Bottini, A., Duc, C., Taborsky, M. & Heg, D. 2011. Behavioural type affects dominance and growth in staged encounters of cooperatively breeding cichlids. Anim. Behav. 81, 313-323.

Riebli, T., Taborsky, M., Chervet, N., Apolloni, N., Zuercher, Y. & Heg, D. 2012. Behavioural type, status and social context affect behaviour and resource allocation in cooperatively breeding cichlids. Anim. Behav. 84, 925-936.

Robertson, D. 1982. Dominance and neophobia in rats. Behav. Neural Biol. 35, 91-95.

Rohwer, S. & Ewald, P. 1981. The cost of dominance and advantage of subordination in a badge signaling system. Evolution 35, 441-454.

Røskaft, E., Järvi, T., Bakken, M., Bech, C. & Reinertsen, R. 1986. The relationship between social status and resting metabolic rate in great tits (*Parus major*) and pied flycatchers (*Ficedula hypoleuca*). Anim. Behav. 34, 838-842.

Schjelderup-Ebbe, T. 1922. Beiträge zur sozialpsychologie des haushuhns. Zeit. für Psychol. 22, 225-252.

Schubert, K. A., Mennill, D. J., Ramsay, S. M., Otter, K. A., Boag, P. T. & Ratcliffe, L. M. 2007. Variation in social rank acquisition influences lifetime reproductive success in black-capped chickadees. Biol. J. Linn. Soc. 90, 85-95.

Seibt, U. & Wickler, W. 2006. Individuality in problem solving: string pulling in two *Carduelis* species. Ethology 112, 493-502.

Self, S. G. & Liang, K.-Y. 1987. Asymptotic properties of maximum likelihood estimators and likelihood ratio tests under nonstandard conditions. J. Am. Stat. Ass. 82, 605-610.

Seyfarth, R. M., & Cheney, D. L. 2002. What are big brains for? Proc. Natl. Acad. Sci. U.S.A. 99, 4141-4142.

Shizuka, D. & McDonald, D. B. 2012. A social network perspective on measurements of dominance hierarchies. Anim. Behav. 83, 925-934.

Shizuka, D. & McDonald, D. B. 2014. A social network perspective on measurements of dominance hierarchies. Anim. Behav. 87, 243-243.

Shizuka, D. & McDonald, D. B. 2015. The network motif architecture of dominance hierarchies. J. R. Soc. Interface 12, 20150080.

Sih, A., Bell, A. & Johnson, J. 2004. Behavioral syndromes: an ecological and evolutionary overview. Trends Ecol. Evol. 19, 372-378.

Smith, S. 1976. Ecological aspects of dominance hierarchies in black-capped chickadees. Auk 93, 95-107.

Smith, S. 1984. Flock switching in chickadees - why be a winter floater. Am. Nat. 123, 81-98.

Smith, S.M., 1991. The black-capped chickadee: Behavioral ecology and natural history. Cornell University Press, Ithaca, NY.

Smith, S. 1994. Social influences on the dynamics of a northeastern black-capped chickadee population. Ecology 75, 2043-2051.

Sol, D., Stirling, D. G. & Lefebvre, L. 2005a. Behavioral drive or behavioral inhibition in evolution: subspecific diversification in holartic passerines. Evolution 59, 2669-2677.

Sol, D., Duncan, R. P., Blackburn, T. M., Cassey, P. & Lefebre, L. 2005b. Big brains, enhanced cognition, and response of birds to novel environments. Proc. Natl. Acad. Sci. U.S.A. 102, 5460-5465.

Stahl, J., Tolsma, P., Loonen, M. & Drent, R. 2001. Subordinates explore but dominants profit: resource competition in high Arctic barnacle goose flocks. Anim. Behav. 61, 257-264.

Thornton, A. & Samson, J. 2012. Innovative problem solving in wild meerkats. Anim. Behav. 83, 1459-1468.

Valderrabano-Ibarra, C., Brumon, I. & Drummond, H. 2007. Development of a linear dominance hierarchy in nestling birds. Anim. Behav. 74, 1705-1714.

Verbeek, M., Drent, P. & Wiepkema, P. 1994. Consistent individual-differences in early exploratory-behavior of male great tits. Anim. Behav. 48, 1113-1121.

Verbeek, M., Boon, A. & Drent, P. 1996. Exploration, aggressive behavior and dominance in pair-wise confrontations of juvenile male great tits. Behaviour 133, 945-963.

Verbeek, M., De Goede, P., Drent, P. & Wiepkema, P. 1999. Individual behavioural characteristics and dominance in aviary groups of great tits. Behaviour 136, 23-48.

Vervaecke, H., de Vries, H. & van Elsacker, L. 2000. Dominance and its behavioral measures in a captive group of bonobos (*Pan paniscus*). Int. J. Primatol. 21, 47-68.

Vervaecke, H., Stevens, J. M. G., Vandemoortele, H., Sigurjonsdottir, H. & De Vries, H. 2007. Aggression and dominance in matched groups of subadult Icelandic horses (*Equus caballus*). J. Ethol. 25, 239-248.

de Vries, H. 1995. An improved test of linearity in dominance hierarchies containing unknown or tied relationships. Anim. Behav. 50, 1375-1389.

de Vries, H. 1998. Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. Anim. Behav. 55, 827-843.

de Vries, H., Stevens, J. & Vervaecke, H. 2006. Measuring and testing the steepness of dominance hierarchies. Anim. Behav. 71, 585-592.

Webster, S. & Lefebvre, L. 2001. Problem solving and neophobia in a columbiform-passeriform assemblage in Barbados. Anim. Behav. 62, 23-32.

Weinrich, M. T., Schilling, M. R. & Belt, C. R. 1992. Evidence for acquisition of a novel feeding behaviour: lobtail feeding in humpback whales, *Megaptera novaeangliae*. Anim. Behav. 44, 1059-1072.

Wilson, E. O. 1975. Sociobiology: the new synthesis. Harvard University Press, Boston, MA.

Wolf, M. & Weissing, F. J. 2012. Animal personalities: consequences for ecology and evolution. Trends Ecol. Evol. 27, 452-461.

Zann, R. A. 1996. The zebra finch: a synthesis of field and laboratory studies. Oxford University Press, Oxford.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. & Graham, M. S. 2009. Mixed effects models and extensions in ecology with R. Springer, New-York.