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Two blue tit Parus caeruleus *populations from Corsica differ in social dominance*

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Although the causes and consequences of social dominance have been examined extensively, avian studies have rarely focused on between-population differences in social dominance. On the island of Corsica, two resident blue tit *Parus caeruleus* populations 25 km apart differ significantly in body size measures, timing and effort of reproduction, and song structure, and some of these population differences have a genetic basis. Because earlier avian studies have shown that social dominance is influenced by body size or mass, we predicted that individuals from these two blue tit populations would also differ in their ability to dominate other individuals. Consistent with this prediction, we found that male blue tits of these two populations differ in social dominance, and that heavier or larger individuals dominate lighter or smaller ones in aviary experiments. We propose that social dominance may serve to maintain phenotypic population differentiation at a micro-geographic scale by acting as a barrier to dispersal.

Social dominance describes the capacity of one individual to cause another individual to retreat in agonistic interactions. Dominant individuals have better success in acquiring resources in intraspecific competition, and therefore may have better survival and reproduction than subordinates (e.g. Kikkawa 1980, Arcese and Smith 1985, Piper 1997, Stahl et al. 2001). For instance, dominant individuals can force subordinates to settle in less suitable habitat causing non-random distributions of individuals within or across populations (e.g. Ketterson and Nolan 1976, Ulfstrand et al. 1981, Ekman and Askenmo 1984, Hogstad 1989, Marra 2000, Burton and Evans 2001, but see Lemel 1989, Rogers et al. 1989). Social dominance is not a fixed trait because dominance status often changes with age, site-familiarity, experience, body condition and mating status (e.g. Krebs 1982, Arcese and Smith 1985, Lundberg 1985, Piper and Wiley 1989, Cristol et al. 1990, Dearborn and Wiley 1993, Martin et al. 1997, Piper 1997, Hogstad 1999, Stahl et al. 2001). In many cases, older individuals dominate less experienced juveniles. Prior occupancy may also often confer a dominance advantage (e.g. Krebs 1982, Sandell and Smith 1991, Piper 1997), whatever the quality of the individuals involved (e.g. Lambrechts and Dhondt 1988). However, because of consistent individual variation in intrinsic traits, some individuals have a higher capacity to dominate others (Piper 1997). For instance, social dominance ability may be influenced by aggression that has a genetic basis (Verbeek et al. 1996), males most often dominate females (e.g. Lundberg 1985, Wiedenmann and Rabenold 1987, Hogstad 1999), or larger individuals dominate smaller ones (e.g. Dearborn and Wiley 1993, Burton and Evans 2001, Stahl et al. 2001, but see Lambrechts and Dhondt 1986). If local populations differ in phenotypic traits, such as body size, the ability to dominate may differ between populations, a supposition that has rarely been tested experimentally (e.g. Foster 1999).

Two resident blue tit *Parus caeruleus ogliastrae* populations on the island of Corsica, only 25 km apart, differ phenotypically, and these phenotypic differences may have a genetic basis (e.g. Blondel et al. 1999, Lambrechts et al. 1999). Blue tits in a valley with patches of rich broad-leaved deciduous oak (valley Mu) breed one month earlier, lay more eggs, and are larger and heavier than blue tits from a valley dominated by poor evergreen habitat (valley Pi) (Lambrechts et al. 1997, Blondel et al. 1999). The two populations also differ in the song types they sing (Doutrelant et al.

2001), and differ in their timing of reproduction in the standardised conditions of outdoor aviaries (Lambrechts et al. 1999, Lambrechts and Perret 2000). Some of these population differences are ultimately attributed to pronounced spatial variation in local selection pressures and reduced exchange between the two valleys favouring phenotypic differentiation at a micro-geographic scale (e.g. Lambrechts et al. 1997, Blondel et al. 1999, Lambrechts et al. 1999).

We hypothesised that social dominance may contribute to the phenotypic differentiation of the two insular blue tit populations by acting as a barrier to dispersal. For instance, both site-related dominance and population differences in phenotypic traits would exclude immigrants from valley Pi to acquire an optimal breeding territory in valley Mu. Birds from valley Mu produce offspring earlier in the season than birds from valley Pi, perhaps causing between-valley differences in the timing of territory establishment in both adults and juveniles. If site-related dominance is important, between-population exchange of individuals may be reduced if locally-bred offspring in valley Mu occupy a territory before immigrants arrive. In addition, it is reasonable to assume that blue tits from valley Mu dominate blue tits from valley Pi because they are larger and heavier.

