Behavioural profile predicts dominance status in mountain chickadees, *Poecile gambeli*

Rebecca A. Fox*, Lara D. Ladage, Timothy C. Roth, II, Vladimir V. Pravosudov

Department of Biology, University of Nevada, Reno

ARTICLE INFO

Individual variation in stable behavioural traits may explain variation in ecologically relevant behaviours such as foraging, dispersal, anti-predator behaviour, and dominance. We investigated behavioural variation in mountain chickadees, a North American parid that lives in dominance-structured winter flocks, using two common measures of behavioural profile: exploration of a novel room and novel object exploration. We related those behavioural traits to dominance status in male chickadees following brief, pairwise encounters. Low-exploring birds (birds that visited less than four locations in the novel room) were significantly more likely to become dominant in brief, pairwise encounters with high-exploring birds (i.e. birds that visited all perching locations within a novel room). On the other hand, there was no relationship between novel object exploration and dominance. Interestingly, novel-room exploration was also not correlated with novel object exploration. These results suggest that behavioural profile may predict the social status of group-living individuals. Moreover, our results contradict the idea that novel object exploration and novel-room exploration are always interchangeable measures of individuals' sensitivity to environmental novelty.

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

Although individual differences in behaviour were long ignored as 'noise' around an adaptive mean (Wilson 1998; Dall et al. 2004), consistent variation in individual behavioural traits such as exploratory behaviour now appears to be associated with variation in many ecologically relevant behaviours, including dispersal distance, anti-predator behaviour, aggression towards conspecifics, nest defence and response to social defeat (Koolhaas et al. 1999; Sih et al. 2004; Groothius & Carere 2005; Reale et al. 2007; Hollander et al. 2008). Broadly, exploratory behaviour has been correlated with survival, and therefore, fitness (Smith & Blumstein 2008), although the direction of the association can be context dependent: in great tits, *Parus major*, the relationship between exploration and survival is always opposite for males and females, and varies depending on environmental conditions (Dingemanse et al. 2004). Consistent with the terminology of Groothius & Carere (2005), we use the term 'behavioural profile' to refer to interindividual behavioural differences. Commonly used proxies for behavioural profiles in nonhuman animals include escape behaviour and exploration of novel objects or environments (Benus et al. 1991; Hessing et al. 1994; Verbeek et al. 1994; Reale et al. 2000; Bolhuis

et al. 2005). A number of studies have shown that individual variation in behavioural profile is both repeatable (e.g. Armitage & van Vuren 2003; Schjolden et al. 2005) and at least moderately heritable (Dingemanse et al. 2002; Cockrem 2007), which, in conjunction with evidence that behavioural profiles influence survival (Dingemanse et al. 2004; Smith & Blumstein 2008), means that such behavioural variation may be susceptible to natural selection.

To understand fully the significance of variation in behavioural profiles, it is crucial to investigate how variation in behavioural profile may affect behaviours directly linked to individual fitness (Smith & Blumstein 2008). In socially living animals, social dominance may strongly influence fitness (e.g. Desrochers 1985; Ekman 1989; Mennill et al. 2004; Otter et al. 2007), and it is thus important to establish whether variation in behavioural profile might be linked to the acquisition of dominance status. Although social interactions are necessary for the formation of dominance hierarchies, individual variation in attributes may also be important in hierarchy formation (Chase et al. 2002). While most work on hierarchy formation has focused on variation in physical attributes, there are reasons to expect that behavioural profiles might also be important. For example, both aggressiveness and response to social defeat can be determinants of individuals' dominance ranks, and these factors are correlated with exploration-based measures of

---

* Correspondence: R. A. Fox, Department of Biology, mail stop 314, University of Nevada, Reno, Reno, NV 89557, U.S.A.
  E-mail address: rfox@unr.edu (R.A. Fox).

behavioural profile (Verbeek et al. 1996, 1999; Dingemanse & de Goede 2004).

Dominance status can affect both survival (e.g. Piper & Wiley 1990) and reproductive success (e.g. Mennill et al. 2004). Among parids, many of which live in dominance-structured flocks for at least part of the year (Ekman 1989), dominant individuals may benefit from greater access to food resources (Hogstad 1989), access to foraging locations that are safer from predators (Desrochers 1985; Ekman 1989), increased likelihood of siring both within-pair and extrapair offspring (Mennill et al. 2004), greater attractiveness to the opposite sex and higher mate retention (Otter & Ratcliffe 1996). Recent evidence also shows that subordinate black-capped chickadees, *Poecile atricapillus*, may be disproportionately affected by food limitation in poor habitats (Otter et al. 2007).

It is also clear that among parids (as well as other birds and mammals), dominants differ both behaviourally and physiologically from subordinates (Verbeek et al. 1999; Barnard & Luo 2002; Pravosudov et al. 2003; Arakawa 2006). Unsurprisingly, dominant black-capped chickadees are more aggressive than subordinates, and are also more likely to approach a feeder when other birds are present (Ficken et al. 1990). In the laboratory, subordinate mountain chickadees cache less food, are less efficient at cache retrieval, show poorer performance on a memory task and have lower rates of hippocampal cell proliferation than dominants (Pravosudov et al. 2003; Pravosudov & Omanska 2005). Subordinate males also show lower maximal corticosterone levels following acute stress (Pravosudov et al. 2003). However, it is not clear whether these behavioural differences between dominants and subordinates reflect pre-existing variations in behavioural profile or arise as a result of social rank acquisition. Work in mice suggests that the acquisition of dominance status may change exploratory behaviour (Arakawa 2006) and learning ability (Barnard & Luo 2002). However, Boogert et al. (2006) found that in starlings, *Sturnus vulgaris*, dominant and subordinate birds differ in learning speed prior to the establishment of dominance relationships between birds. Additionally, studies of great tits also show that individual differences in exploratory behaviour and stress responsiveness may predict aggression towards conspecifics (Verbeek et al. 1996), and dominance following pairwise encounters, in aviary groups, and in the wild (Verbeek et al. 1996, 1999; Dingemanse & de Goede 2004). Similar results have been found in salmonid fish (Pottinger & Carrick 2001; Schjolden et al. 2005).

