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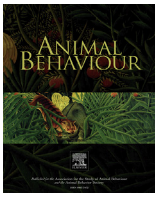

Personality does not predict social dominance in wild groups of black-capped chickadees

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Dominance hierarchies characterize social groups of various species and can significantly influence individual fitness. Personality traits, consistent behavioural differences between individuals, have been proposed to influence individuals' social status. However, few studies so far have investigated the link between personality traits and dominance in groups of animals in the wild. Here, we investigated the relationship between three personality traits hypothesized to be linked to the proactive–reactive axis (i.e. exploration, activity and object neophilia) and dominance in wild groups of black-capped chickadees, *Poecile atricapillus*, a resident passerine bird that overwinters 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 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 dominance, and there was no evidence that they correlated as part of a syndrome. These results suggest that proactive–reactive personality traits do 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.

Social dominance has been shown to strongly influence individual fitness in group-living animals of various taxa (reviewed in Ellis, 1995; Huntingford & Turner, 1987). Two main hypotheses have been proposed to explain the formation of dominance hierarchies: dominance ranks could be predetermined by differences in 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, Tovey, Spangler-Martin, & Manfredonia, 2002). While much work has focused on the association of hierarchical relationships with physical attributes of individuals such as body size, sex and age, the influence of behavioural attributes on dominance is less clear.

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 Bell, Hankison, & Laskowski, 2009; Dall & Griffith, 2014). Consistent individual differences in behaviour may affect animal life-history traits and interactions with the environment in several ways, for instance by affecting growth, fecundity, response to predators, food sources or habitat, and social or sexual interactions with conspecifics (Biro & Stamps, 2008; Réale, Reader, Sol, McDougall, & Dingemanse, 2007). 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 (Réale et al., 2007; Sih, Bell, & Johnson, 2004; Wolf & 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). Following this axis, individuals with proactive personality type exhibit high aggressiveness, high activity, high propensity to take risks, and fast and superficial exploration, whereas reactive individuals are characterized by low aggressiveness, low activity, low propensity to take risks and slow but thorough exploration (Koolhaas et al., 1999). Proactive individuals are suggested to exhibit a fast lifestyle (Réale et al., 2010). Because proactivity may positively correlate with competitive ability, we would expect positive relationships between proactive traits and

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dominance rank. Indeed, some studies have reported that dominant individuals tend to be more proactive (David, Auclair, & Cézilly, 2011), exploratory (Cole & Quinn, 2012; Favati, Leimar, & Lovlie, 2014; Verbeek, Boon, & Drent, 1996) and active when presented with a novel object or refuge (Colléter & Brown, 2011; Dahlbom, Lagman, Lundstedt-Enkel, Sundstrom, & Winberg, 2011) and more aggressive towards conspecifics (Riebli et al., 2011; Verbeek et al., 1996) than subordinates (reviewed by Briffa, Sneddon, & Wilson, 2015).

Experiments investigating social dominance and personality in group settings, however, report conflicting results, with some having found significant correlations between dominance and personality traits (Cole & Quinn, 2012; David et al., 2011; Dingemanse & de Goede, 2004; Verbeek, de Goede, Drent, & Wiepkema, 1999), and others no significant effects (Boogert, Reader, & Laland, 2006; Funghi, Leitao, Ferreira, Mota, & Cardoso, 2015; Kurvers et al., 2009; Réale, Gallant, Leblanc, & Festa-Bianchet, 2000; Riebli et al., 2012). Moreover, with only a few noticeable exceptions (Cole & Quinn, 2012; Dingemanse & de Goede, 2004; Réale et al., 2000), 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 more similar 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.

In this study, we examined the relationship between social dominance in wild animal groups, and exploration, activity and neophilia, three personality traits hypothesized to characterize the proactive–reactive axis. We also tested for the presence of a proactive–reactive behavioural syndrome using our three personality traits, as this syndrome (or any other, to our knowledge), has never been investigated in our study species, the black-capped chickadee, *Poecile atricapillus*. Black-capped chickadees are small resident parids widespread in North America. They form nonbreeding flocks in autumn and winter, with an average group size of eight individuals (Odum, 1942; Ratcliffe, Mennill, & Schubert, 2007; Smith, 1991). These flocks are typically characterized by stable membership and are organized into strict linear dominance hierarchies (Hartzler, 1970; Ratcliffe et al., 2007; Smith, 1976, 1991). Linear hierarchies occur predominantly in small social groups, and their two main criteria are asymmetry of dyadic relationships and transitivity of dominance relationships (Appleby, 1983; Chase, 1980; Shizuka & McDonald, 2012). In black-capped chickadee hierarchies, males are usually dominant over females, and adults tend to dominate young birds (Desrochers, Hannon, & Nordin, 1988; Odum, 1942; Ratcliffe et al., 2007; Smith, 1991); dominants have also been found to be leaner than subordinates (Schubert et al., 2007), but the impact of personality traits on dominance rank is not well understood. We predicted that dominant birds would exhibit more proactive personality types (i.e. be more exploratory, active and neophilic than subordinate individuals).