To contribute to a better understanding of processes related to population differentiation, we examined population effects on social dominance. We tested the simple prediction that, because of population differences in body size or mass, male blue tits from valley Mu dominate male blue tits from valley Pi also after controlling for site familiarity. Because exchanges of blue tits between the two valleys are rare events in natural conditions (Blondel et al. 1999), we carried out our study on captive blue tits.

Material and methods

Male Corsican blue tits were trapped during two sessions in the autumn of 2000 (8–12 November and 11–14 December). In valley Mu, 13 males (4 adults, 9 juveniles) were captured at or near the broad-leaved deciduous study sites described in Lambrechts et al. (1997), eight of them in November. In valley Pi, 13 males (8 adults, 5 juveniles) were trapped at or near the evergreen oak and alder study sites described in Lambrechts and Dias (1993), six of them in November. All individuals were ringed with a unique combination of colour and aluminium rings to allow individual recognition. We measured tarso-metatarsus length (hereafter called tarsus length), flattened wing to the nearest 0.1 mm, and mass to the nearest 0.1 g (cf. Blondel et al. 1999, Lambrechts et al. 2000). For one bird from valley Mu, body mass was not measured in the field. Morphological measures did not differ between the two trapping sessions (all $P > 0.30$), and the dates the birds were trapped did not differ between the two valleys ($P > 0.30$).

Birds were transported in individual cages to the mainland (CNRS campus in Montpellier; 43°38′N, 03°52′E), where they were held in outdoor aviaries following the procedures described in Lambrechts and Dias (1993) and Lambrechts et al. (1996). Prior to the dominance tests, males were kept in such a way that interactions with other individuals were avoided. Blue tits were aged as born in the same year or older using feather criteria (Perrins 1979). Blood samples were taken from the tarsal vein and stored in Queen's lysis buffer (Seutin et al. 1991). Birds were sexed using DNA analyses following the procedures described in Griffiths et al. (1998). Birds were weighed and measured again in captivity.

Social dominance measurements

To determine the dominance status, one blue tit from valley Mu was placed together with one blue tit from valley Pi in a test aviary. The birds were simultaneously introduced into the aviary to control for site-familiarity. Twelve dyads were created initially. These dyads were placed in test aviaries just after they arrived on the CNRS campus. The dyads were formed 19 ± 9 days before observations on social dominance started. Some of these birds were tested again with another individual ($N = 6$). Eighteen dyads, each consisting of a male from valley Mu and a male from valley Pi, were observed between 12 December 2000 and 6 February 2001. Because of differences in the age structure between the Mu and Pi samples, four dyads combined yearlings from valley Mu with adults from valley Pi.

Data on social dominance were gathered by the same observer (CB) who did not know the origin of the birds during the trials and did not help with the trapping sessions on Corsica. The dominance status of a bird was determined using both active and passive interactions (e.g. see Stokes 1962, de Laet 1984, Hegner 1985, Lambrechts and Dhondt 1986, Piper 1997). In active interactions, the dominant male chased the subordinate male away (displacement, supplanting). In passive interactions, the subordinate male clearly waited to feed until the dominant male left the feeder. We observed that dominant males that won during active interactions also forced the subordinate males to wait near the feeder. To stimulate active interactions, food (cake, mealworms) was removed for 1.5 hours before the start of the observations (cf. Hegner 1985, Dufour and Weatherhead 1998). During the observation period, birds were provided with wax moth larvae, a favoured prey of captive blue tits (own observations). In sixteen dyads active interactions were observed, with an average rate of 11.1 ± 12.6 active interactions per dyad. Dominant males won in 96.6% of the active encounters observed. In one dyad, only passive interactions were observed. In another dyad with birds that were tested for the first time the males did not interact at all, so this dyad was not considered in analyses related to social dominance. Each dyad was observed during 5.5 ± 1.4 days, on average, for 5–20 min in the morning.

Statistical analyses were carried using the SAS V8.02 computer program. When applying binomial tests, we supposed that, if chance would determine the dominance relationships, a bird from one valley had a 50% chance to be dominated by a bird from the other valley. To look at relationships between dominance and body size measures, we related the percent of interactions won by Mu birds to the difference in body size measures between Mu and Pi birds using GLM analyses. We predicted positive relationships between social dominance and body size measures, and since birds from valley Mu were larger than individuals from valley Pi (see introduction and below), we performed one-tailed tests.