The objectives of the current study were to characterize behavioural profiles in a North American parid, the mountain chickadee, and to test whether individual differences in behavioural profile relate to the acquisition of dominance status. We chose the mountain chickadee as a study species because we were specifically interested in how behavioural profile relates to the acquisition of dominance status in a species with fixed flock membership and a rigidly linear dominance hierarchy (by contrast, flocks of great tits, the other parid species in which the relationship between behavioural profile dominance has explicitly been studied, are fluid in both membership and dominance structure, with reversals of dominance status being common; Ekman 1989). Such differences in social structure may be extremely important when considering the effect of behavioural profile on the acquisition of dominance status. In great tits, a species in which challenges to dominants and dominance reversals are common (Ekman 1989), sensitivity to social defeat (which is correlated with exploratory behaviour; Verbeek et al. 1999) is crucially important in determining whether individuals are able to maintain their dominance status. In mountain chickadees, the dominance hierarchy appears to be rigid, and challenges to dominant birds are exceptionally rare (Ekman 1989), so sensitivity to social defeat seems likely to be far less important in relation to the acquisition and maintenance of

dominance status, and thus (assuming that social defeat is generally related to exploration), the relationship between exploration and dominance may be different.

To classify behavioural profiles in mountain chickadees, we chose to use measures of exploratory behaviour (both exploration of a novel flight room and behaviour towards an unfamiliar object placed in the home cage) because similar measures have been used in studies of dominance in another parid species (Verbeek et al. 1996, 1999). Although we relied on measures of exploration collected at a single time point and did not explicitly evaluate the repeatability of exploratory behaviour in mountain chickadees, we are confident that exploratory behaviour remained reasonably consistent over the timescale of the experiment. No more than 3 weeks elapsed between testing in the novel room and dominance testing, and a number of studies examining exploration in nonhuman animals have shown that within individuals, exploratory behaviour and other indexes of 'boldness' typically show substantial repeatability over periods of weeks to months, and in many cases much longer (e.g. Verbeek et al. 1994; Dingemanse et al. 2002; Armitage & Van Vuren 2003; Schjolden et al. 2005; Quinn & Cresswell 2005).

Behaviour in novel environments has been linked to the establishment of dominance relationships in both birds and fish, although the direction of the relationship between exploration of or adjustment to a novel environment and the acquisition of dominance status varies. In great tits, birds that explore a novel environment more quickly generally become dominant in staged dyadic encounters (Verbeek et al. 1996), but are subordinate to slow-exploring birds when housed in multi-individual groups in aviaries (Verbeek et al. 1999). This is thought to be related to the fact that fast-exploring birds are more aggressive, but take longer to recover from social defeat (Verbeek et al. 1999). In rainbow trout, *Oncorhynchus mykiss*, individuals that acclimate more quickly to a novel tank dominate fish that are slower to acclimate (Schjolden et al. 2005). Among chickadees, dominant individuals are typically more risk averse than subordinates and prefer to forage in less exposed locations (e.g. Desrochers 1985; Ekman 1989). Assuming that this behavioural difference between dominants and subordinates exists prior to the establishment of dominance relationships, we predicted that mountain chickadees that showed lower levels of exploratory behaviour would dominate more exploratory birds, based on the finding that exploration and other indexes of what is commonly referred to as 'boldness' are generally positively correlated with risk taking (van Oers et al. 2004b; Sih et al. 2004; Bell 2005; Quinn & Cresswell 2005).

METHODS

Animals

Subjects were 48 juvenile male mountain chickadees that were captured around Sagehen creek, Tahoe National Forest, CA (near Truckee, CA), U.S.A., on 11–12 September 2007 using mist nets near feeders. Birds for this study were captured at a network of 40 feeders situated at spatially distinct locations spread over a distance of approximately 11 km along two forest roads. Based on extensive observations at these feeders over the last 8 years, it is highly unlikely that birds trapped at different feeders on the same day belonged to the same flock (V. V. Pravosudov, unpublished data). We captured birds at 16 feeders (11 feeders on 11 September and 5 feeders that were separated from the original 11 by several km on 12 September), and thus the birds that we captured were almost certainly from at least 16 distinct flocks with nonoverlapping membership. Birds were transferred to the laboratory at the University of Nevada, Reno, U.S.A., and were housed individually in

wire-mesh cages ($60 \times 42 \times 60$ cm), which were visually, although not acoustically, isolated from one another by solid metal partitions between cages. Birds were maintained on a 10:14 h light:dark cycle at a constant 20 °C temperature and a mixture of pine nuts, shelled and unshelled sunflower seeds, crushed peanuts, and Roudybush bird pellets (Roudybush Inc., Woodland, CA, U.S.A.) was available ad libitum. Each bird was also given 6–10 mealworms daily, and ad libitum water was provided.

After 7 days in captivity, we collected one capillary tube (75 μl) of blood from the brachial vein of each bird for genetic sex determination. DNA was extracted from samples using a Qiagen DNEasy kit (Qiagen Inc., Valencia, CA, U.S.A.). Sex was determined by amplifying a portion of the sex-linked CHD genes (CHD-W in females and CHD-Z in both sexes) in a polymerase chain reaction using microsatellite primers P2 and P8 (Griffiths et al. 1998). Sex was confirmed by visual examination of the gonads after birds were killed with an overdose of sodium pentobarbital as part of another experiment. Results of the visual and genetic sexing matched 100%.

Exploration Tests

After birds had been housed in individual cages and visually isolated from other birds for 3 weeks, each bird was given two tests of exploratory behaviour based on the methods of Verbeek et al. (1994). We waited 3 weeks to administer behavioural tests because our previous research has shown that the level of the stress hormone, corticosterone, returns to its normal, undisturbed level after 3 weeks in captive settings, suggesting that the birds become habituated to captive housing in approximately 3 weeks (Pravosudov et al. 2003).