METHODS

Study Sites and Subjects

Our 15 study sites were located within the vicinity of the cities of Ottawa (ON) and Gatineau (QC). We established one feeder location per site. All sites were separated from each other by a distance of at least 2 km to prevent any overlap between groups' homes ranges (about 10–20 ha; reviewed in Smith, 1991). These locations indeed seemed to be independent as we never caught or observed a bird from another site on a given location. Birds were caught using a mist net or Potter trap from 3 November to 6 December 2013 and from 26 September to 9 December 2014. Individuals were fitted with a metal leg band, a colour band and a coloured passive integrated transponder (PIT tag). We recorded body mass (g), as well as wing, tail and tarsus lengths (mm). Body condition 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, Cram, & Quinn, 2011; Cole & 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, Smith, & Van Buskirk, 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, 1989; Desrochers et al., 1988; D. J. Mennill, personal communication). We compared results obtained using a discriminant function already available from the same geographical area for this species (D. J. Mennill, personal communication) with those from DNA sexing analyses on a subsample of birds in our study population. Out of 29 individuals, 28 (96.6%) were sexed accurately. We thus concluded that this discriminant function was sufficiently accurate and used it to sex other birds (71% identifiable) in our population.

Personality Assays

We measured three personality traits in the field: exploration of a novel environment, activity and object neophilia. The behaviours were recorded at 15 study sites after banding and measurement, using an open-field test modified from Kluen, Kuhn, Kempenaers, and Brommer (2012). Each bird was tested individually in a standard commercial bird cage (40 × 60 × 40 cm; see also Stuber et al., 2013), which had three perches positioned at the bottom, middle and uppermost levels, and opaque panels on the back and sides. The open-field assay was videorecorded for subsequent analyses, with no observer around the cage during the test. The assay lasted 14 min and was divided in three phases, measuring exploration (first 10 min), activity (2 min) and neophilia (2 min). Interobserver reliability when scoring behaviours from the videos was assessed using correlation coefficients (Martin & Bateson, 2007), and were all >0.95.

Exploration Behaviour

During the first phase of the open-field assay, considered to be the 'novel environment test', we recorded the time needed to visit the four corners of the cage (in seconds). We considered this measure to be analogous to the classical captive test using the time required to visit a certain number of artificial trees (Drent, van Oers, & van Noordwijk, 2003; Verbeek, Drent, & Wiepkema, 1994). The novel environment exploration period was fixed at 10 min (Drent et al., 2003; Kozlovsky, Branch, Freas, & Pravosudov, 2014; Kurvers et al., 2009; Verbeek et al., 1994). Birds that did not visit all four corners within 10 min were given a maximum latency of 600 s (i.e. 10 min; Verbeek et al., 1994).

Activity

While the exploration variable quantified the time needed to visit four novel locations in the cage, the activity variable measured the extent to which a bird moved in the cage, without regard as to the novelty of each location visited. After the first 10 min of the test, we recorded the bird's activity level for 2 min (see also Kluen et al., 2012; Kozlovsky et al., 2014, for an initial exploration period lasting up to 10 min). We used the number of movements through the cage, by counting hops and short flights, as an estimate of overall activity level

(Bókony, Kulcsar, Toth, & Liker, 2012; Overington, Cauchard, Côté, & Lefebvre, 2011). This behaviour was scored using the software JWatcher Video version 1.0 (see Blumstein & Daniel, 2007).

Neophilia

We quantified neophilia as the latency to approach a novel object in a familiar environment (Greenberg, 2003; Mettke-Hofmann, Winkler, & Leisler, 2002; Miranda, Schielzeth, Sonntag, & Partecke, 2013). During the third phase of the open-field assay, we introduced a novel object (a small pink cardboard box) and hooked it to the roof of the cage. We chose a pink-coloured object, following Kluen et al. (2012) (see also Fox, Ladage, Roth, & Pravosudov, 2009; Herborn et al., 2010; Verbeek et al., 1994), 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 s (i.e. 2 min). 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 cannot be completely excluded.

Dominance

To assess dominance hierarchies, we recorded dyadic interactions between banded birds at feeding platforms (30 × 30 cm) (e.g. Ratcliffe et al., 2007), one per site at each of eight sites, from 9 February to 24 March 2015. Wooden platforms were installed on 2 m poles during the banding period in the autumn to allow acclimation prior to observations. We placed a handful of sunflower seed on the platform and recorded dominance interactions by video throughout the day. An individual was considered the winner of an interaction when it (1) supplanted or chased an opponent, (2) resisted an attack by an opponent, (3) elicited a submissive posture in an opponent or (4) fed while an opponent waited to take a seed (Ficken, Weise, & Popp, 1990; Otter, Ratcliffe, Michaud, & Boag, 1998; Ratcliffe et al., 2007).