The first test measured exploratory behaviour in an unfamiliar room. Each bird was released into an experimental room ($325 \times 218 \times 312$ cm) and its behaviour observed through a one-way Plexiglas window. The room contained two artificial 'trees' with 20 perching sites. Additionally, 36 wood blocks with attached perches were attached by Velcro to two opposite walls (18 perches on each wall). No food was available in the testing room. Every home cage was connected to the experimental room by a door covered by a flap, so that birds could enter the experimental room without handling. The experimenter manipulated the lights and opened the flap so that the bird could enter or leave by flying from the dark to the light. Birds remained in the room until they had visited both trees and at least one perching site on each wall, or for 30 min, whichever was sooner. For each bird, we measured the number of perching sites visited during the 30 min time period. Birds could therefore visit a minimum of zero sites (if the bird hung from the ceiling or a wall without perches for the entire test period) and a maximum of four sites (if the bird visited both 'trees' and both walls containing perches). For those birds that visited all four perching sites, we recorded exploration time (the time required for a bird to visit all four perching locations). We also recorded the number of hops a bird made between perches during each visit to a given tree or wall (hereafter 'hops per site visit'). Our testing technique differs somewhat from the technique used by Dingemanse et al. (2004) to assess exploratory behaviour in wild-captured great tits. Dingemanse et al. (2004) used the number of flights and hops (which in great tits are known to be tightly correlated with arrival time) during the first 2 min in the novel room as a proxy for exploratory behaviour. As we did not know a priori whether activity in the novel room would be correlated with arrival time in mountain chickadees, we also measured the number of sites visited during the testing period as an alternative index of exploration. Birds were considered high-exploring if they visited all four perching locations within 30 min, and low-exploring if they did not. Additionally, although 30 min is longer than the

time typically allotted for novel-environment tests (Verbeek et al. 1994 allotted 10 min, as did Martins et al. 2007), we argue that the environment was still likely to have been quite novel to the chickadees even after half an hour. It typically takes two to three 1 h sessions in the flight room for birds to become habituated enough to the room to perform well on memory tasks (e.g. Pravosudov et al. 2003). Additionally, 12 birds failed to visit all four perching locations, suggesting that they may still have been somewhat neophobic.

The second test measured novel object exploration. Birds were videotaped for 10 min following the introduction of a novel object (a plastic Pink Panther keychain, approximately 8 cm long by 1.5 cm wide) into the home cage. An experimenter hung the novel object from the perch at the front of each bird's home cage, approximately 10 cm from the cage wall. Birds could easily reach the object while standing on the perch. We scored approach behaviour towards the novel object during a 10 min period on a scale of 1 to 4. Birds assigned a score of 1 never landed on the perch with the novel object. Birds assigned a score of 2 landed on the perch with the object but did not approach it. Birds assigned a score of 3 approached to within less than a body length of the novel object, and birds assigned a score of 4 approached the object and made bill contact with it (most birds did so while standing on the perch on which the object was hanging). Timing began immediately after the experimenter placed the object in the cage. To control for the possibility that differences in birds' behaviour towards the novel object actually reflected something other than sensitivity to the novel object (e.g. differences in sensitivity to the experimenter's manipulation of the home cage or differences in innate motivation to interact with objects placed in the home cage), birds were first given a control test with a familiar object. A balsa wood toy for small birds (Balsa Buddies Sun, Birdalog.com) was hung from the front wall of each bird's home cage for 3 days to habituate birds to the object. Following the habituation period, each bird was videotaped for 10 min after the experimenter hung the familiar object from the front perch of the home cage, and we again scored approach behaviour.

To analyse temperament structure in mountain chickadees, we examined the relationship between sites visited in the novel room, novel object approach scores and average number of hops per perching site visit. We used nonparametric measures because the data were not normally distributed (Shapiro–Wilk's test of normality: sites visited:$W = 0.56$, $P < 0.0001$; novel object approach score: $W = 0.80$, $P = <0.0001$; hops per visit: $W = 0.72$, $P < 0.0001$). P values ≤ 0.05 were considered to be statistically significant. All tests were two tailed. SAS was used for all statistical analyses (SAS Systems, Cary, NC, U.S.A.).

Dominance Tests

No more than 3 weeks after birds were tested in the novel-room, pairs of males underwent staged dyadic encounters. To determine within-pair dominance rank, we introduced pairs of unfamiliar males from different nonoverlapping social groups into the experimental flight room (the same room used during the initial novel-environment exploration tests). Although birds used in the dominance tests had never been in visual or physical contact with one another before testing, these birds were not acoustically isolated in the laboratory before testing, and thus, they may not have been totally 'unfamiliar' with one another.

Birds were allowed to enter the room without handling, and were observed through the one-way Plexiglas window. We determined dominance rank by recording typical dominance interactions including aggressive interactions (the dominant bird attacked the subordinate while the subordinate bird offered no resistance)

and passive displacements (the subordinate bird always gives way to the dominant bird; Lahti 1998; Pravosudov & Lucas 2000; Pravosudov et al. 2003). We always observed birds for at least 5 min (allowing for multiple interactions) before ending the dominance test, although dominance in pairs of male mountain chickadees is generally apparent after a single interaction, and reversals have not been observed following multiple interactions (Pravosudov & Lucas 2000; Pravosudov et al. 2003). In chickadees, dominance hierarchies are strictly linear without reversals, and the relationship between any two given birds reflects their dominance relationship within a social group (Ekman 1989; Hogstad 1989; Lahti 1998; Pravosudov & Lucas 2000; Ratcliffe et al. 2007). After we established the dominance status of each bird, birds were returned to their home cages. Because we recorded which bird behaved in a subordinate fashion (i.e. was chased by the other male, or repeatedly yielded perching locations to the other male), the outcomes of these dyadic encounters represent a measure of dominance status, rather than a simple measure of aggression per se. In fact, in several cases, the dominance relationship appeared to be established (i.e. one bird was repeatedly displaced by the other) with little or no overt aggression towards the subordinate bird on the part of the dominant individual.