To construct hierarchies with the recorded interactions, we calculated a David's score for each banded individual of a group (David, 1987; Gammell, de Vries, Jennings, Carlin, & Hayden, 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 (Cole & Quinn, 2012; Dingemanse & de Goede, 2004), regardless of their sex (i.e. male, female or unknown). As restricting analyses to males produced qualitatively similar results, we only present results with both sexes included.

To calculate the David's score, we used the procedure from Gammell et al. (2003) with correction from de Vries (1998; de Vries, Stevens, & Vervaecke, 2006). When calculating David's scores, using the dyadic proportion of wins (P_{ij}) by individual i during its interactions with another individual j 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 (Gammell et al., 2003; de Vries, 1998). 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; de Vries et al., 2006). The dyadic dominance index D_{ij} is suggested to be a better estimator of the win probability (de Vries et al., 2006). We did not proceed with normalization of the David's score as proposed by de Vries et al. (2006) because we observed different group sizes (N ranging from 3 to 12; mean ± SE = 6.9 ± 0.8). With normalization, some dominants and subordinates from flocks of different sizes would have received equivalent normalized scores despite their difference in status (i.e. equivalent scores for dominants of smaller groups and subordinates of larger groups). The adjusted David's score, hereafter ‘dominance score’, was calculated using the R package ‘steepness 0.2–2’ (Leiva & de Vries, 2014). 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, Petit, & Vézina, 2012).

The degree of linearity of dominance hierarchies often has been measured using Landau's h (Landau, 1951) and de Vries' 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 & Cords, 2011; Shizuka & McDonald, 2012). The presence of unknown dyadic relationships is a common problem in empirical studies, especially when studying 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 dominant–subordinate relationship was already established, and thus subordinates would keep a safe distance from dominants to prevent agonistic interactions (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 the video cameras did not record interactions outside of the feeding platform. 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 (Appleby, 1983; Chase, 1980; Shizuka & McDonald, 2012). Asymmetry occurs when there is a clear dominant–subordinate relation between dyad members (i.e. one individual consistently wins over the other) whereas 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 over no one (A > B > C; Fig. 1) (Appleby, 1983; Chase, 1980). 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 (Fig. 1) (Appleby, 1983; Chase, 1980).

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 & Wensing, 1987). This index has been used in studies on

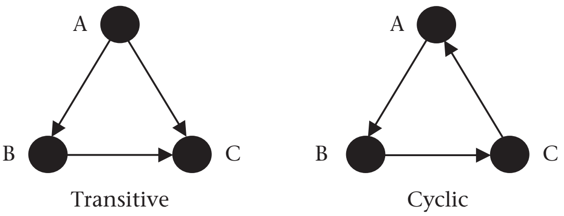

Figure 1. Configuration of transitive and cyclic (intransitive) triads among individuals A, B and C.

a variety of species to quantify the asymmetry of wins within pairwise relationships (e.g. Côté, 2000; Chiarati, Canestrari, Vera, Marcos, & Baglione, 2010; Vervaecke, Stevens, Vandemoortele, Sigurjónsdóttir, & de Vries, 2007; Vervaecke, de Vries, & van Elsacker, 2000). The DCI is obtained 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 within the dyad: $\mathrm{DC} = (\mathrm{H} - \mathrm{L})/(\mathrm{H} + \mathrm{L})$. It ranges from 0 (equal exchange) to 1 (completely unidirectional). 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' (same number of wins for both dyad members) (Chiarati et al., 2010; Vervaecke et al., 2000, 2007). Second, 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 (Fig. 1) relative to all triads (P_t) and the 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 some dyads do not interact (Shizuka & McDonald, 2012).

Statistical Analyses

We assessed within-year repeatability of the personality variables using all trials, and including 20 individuals with two assays separated by 3–10 weeks in 2015 ($N = 149$–153). We calculated adjusted repeatability (i.e. repeatability controlling for confounding effects as random or fixed effects; Nakagawa & Schielzeth, 2010) using linear mixed-effects models (LMMs) and the R package 'lme4' (Bates, Maechler, Bolker, & Walker, 2010). We used one personality measure as the response variable with individual identity as a random intercept nested in group (one group per site), and Julian date, time, method of capture (mist net or trap) and trial number (1 or 2) as fixed terms. We used log-transformed response variables when the transformation improved normality of the model's residuals. Statistical significance was tested using a likelihood ratio test (LRT) (Bolker et al., 2009), and *P* values were adjusted for boundary effects by halving them (Dominicus, Skrondal, Gjessing, Pedersen, & Palmgren, 2006). Confidence intervals were generated using parametric boostrapping with 1000 iterations (Nakagawa & Schielzeth, 2010) with the function 'confit' in the package 'stats' (R Core Team, 2015).