We tested 12 pairs of birds consisting of one lower-exploring bird and one higher-exploring bird (i.e. birds that had visited four sites were paired with opponents that had visited either two or three sites). We also staged encounters between 13 pairs consisting of two high-exploring birds (i.e. birds that had visited all four sites within the novel room) with different exploration times. We analysed the outcomes of dyadic encounters between birds of different exploration types and between high-exploring birds with different exploration times separately, and we used birds only once in a given set of dyadic encounters. Birds were at least loosely size-matched by wing length (average difference in wing length between opponents differing in exploration type: 1.33 ± 0.48 mm; average difference in wing length between high-exploring opponents differing in arrival time: 0.45 ± 0.16 mm). Wing lengths of birds tested ranged from 68.5 to 74.5 mm.

Ethical Note

Birds were collected under U.S. Fish and Wildlife (MB022532) and California State (802017-05) scientific collecting permits. All experiments were performed under Animal Care and Use Protocol no. A05/06-39, approved by the University of Nevada, Reno Institutional Animal Care and Use Committee.

RESULTS

Behavioural Traits

All birds visited at least two perching sites in the novel room. Twelve birds failed to visit all four perching locations during the 30 min observation period and were classified as low-exploring (Fig. 1a). Of these 12 low-exploring birds, nine birds visited only two locations in the room, while the remaining three birds visited three perching sites. The remaining 36 birds visited all four perching locations within the room and were classified as high-exploring. Among high-exploring birds, latencies to visit all four perching locations within the room (i.e. exploration time) ranged from 4.38 min to 27.3 min, and appeared to follow a roughly bimodal distribution (Fig. 1b).

Low-exploring birds (those with novel-room scores of 2 and 3 sites visited) tended to make more hops during a single site visit than high-exploring birds, although the difference was not statistically significant (Kruskal–Wallis test: $\chi^2_2 < = 5.19$, $P = 0.075$;
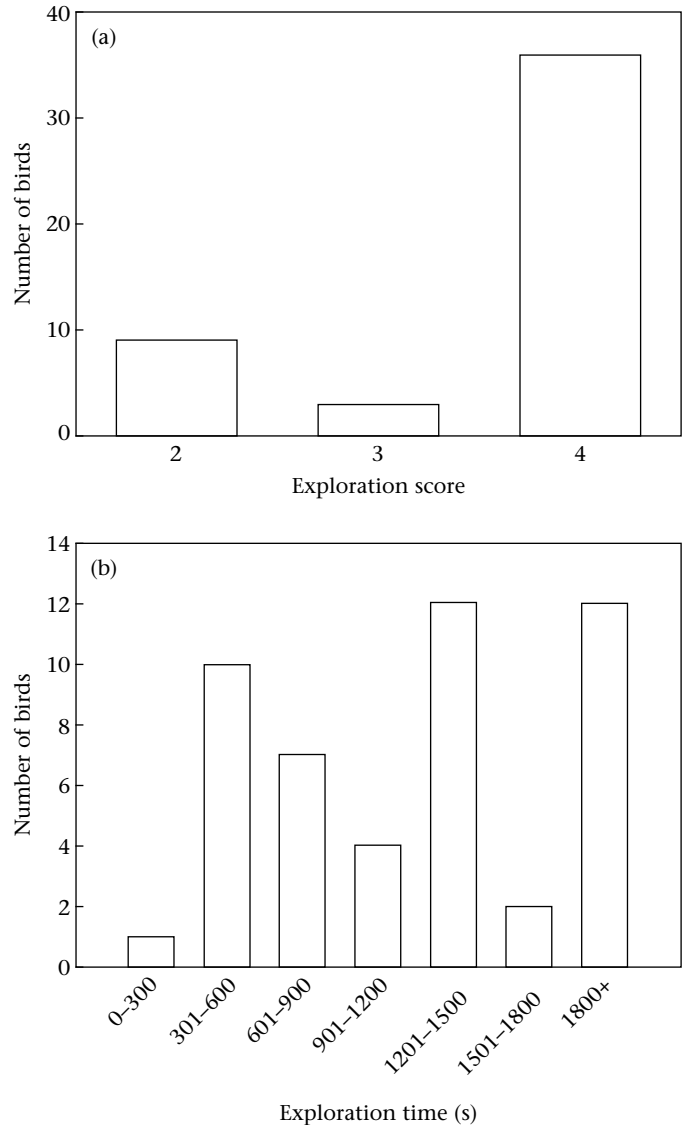

Figure 1. Distribution of (a) exploration scores and (b) exploration times for 48 mountain chickadees. Exploration score was based on the number of perching sites (range 0–4) visited in a novel room during a 30 min period.

Fig. 2). Two outliers were excluded from this analysis: among the 46 males included in the analysis, the average number of hops per visit ranged from 0.33 to 9.87; the two outlier males (a high-exploring male and a low-exploring male) averaged 17.70 and 51.30 hops per visit, respectively.

With regard to behaviour towards a novel object, all birds received a score of at least 2, indicating that they, at minimum, landed on the perch with the novel object. Novel object scores were fairly evenly distributed within the population (Fig. 3), with 12 birds receiving a score of 2 (landed on the perch with the object), 19 birds receiving a score of 3 (approached within one body length of the object), and 17 birds receiving a score of 4 (contacted the object with the bill).