We investigated the presence of correlations between pairs of personality traits using pairwise correlations with Bonferroni correction for multiple testing (Rice, 1989) after attempting to reduce the traits using a principal component analysis. 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 and time) on each personality trait, and to include these variables in the dominance versus personality analyses only if significant. For this analysis we used an LMM with each personality trait as the response variable, group as a random intercept and the potential confounding variables as fixed factors. We examined the predictive value of known determinants of dominance (age, sex, body condition, body size; Ratcliffe et al., 2007; Smith, 1991) in LMMs including a random intercept for group and either David's score or weighted ranks as the response variable. For the analyses of dominance versus personality, we carried out LMMs 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 and time. We fitted linear mixed models using the 'lmer' function in the 'lme4' package (Bates et al., 2010). All analyses were conducted in R v.3.2.1 and v.3.2.3 (R Core Team, 2015).

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 (1758 and 1759).

RESULTS

Characterization of Personality Traits

Two behaviours assessed in the personality assays were significantly repeatable: exploration ($R = 0.39$, CI = 0.23–0.46, $P = 0.005$) and neophilia ($R = 0.36$, CI = 0.13–0.45, $P = 0.037$). Activity was also significantly repeatable, but its repeatability value was lower and the lower confidence interval was very close to zero ($R = 0.27$, CI $\leq$ 0.01–0.40, $P = 0.043$). There was no evidence for a behavioural syndrome in our data: each personality trait loaded onto a distinct principal component (PC1: eigenvalue <1, only 46% variance explained), and there was no significant correlation between any of the personality traits (Table 1). Moreover, none of the personality traits were significantly associated with sex, age, body condition, wing length, date or time of test (Table 2). Inter-site variability for each personality variable is presented in the Appendix.

Table 1
Correlations between pairs of personality traits

Pairs of personality traits	Pearson *r*	*df*	*P*[*]
Exploration – neophilia	0.05	76	0.646
Exploration – activity	−0.19	75	0.090
Neophilia – activity	−0.06	78	0.596

[*] *P* value of each correlation before Bonferroni correction.

Table 2
Potential confounding variables of exploration, activity and neophilia from three linear mixed models including random intercept 'group'

Fixed terms	Estimate	±SE	*df*	*F*	*P*
Exploration					
Sex	33.14	95.47	45.07	0.120	0.730
Age	12.28	58.51	45.07	0.044	0.835
Body condition	36.93	41.23	45.07	0.802	0.375
Wing length	−1.894	18.19	45.07	0.011	0.918
Date	2.026	1.233	45.07	2.701	0.107
Time of test	4.417	17.49	45.07	0.064	0.802
Activity					
Sex	7.645	8.183	46.87	0.873	0.355
Age	−5.215	4.872	46.95	1.145	0.290
Body condition	2.236	3.512	40.38	0.405	0.528
Wing length	−2.167	1.588	44.99	1.863	0.179
Date	−0.076	0.103	16.80	0.535	0.475
Time of test	1.998	1.513	32.98	1.744	0.196
Neophilia					
Sex	1.144	18.23	46.01	0.004	0.950
Age	14.67	11.22	46.01	1.709	0.198
Body condition	−2.240	7.849	46.01	0.081	0.777
Wing length	−2.313	3.493	46.01	0.438	0.511
Date	0.138	0.232	46.01	0.355	0.554
Time of test	0.117	3.357	46.01	0.001	0.972

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

Dominance Hierarchies

Dominance hierarchies in our black-capped chickadee 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 mean DCI ± SE was 0.91 ± 0.03. Out of 183 known dyads, 173 were asymmetric, with 154 exhibiting ‘one-way relationships’ and 19 showing ‘two-way relationships’, whereas 10 did not show a clear dominant–subordinate relation. All triads were transitive ($P_t = t_{\text{tri}} = 1$) in three groups, whereas five other groups were significantly more transitive than expected by null models (mean $P_t = 0.94$, mean $t_{\text{tri}} = 0.76$, $P < 0.05$). The number of interactions per dyad was variable with a mean ± SE of 3.00 ± 0.22.

A dominance score was calculated for 66 individuals from eight groups. Sex had a strong significant influence on dominance (Table 3), with males dominating females in more than 95% of the cases. Within males, there was a nonsignificant tendency for larger individuals to have higher dominance scores, correcting for age and body condition (LMM estimate ± SE = 1.767 ± 0.936, $F_{1,26} = 3.56$, $P = 0.070$), but this trend was not detected using weighted ranks (LMM estimate ± SE = -0.046 ± 0.028, $F_{1,26} = 2.66$, $P = 0.115$). Dominance was not significantly affected by age class or body condition (Table 3).