There was no association between novel object approach score and the number of sites visited in the novel room (Kruskal–Wallis test: $\chi^2_2 = 1.60$, $P = 0.45$). There was no difference between birds with novel object approach scores of 2, 3 or 4 with regard to their approach scores when tested with the familiar object (Kruskal–Wallis test: $\chi^2_2 = 0.87$, $P = 0.64$), indicating that novel object approach scores were unlikely to be confounded with variation in
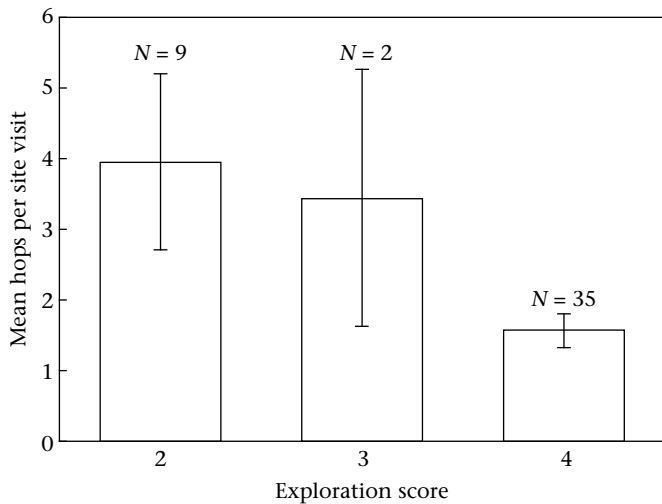
Figure 2. Association between the number of sites visited (exploration score) and the mean number of hops per site visit for mountain chickadees in the novel room. N = number of birds; two outliers are excluded.

how birds responded to the experimenter or with differences in innate motivation to explore objects placed in the cage. However, birds were apparently habituated to the familiar object: only 17 birds contacted the novel object with their bills, while 34 birds touched the familiar object. This difference was highly significant ($\chi_1^2 = 12.09$, $P = 0.001$).

Behavioural Profile and Dominance

In staged dyadic encounters between birds of different exploration type, birds with lower exploration scores were more likely to become dominant. Birds that became dominant following these encounters had previously visited an average ± SE of 2.5 ± 0.23 sites in the novel room, while birds that became subordinate had visited an average of 3.58 ± 0.23 sites in the novel room (Fig. 4). This difference was significant (Wilcoxon two-sample test:
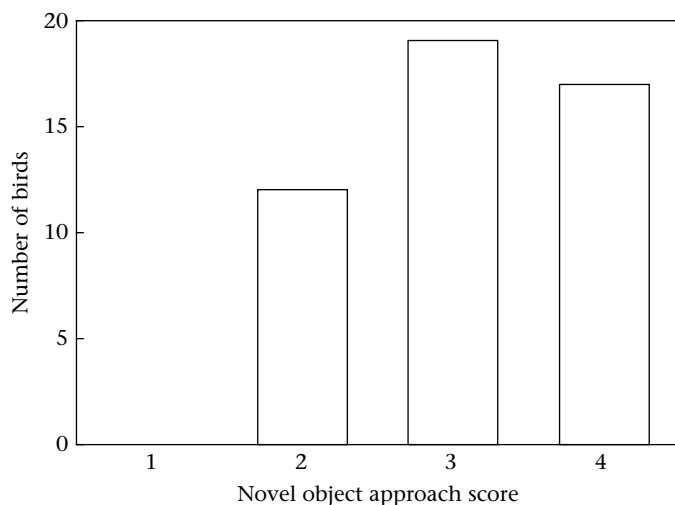
Figure 3. Distribution of novel object approach scores for 48 male mountain chickadees. A novel object was suspended from a perch in each bird's home cage for 10 min, and each bird was scored according to how closely it approached the novel object: 1 = bird did not land on the perch with the object ($N = 0$); 2 = bird landed on the perch but failed to approach the object ($N = 12$); 3 = bird approached to within one body length of the object ($N = 19$); 4 = bird touched the object with its bill ($N = 17$).

$U = 106.00$, $N_1 = N_2 = 12$, $P = 0.005$). We used a binomial test to test whether, across pairs, low-exploring birds were more likely to win dominance encounters with high-exploring birds. In 10 of 12 dyadic encounters between birds of different exploration score, the lower-exploring bird became dominant, a significantly greater proportion than expected by chance (binomial test: $N = 12$, $x \geq 10$, $P = 0.038$; Fig. 5).

While exploration type clearly affected the outcomes of staged dominance encounters between low- and high-exploring birds, variation in exploration time (another commonly used proxy for exploratory behaviour; Verbeek et al. 1994) had no significant effect on the outcome of dominance encounters between two high-exploring birds (Wilcoxon two-sample test: $U = 154.00$, $N_1 = N_2 = 13$, $P = 0.29$). There was no association between the other measures of behavioural profile and the outcome of dominance encounters either in encounters between birds with different exploration scores (Wilcoxon two-sample test: hops per site visit: $U = 167.00$, $N_1 = N_2 = 12$, $P = 0.34$; novel object approach score: $U = 158.00$, $N_1 = N_2 = 12$, $P = 0.64$), or in encounters between high-explorers that differed in exploration time (Wilcoxon two-sample test: hops per site visit: $U = 157.00$, $N_1 = N_2 = 13$, $P = 0.36$; novel object approach score: $U = 158.00$, $N_1 = N_2 = 13$, $P = 0.35$).

DISCUSSION

Characterization of Behavioural Profile in Mountain Chickadees

Mountain chickadees showed considerable interindividual variation in exploratory behaviour. Individuals showed substantial differences in the extent to which they explored a novel environment (i.e. number of perching sites visited in the novel room), the extent to which they explored individual perching sites within the novel environment (i.e. number of hops per site visit) and their behaviour towards novel objects. There was also a tendency for the number of perching sites visited during the novel-room test to be negatively correlated with the average number of perch hops per site visit, suggesting that low-exploring birds explored individual perching sites more thoroughly than did high-exploring birds. This finding may be parallel to the results of Verbeek et al. (1994), who found that great tits that took longer to explore a novel room did so partly because they explored the room more thoroughly. However, our finding could also simply be an artefact of low-exploring birds visiting fewer sites in the novel room than high-exploring birds, causing their perch hops to be spread among fewer possible sites.

The distribution of exploration types among the 48 males tested, with only three males showing what might be considered an intermediate level of exploration (i.e. visiting three of the possible four locations in the room), parallels the roughly bimodal distribution of exploratory behaviour and other measures of 'coping style' that have been widely reported in studies of fish (e.g. Schjolden et al. 2005), birds (e.g. Verbeek et al. 1994) and mammals (e.g. Benus et al. 1991). Four times as many males in our laboratory population were classified as high-exploring as were classified as low-exploring. Whether this finding reflects the actual distribution of behavioural profiles within the wild population from which these birds were drawn or merely reflects the fact that high-exploring birds may have been more likely to enter our mist nets is unknown.

Behaviour towards novel objects is another measure that is commonly used in studies of behavioural profiles or 'personalities' in animals. Novel object approach scores were much more evenly distributed than exploration types among our male mountain chickadees. Moreover, we found no relationship between exploration type and novel object scores: high-exploring birds were no
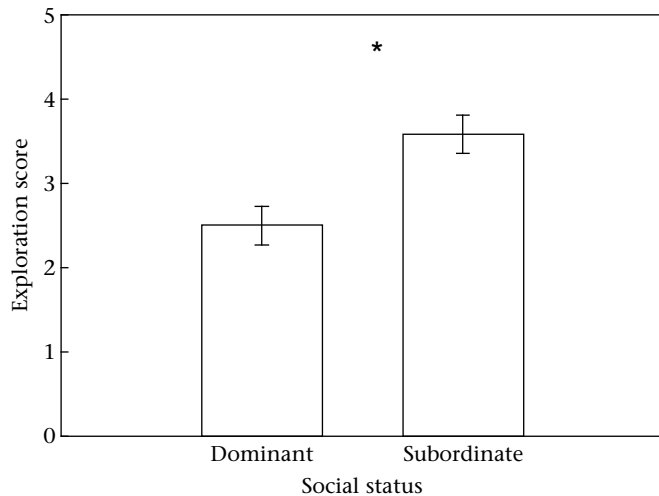
Figure 4. Association between the number of sites visited in the novel room (exploration score) and the social status of male mountain chickadees during subsequent staged dyadic encounters. $N = 12$ dyads. $*P < 0.05$.

more likely than low-exploring birds to make physical contact with an unfamiliar object placed in their home cage. This finding does not simply reflect a broad-based insensitivity to the novelty of objects: twice as many birds touched the familiar object with their bills as touched the novel object, suggesting that birds were more fearful of the unfamiliar object. Therefore, our results suggest that while mountain chickadees are sensitive to whether an object is familiar, and individual birds vary in their willingness to approach unfamiliar objects, this variation is not predicted by exploration type. It seems likely that in mountain chickadees, exploration type and novel object approach score are proxies for two different stable behavioural traits. Martins et al. (2007) found an identical result in zebra finches, *Taeniopygia guttata*, in which the correlation between the scores from novel environment and novel objects tests was not significantly different from zero. Similarly, Moretz et al. (2007) found that in zebrafish, *Danio rerio*, various measures of 'boldness' were not consistently correlated across laboratory strains. Additionally, in another parid species, research has shown
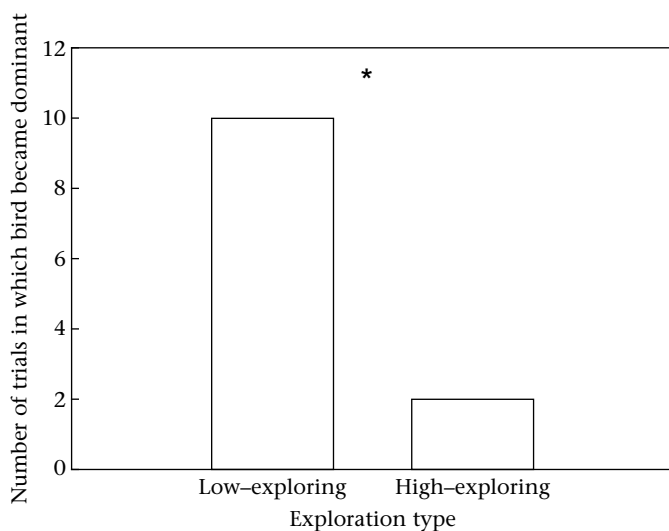
Figure 5. Number of staged dyadic encounters between male mountain chickadees in which the low-exploring bird ($N = 10$) or the high-exploring bird ($N = 2$) became dominant. $*P < 0.05$.

that novel-environment exploration and novel object exploration may have different genetic bases, although both traits are at least moderately heritable and show some correlation with one another (van Oers et al. 2004a). Both our findings and the results of Martins et al. (2007), Moretz et al. (2007) and van Oers et al. (2004a) suggest that researchers should be cautious in assuming that various measures of 'boldness' or 'exploration' are interchangeable, an assumption that seems to be fairly pervasive in reviews and meta-analyses dealing with the ecological implications of behavioural profile or temperament in animals (e.g. Gosling 2001; Reale et al. 2007; Smith & Blumstein 2008).

Behavioural Profiles and Dominance in Mountain Chickadees

While some research has shown that behavioural differences between dominants and subordinates may arise as a result of the establishment of dominance relationships (Barnard & Luo 2002; Arakawa 2006), our results suggest that dominant individuals may also differ behaviourally from subordinates prior to the establishment of social rank. Specifically, birds that were classified as low-exploring prior to the staged dyadic encounters dominated high-exploring birds in almost all cases. Parallel results have been seen in fish, although the direction of the relationship between reactivity to the stress of being in a novel environment and dominance may be different. In juvenile rainbow trout, fish that mount a low plasma cortisol response to being moved to a novel tank are significantly more likely to become dominant in staged dominance encounters with high-responding conspecifics (Schjolden et al. 2005). While we do not know whether differences in exploration type may be associated with differences in stress responsiveness in mountain chickadees, this seems like a reasonable hypothesis: in Japanese quail, *Coturnix japonica*, chickens, *Gallus domesticus*, and great tits, birds that behave more fearfully in tests of novel-environment exploration typically mount a greater corticosterone response to acute stress (reviewed in Cockrem 2007).