Dominance and Personality Traits

Our results showed no significant relationship between dominance and any of the personality traits (Table 4, Fig. 2). Repeating analyses excluding individuals with ceiling values (i.e. failing to contact all four corners in the exploration assay within 600 s or failing to approach the object in the neophilia assay within 120 s) also returned nonsignificant results: exploration (David's score: LMM estimate ± SE = -0.003 ± 0.008, $F_{1,47} = 0.178$, $P = 0.675$; weighted ranks: LMM estimate ± SE = -0.00004 ± 0.0003, $F_{1,47} = 0.022$, $P = 0.883$); neophilia (David's score: LMM estimate ± SE = -0.028 ± 0.055, $F_{1,35} = 0.262$, $P = 0.612$; weighted ranks: LMM estimate ± SE = 0.001 ± 0.002, $F_{1,35} = 0.580$, $P = 0.451$).

DISCUSSION

The main aim of this study was to investigate the relationship between three personality traits (exploration, activity and neophilia) and social dominance measured in natural groups in the wild. We found that hierarchies in our study groups were linear, with transitive and asymmetric dominance relationships. All personality traits exhibited repeatability values in the range of those observed in other species for these traits (Bell et al., 2009). However, our results did not reveal any significant correlations between the three personality traits and dominance measures.

Table 3
Predictors of dominance (David's score or weighted ranks) from two linear mixed models including fixed factors sex, age and body condition, as well as random intercept ‘group’

Fixed effect	Estimate	±SE	*df*	*F*	*P*
Dominance score (David's score)					
Sex	13.32	2.544	39	27.44	**<0.001**
Age	−1.761	2.206	39	0.637	0.430
Body condition	−0.769	2.095	39	0.135	0.715
Weighted ranks					
Sex	−0.420	0.078	39	29.24	**<0.001**
Age	0.065	0.067	39	0.928	0.341
Body condition	0.022	0.064	39	0.123	0.728

Reference categories with estimates set to 0 are sex (=female) and age (=adult). Significant *P* values are presented in bold.

Table 4
Results of linear mixed models including one of the two dominance measurements (dominance score or weighted ranks) as response variable, group as a random intercept and exploration, activity or neophilia as fixed factor (one per model)

Fixed effect	Estimate	±SE	*df*	*F*	*P*
Dominance score (David's score)					
Exploration	−0.002	0.006	60	0.114	0.736
Activity	0.006	0.075	61	0.0069	0.934
Neophilia	−0.026	0.029	60	0.801	0.374
Weighted ranks					
Exploration	−0.0001	0.0002	60	0.186	0.668
Activity	0.001	0.002	61	0.244	0.623
Neophilia	0.001	0.001	60	0.672	0.416

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 (Desrochers et al., 1988; Glase, 1973; Hartzler, 1970; Smith, 1976). 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 previous studies of black-capped chickadees and parids in general (Odum, 1942; Ratcliffe et al., 2007; Smith, 1991).

We found no significant correlations between pairs of personality traits, and thus no evidence of a behavioural syndrome in our data, suggesting that the proactive–reactive axis does not exist in black-capped chickadees, is composed of different personality traits, or was not present in our population during the nonbreeding season. Other personality traits are known to be repeatable in black-capped chickadees (capture order: Guillette, Bailey, Reddon, Hurd, & Sturdy, 2010; object neophobia: An, Kriengwatana, Newman, MacDougall-Shackleton, & MacDougall-Shackleton, 2011), but to our knowledge there has been no other attempt at examining the proactive–reactive axis, or any other behavioural syndrome in this species, and thus we cannot distinguish among these possibilities. Within close relatives of the black-capped chickadee, studies on great tits, *Parus major*, showed positive correlations between exploratory behaviour and aggressiveness (Verbeek et al., 1996) or risk taking (van Oers, Drent, de Goede, & van Noordwijk, 2004), while studies on mountain chickadees, *Poecile gambeli* (Fox et al., 2009) and blue tits, *Cyanistes caeruleus* (Herborn et al., 2010) found no correlation between exploratory tendency and object neophobia, suggesting that the components of proactivity syndromes may vary between species. Similarly, discrepancies in trait correlations were found between populations of the same species exposed to different environments (e.g. in three-spined sticklebacks, *Gasterosteus aculeatus*: Bell, 2005; Bell & Sih, 2007; Dingemanse et al., 2007), suggesting that behavioural syndromes may be population dependent and vary along selective factors.

As all three of our personality traits were measured over a short time frame in the field, we cannot exclude the possibility that one or more of our variables were influenced by a stress response caused by handling or the novelty of the test context (Carter, Feeney, Marshall, Cowlishaw, & Heinsohn, 2013), which is also a potential issue with animals transported only briefly to captivity for behavioural assessment (Archard & Braithwaite, 2010). Studies assessing the ecological relevance of tests of individual responses to novelty suggest that rapid assays may indeed be representative of natural behaviour; for instance, exploration in a captive cage test correlated with the number of feeders visited in the field in blue tits (Herborn et al., 2010). However this relationship was not found in wild zebra finches, *Taeniopygia guttata* (McCowan, Mainwaring, Prior, & Griffith, 2015). Clearly, more studies investigating the ecological relevance of short-term personality assays conducted in the field are needed to refine our characterization of repeatable behavioural axes.

Our results showed no significant relationship between dominance in wild groups of black-capped chickadees and personality traits, namely exploration of a novel environment, activity and object neophilia. Some studies have reported that personality traits can predict social dominance, although most of these studies used status derived from contests between dyads in captivity (An et al., 2011; Dahlbom et al., 2011; Favati et al., 2014; Fox et al., 2009; Riebli et al., 2011; Verbeek et al., 1996). However, the relevance of experiments on isolated pairs for understanding dominance in animals groups has been questioned (e.g. Chase, Tovey, & Murch, 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 led to several changes in dominance and leadership status (Beauchamp, 2000). Moreover, Chase et al. (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 an increased probability of losing later ones; Chase, Bartolomeo, & Dugatkin, 1994; Hsu & Wolf, 1999) found in isolated pairs either disappeared or were significantly reduced when examining pairs within social contexts (Chase et al., 2003). Furthermore, studies on the same species found different relationships between dominance and behavioural traits when testing animals under dyadic versus group conditions: opposite relationships between exploratory behaviour and dominance were found in great tits (Verbeek et al., 1996, 1999), and different trends between aggressive behavioural types and the likelihood of obtaining a dominant position were found in cichlid fish depending of the social context (Riebli et al., 2011, 2012). It therefore appears that personality traits and attributes in general (i.e. behavioural and physical) do not have the same predictive value of dominance encounters for animals within social groups. This may explain why, by looking at individuals within their social groups rather than only within 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 have also yielded conflicting results. For the most part, no significant association was found between dominance and various behavioural traits: docility and trappability in bighorn sheep, *Ovis canadensis* (Réale et al., 2000); neophobia in starlings, *Sturnus vulgaris* (Boogert et al., 2006); exploration, activity and novel object response in barnacle geese, *Branta leucopsis* (Kurvers et al., 2009); aggressive propensity in cichlid fish (Riebli et al., 2012); and exploration, neophobia, fear and sociability in common waxbills, *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 (Cole & Quinn, 2012; Dingemanse & de Goede, 2004; Verbeek et al., 1999). 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. While black-capped chickadees live in stable tight social units and form highly linear dominance hierarchies (Ekman, 1989; Hartzler, 1970; Ratcliffe et al., 2007; Smith, 1976, 1991; also the present study), great tits live in a more loosely organized system of fission–fusion flocks (Aplin, Farine, Morand-

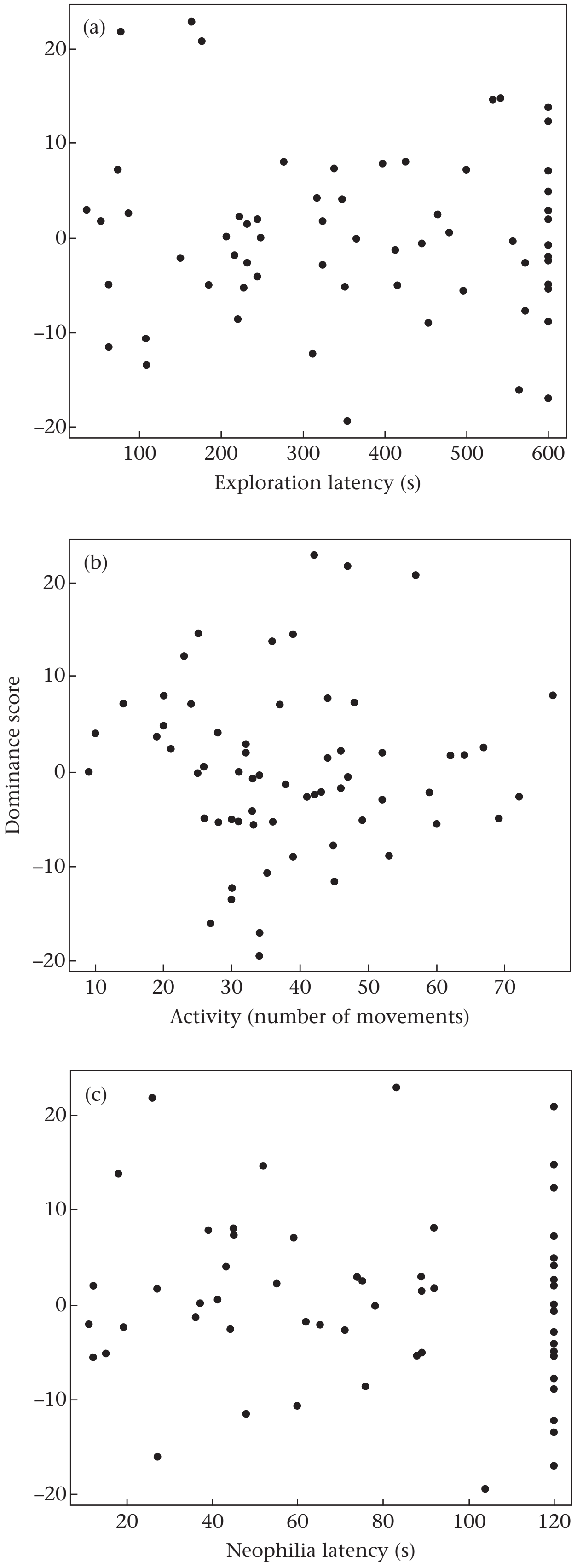

Figure 2. Dominance score (i.e. David's score) in relation to (a) exploration of a novel environment (latency to explore the four corners of the cage, $N = 62$), (b) activity (number of hops and short flights, $N = 63$) and (c) object neophilia (latency to approach the object, $N = 62$).