It is also possible that there is no direct causal link between exploration type and the acquisition of dominance status, or even between stress responsiveness and the acquisition of dominance status. Instead, as suggested by Pottinger & Carrick (2001), stress responsiveness and exploratory behaviour may simply covary with some other trait that more directly affects competitive ability, such as aggression (e.g. Verbeek et al. 1996; Armitage & Van Vuren 2003; Bolhuis et al. 2005) or response to social defeat (Verbeek et al. 1999). In captive-reared great tits, more exploratory birds are more aggressive and tend to dominate less exploratory birds in dyadic encounters (Verbeek et al. 1996). However, less exploratory birds take less time to recover from social defeat and are more likely to acquire high status when housed in larger groups (Verbeek et al. 1999). Dingemanse & de Goede (2004) found similar results in wild great tits: while 'fast'-exploring territorial males dominate 'slow'-exploring territorial males at feeding trays, among flock-living nonterritorial males, the 'slow' males dominate, presumably because they are better able to cope with the stress of living in a large group. Although the social structure of mountain chickadee flocks differs greatly from that of great tits (Ekman 1989), making direct comparison difficult, low-exploring male mountain chickadees, like slow-exploring great tits, may be better able to cope with social stress and therefore might perform better in dyadic encounters, even though they are apparently more reactive to environmental novelty than high-exploring males. It is also possible that low-exploring chickadees are more aggressive than high-exploring chickadees. Both of these hypotheses warrant further testing. However, our results clearly show that, at least in mountain chickadees, some behavioural differences between dominant and subordinate birds exist prior to the establishment of

dominance relationships. Specifically, dominant chickadees are more risk averse than subordinate birds (Desrochers 1985; Ekman 1989), and it now seems likely that this behavioural difference may actually precede the establishment of social relationships within winter flocks.

Furthermore, during establishment of dominance relationships, differences in exploration type appeared to be more salient than differences in exploration time (i.e. latency to visit all four perching locations) between high-exploring birds in our study, even when differences in exploration time were substantial. While exploration type was a significant predictor of dominance in encounters between low- and high-exploring birds, latency to visit all four perching locations in the novel room did not predict dominance status in encounters between two high-exploring birds. This finding suggests that low-explorers and high-explorers are more different from one another behaviourally than are high-explorers with very different exploration times.

Taken together, the results of the present study suggest that variation in behavioural profile may affect the establishment of dominance relationships and that measurements of exploratory behaviour are a potentially useful tool for characterizing behavioural profiles in parids. Additionally, our results strongly suggest that the observed differences in risk sensitivity between dominant and subordinate chickadees may be present before dominance relationships are established. In a broader sense, the present study adds further weight to a substantial body of research that suggests that behavioural profiles or animal 'personalities' affect behaviours directly linked to fitness, including the acquisition of dominance status, antipredator behaviour, and dispersal (Verbeek et al. 1996; Wilson 1998; Armitage & Van Vuren 2003; Dingemanse et al. 2003; Quinn & Cresswell 2005), and that, therefore, the study of behavioural profiles is important for understanding the evolutionary maintenance of behavioural variation both within and between species and populations, as suggested by Dingemanse & Reale (2005).

References

Arakawa, H. 2006. Changes in the pattern of exploratory behavior are associated with the emergence of social dominance relationships in male rats. *Developmental Psychobiology*, **48**, 39–47.

Armitage, K. B. & Van Vuren, D. H. 2003. Individual differences and reproductive success in yellow-bellied marmots. *Ethology, Ecology and Evolution*, **15**, 207–233.

Barnard, C. J. & Luo, N. 2002. Acquisition of dominance status affects maze learning in mice. *Behavioural Processes*, **60**, 53–59.

Bell, A. 2005. Behavioural differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*). *Journal of Evolutionary Biology*, **18**, 464–473.

Benus, R. F., Bohus, B., Koolhaas, J. M. & van Oortmerssen, G. A. 1991. Heritable variation for aggression as a reflection of individual coping strategies. *Experientia*, **47**, 1008–1019.

Bolhuis, J. E., Schouten, W. G. P., Schrama, J. W. & Weigant, V. M. 2005. Individual coping characteristics, aggressiveness and fighting strategies in pigs. *Animal Behaviour*, **69**, 1085–1091.

Boogert, N. J., Reader, S. M. & Laland, K. N. 2006. The relation between social rank, neophobia, and individual learning in starlings. *Animal Behaviour*, **72**, 1229–1239.

Chase, I. D., Tovey, C., Spangler-Martin, D. & Manfredonia, M. 2002. Individual differences versus social dynamics in the formation of animal dominance hierarchies. *Proceedings of the National Academy of Sciences, U.S.A.*, **99**, 5744–5749.

Cockrem, J. F. 2007. Stress, corticosterone responses, and avian personalities. *Journal of Ornithology, Supplement*, **148**, S169–S178.

Dall, S. R. X., Houston, A. I. & McNamara, J. M. 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology Letters*, **7**, 734–739.

Desrochers, A. 1985. Sex, dominance, and microhabitat use in wintering black-capped chickadees: a field experiment. *Ecology*, **70**, 636–645.

Dingemanse, N. J. & de Goede, P. 2004. The relation between dominance and exploratory behavior is context-dependent in wild great tits. *Behavioral Ecology*, **15**, 1023–1030.

Dingemanse, N. J. & Reale, D. 2005. Natural selection and animal personality. *Behaviour*, **142**, 1165–1190.

Dingemanse, N. J., Both, C., Drent, P. J., van Oers, K. & van Noordwijk, A. J. 2002. Repeatability and heritability of exploratory behaviour in great tits from the wild. *Animal Behaviour*, **64**, 929–938.

Dingemanse, N., Both, C., van Noordjwijk, A. J., Rutten, A. L. & Drent, P. J. 2003. Natal dispersal and personalities in great tits (*Parus major*). *Proceedings of the Royal Society of London, Series B*, **270**, 741–747.

Dingemanse, N. J., Both, C., Drent, P. J. & Tinbergen, J. M. 2004. Fitness consequences of avian personalities in a fluctuating environment. *Proceedings of the Royal Society of London, Series B*, **271**, 847–852.