Ferron, & Sheldon, 2012; Ekman, 1989). Among other characteristics, these flocks express unstable membership and site-dependent social dominance (Ekman, 1989). 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), which are similar to our measures of exploration, activity and object neophilia.

Overall, there is increasing evidence that differences in intrinsic individual characteristics 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, Zapata, Samaniego, & Soto-Gamboa, 2013). Indeed, theoretical and modelling work found that individual attributes were not sufficient to account for hierarchy linearity observed in groups of animals (Beacham, 2003; Chase, 1974, 1980; Landau, 1951). Furthermore, Verbeek et al. (1999) showed, in a study on the formation of great tit dominance hierarchies, that stable organization resulted from a gradual process, established after a dynamic phase characterized by a peak in the frequency of interactions 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 et al. (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. Therefore, it 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; David et al., 2011; Valderrabano-Ibarra, Brumon, & Drummond, 2007).

The current study is the first, to our knowledge, to address the potential relationship between social dominance and personality in wild avian groups exhibiting a linear dominance hierarchy, as well as the first to test for the presence of any behavioural syndrome in the black-capped chickadee, a commonly studied passerine bird. We found no significant relationships between dominance and three personality traits, suggesting that these personality traits do 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 social 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.

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Appendix

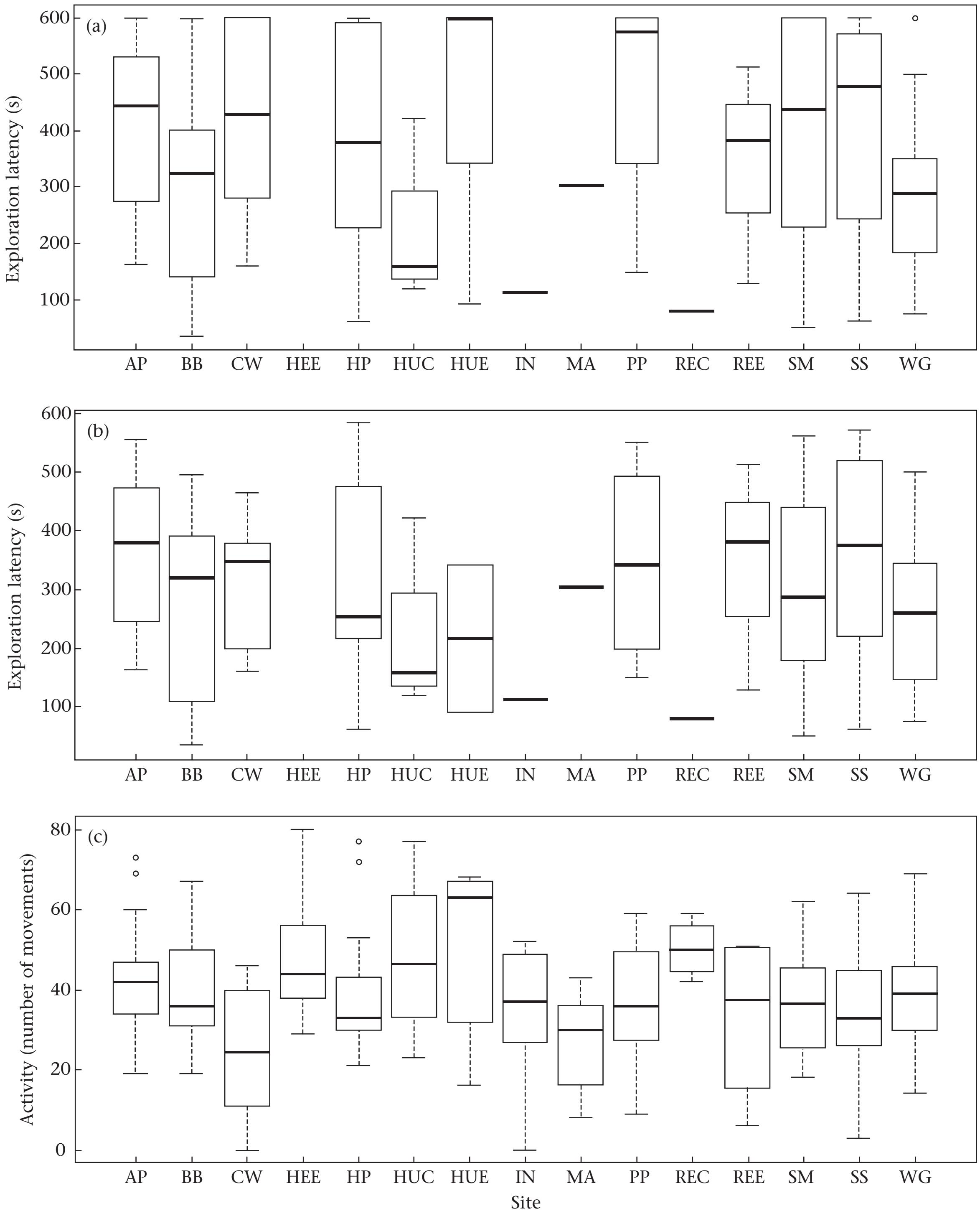

Figure A1. Inter-site variability of the personality measures for the 15 sites where personality assays were carried out: (a) exploration of a novel environment (latency to explore the four corners of the cage); (b) exploration excluding ceiling latencies (i.e. 600 s); (c) activity (number of hops and short flights); (d) object neophilia (latency to approach the object) and (e) object neophilia excluding ceiling latencies (i.e. 120 s). Individuals for which dominance was not recorded are also included.

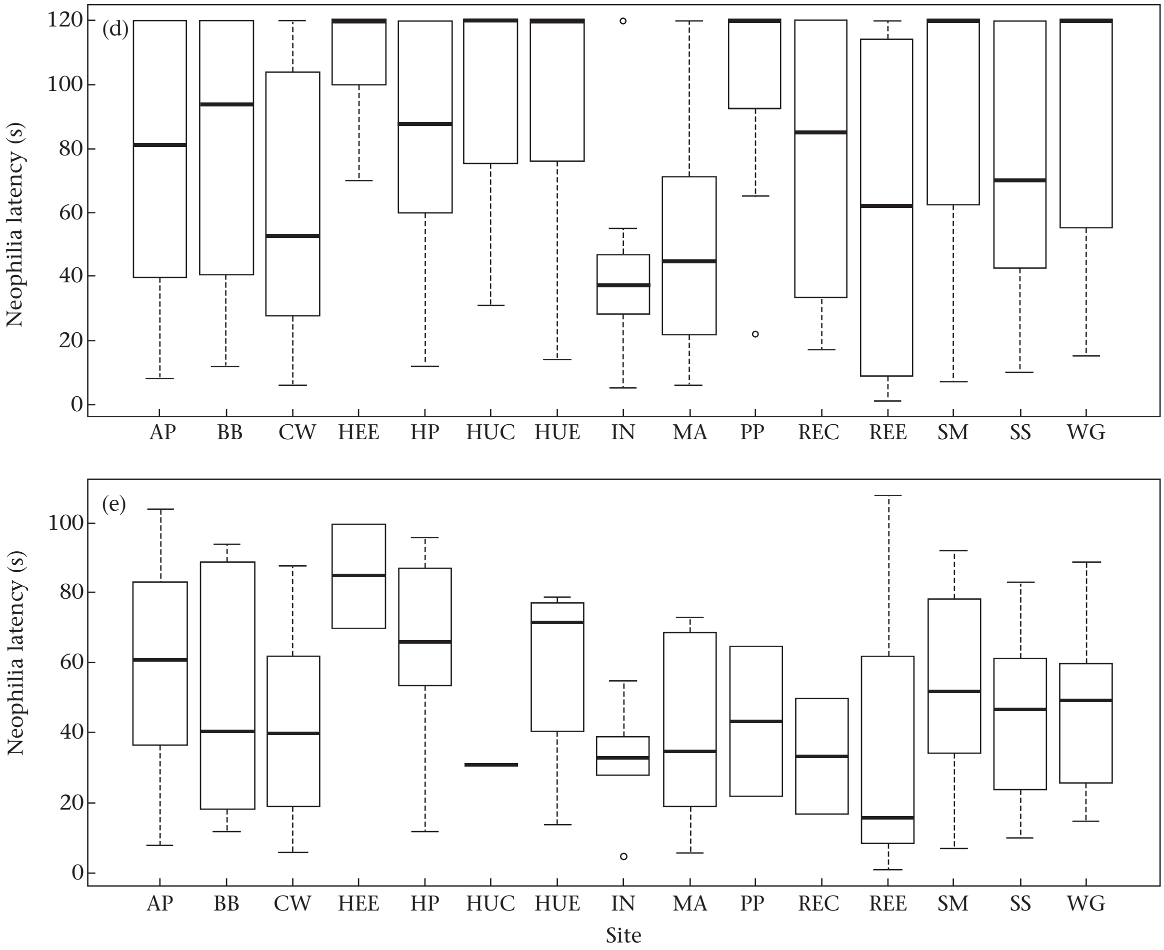

Figure A1. (*continued*).