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

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

Gosling, S. D. 2001. From mice to men: what can we learn about personality from animal research? *Psychological Bulletin*, **127**, 45–86.

Griffiths, R., Double, M. C., Orr, K. & Dawson, R. J. G. 1998. A DNA test to sex most birds. *Molecular Ecology*, **7**, 1071–1075.

Groothius, T. G. G. & Carere, C. 2005. Avian personalities: characterization and epigenesis. *Neuroscience and Biobehavioral Reviews*, **29**, 137–150.

Hessing, M. J. C., Hagelso, A. M., Schouten, W. G. P., Wiepkema, P. R. & van Beek, J. A. M. 1994. Individual behavioral and physiological strategies in pigs. *Physiology & Behavior*, **55**, 39–46.

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

Hollander, F. A., van Overveld, T., Tokka, I. & Matthysen, E. 2008. Personality and nest defence in the great tit (*Parus major*). *Ethology*, **114**, 405–412.

Koolhaas, J. M., Korte, S. M., de Boer, S. F., van der Vegt, B. J., van Reenen, C. G., Hopster, H., de Jong, I. C., Ruis, W. & Blokhuis, H. J. 1999. Coping styles: current status in behavior and stress-physiology. *Neuroscience and Biobehavioral Reviews*, **23**, 925–935.

Lahti, K. 1998. Social dominance and survival in flocking passerine birds: a review with an emphasis on the willow tit *Parus montanus*. *Ornis Fennica*, **75**, 1–17.

Martins, T. L. F., Roberts, M. L., Giblin, I., Huxham, R. & Evans, M. R. 2007. Speed of exploration and risk-taking behavior are linked to corticosterone titres in zebra finches. *Hormones and Behavior*, **52**, 445–453.

Mennill, D. J., Ramsay, S. M., Boag, P. T. & Ratcliffe, L. M. 2004. Patterns of extrapair mating in relation to male dominance status and female nest placement in black-capped chickadees. *Behavioral Ecology*, **5**, 757–765.

Moretz, J. A., Martins, E. P. & Robison, B. D. 2007. Behavioral syndromes and the evolution of correlated behavior in zebrafish. *Behavioral Ecology*, **18**, 556–562.

van Oers, K., Drent, P. J., de Jong, G. & van Noordwijk, A. J. 2004a. Additive and nonadditive variation in avian personality traits. *Heredity*, **93**, 496–503.

van Oers, K., Drent, P. J., de Goede, P. & van Noordwijk, A. J. 2004b. Realized heritability and repeatability of risk-taking behaviour in relation to avian personalities. *Proceedings of the Royal Society of London, Series B*, **271**, 65–73.

Otter, K. & Ratcliffe, L. 1996. Female initiated divorce in a monogamous songbird: abandoning mates for males of higher quality. *Proceedings of the Royal Society of London, Series B*, **263**, 351–355.

Otter, K. A., Atherton, S. E. & van Oort, H. 2007. Female food solicitation calling, hunger levels, and habitat differences in the black-capped chickadee. *Animal Behaviour*, **74**, 847–853.

Piper, W. H. & Wiley, R. H. 1990. The relationship between social dominance, subcutaneous fat, and annual survival in wintering white-throated sparrows. *Behavioral Ecology and Sociobiology*, **26**, 201–208.

Pottinger, T. G. & Carrick, T. R. 2001. Stress responsiveness affects dominant-subordinate relationships in rainbow trout. *Hormones and Behavior*, **40**, 419–427.

Pravosudov, V. V. & Lucas, J. R. 2000. The effect of social dominance on fattening and food-caching behaviour in Carolina chickadees. *Animal Behaviour*, **60**, 483–493.

Pravosudov, V. V. & Omanska, A. 2005. Dominance-related changes in spatial memory are associated with changes in hippocampal cell proliferation rates in mountain chickadees. *Journal of Neurobiology*, **62**, 31–41.

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

Quinn, J. L. & Cresswell, W. 2005. Personality, anti-predation behaviour and behavioural plasticity in the chaffinch *Fringilla coelebs*. *Behaviour*, **142**, 1377–1402.

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* (Ed. by K. A. Otter), pp. 131–146. Oxford: Oxford University Press.

Reale, D., Gallant, B. Y., Leblanc, M. & Festa-Bianchet, M. 2000. Consistency of temperament in bighorn ewes and correlates with behaviour and life history. *Animal Behaviour*, **60**, 589–597.

Reale, D., Reader, S. M., Sol, D., McDougall, P. T. & Dingemanse, N. J. 2007. Integrating animal temperament with ecology and evolution. *Biological Reviews*, **82**, 291–318.

Schjolden, J., Stoskhus, A. & Winberg, S. 2005. Does individual variation in stress responses and agonistic behavior reflect divergent stress coping strategies in juvenile rainbow trout? *Physiological and Biochemical Zoology*, **78**, 715–723.

Sih, A., Bell, A. M., Johnson, J. C. & Ziemba, R. M. 2004. Behavioural syndromes: an integrative overview. *Quarterly Review of Biology*, **79**, 241–277.

Smith, B. R. & Blumstein, D. T. 2008. Fitness consequences of personality: a meta-analysis. *Behavioral Ecology*, **19**, 448–455.

Verbeek, M. E. M., Drent, P. J. & Wiepkema, P. R. 1994. Consistent individual differences in early exploratory behaviour of male great tits. *Animal Behaviour*, **48**, 1113–1121.

Verbeek, M. E., Boon, A. & Drent, P. J. 1996. Exploration, aggressive behaviour, and dominance in pair-wise confrontations of juvenile male great tits. *Behaviour*, **133**, 23–48.

Verbeek, M. E., DeGoede, P., Drent, P. J. & Wiepkema, P. R. 1999. Individual behavioral characteristics and dominance in aviary groups of great tits. *Behaviour*, **136**, 23–48.

Wilson, D. S. 1998. Adaptive individual differences within single populations. *Philosophical Transactions of the Royal Society of London, Series B*, **353**, 199–205.