Results

Blue tits from valley Mu were larger and heavier than those from valley Pi, with a significant difference in field body mass (Mu: 10.5 ± 0.6, $N = 12$ vs. Pi: 9.7 ± 0.4, $N = 13$, $t = 3.86$, $P < 0.002$), and non-significant between-population differences in tarsus length (Mu: 16.40 ± 0.33, $N = 13$ vs. Pi: 16.24 ± 0.39, $N = 13$, $t = 1.12$, $P = 0.28$) and wing length (Mu: 63.8 ± 1.5, $N = 13$ vs. Pi: 62.8 ± 1.8, $N = 13$, $t = 1.51$, $P = 0.14$) (see Table 1).

The heavy birds from valley Mu showed a non-significant increase in body mass in captivity (increasing to 10.7 ± 0.8, paired t-test $= 1.21$, $P = 0.25$, 10 birds), whereas birds from valley Pi became significantly heavier in captivity (increasing to 10.2 ± 0.9, paired t-test $= 2.53$, $P = 0.03$, 11 birds). Thus, body mass was not lower in captivity than in the field.

As predicted, blue tits from valley Mu dominated blue tits from valley Pi in 13 of the 17 dyads (binomial test: $Z = 2.67$, $P = 0.004$, one-tailed). This result did not change when males that were tested for the first time only were analysed, with blue tits from Mu dominating blue tits from Pi in 9 of the 11 dyads (binomial test: $Z = 2.11$, $P = 0.017$, one-tailed).

The dominant males were significantly heavier and larger than the subordinate males (Table 2). In addition, the percent of active encounters won by blue tits from valley Mu was significantly positively correlated

Table 1. Paired comparisons of morphological traits of birds from valley Mu and birds from valley Pi. (A) = All dyads tested, (B) = Dyads with birds tested for the first time. Morphological measures were body mass at the time the males were trapped in the field, body mass measured in captivity after the dominance trials stopped, tarsus length, and wing length. Sample sizes in parentheses. P = Probabilities (all two-tailed).

	Mu	Pi	Paired t-test	P
(A)				
Field body mass	10.5 ± 0.5 (15)	9.6 ± 0.3 (15)	6.04	< 0.0001
Captive body mass	10.6 ± 0.7 (17)	10.2 ± 0.8 (17)	1.85	0.083
Tarsus	16.30 ± 0.31 (17)	16.16 ± 0.40 (17)	1.34	0.20
Wing	63.7 ± 1.35 (17)	62.3 ± 1.81 (17)	2.28	0.037
(B)				
Field body mass	10.5 ± 0.6 (10)	9.7 ± 0.4 (11)	4.53	0.0014
Captive body mass	10.7 ± 0.8 (11)	10.2 ± 0.9 (11)	1.73	0.11
Tarsus	16.38 ± 0.35 (11)	16.21 ± 0.39 (11)	1.21	0.26
Wing	63.6 ± 1.5 (11)	62.6 ± 1.92 (11)	1.18	0.27

Table 2. Paired comparisons of morphological traits of dominant and subordinate males. (A) = All dyads tested, (B) = Dyads with birds tested for the first time. Morphological measures were body mass at the time the males were trapped in the field, body mass measured in captivity after the dominance trials stopped, tarsus length, and wing length. Sample sizes in parentheses. P = Probabilities (all two-tailed).

	Dominant	Subordinate	Paired t-test	P
(A)				
Field body mass	10.5 ± 0.4 (15)	9.6 ± 0.3 (15)	7.34	< 0.0001
Captive body mass	10.7 ± 0.7 (17)	10.1 ± 0.7 (17)	2.75	0.014
Tarsus	16.33 ± 0.30 (17)	16.13 ± 0.40 (17)	1.97	0.067
Wing	64.0 ± 1.28 (17)	62.0 ± 1.62 (17)	3.48	< 0.01
(B)				
Field body mass	10.5 ± 0.5 (10)	9.6 ± 0.3 (10)	5.99	< 0.001
Captive body mass	10.9 ± 0.7 (11)	10.1 ± 0.8 (11)	3.21	< 0.01
Tarsus	16.42 ± 0.31 (11)	16.17 ± 0.39 (11)	2.02	0.07
Wing	64.0 ± 1.41(11)	62.3 ± 1.69 (11)	2.39	< 0.05

with the degree of difference in captive body mass ($F_{1,14} = 2.14$, $P = 0.025$, one-tailed), but not significantly correlated with the degree of difference in field body mass ($F_{1,12} = 1.16$, $P = 0.13$, one-tailed), tarsus length ($F_{1,14} = 1.61$, $P = 0.065$, one-tailed) or wing length ($F_{1,14} = 0.65$, $P = 0.26$, one-tailed). When birds that were tested for the first time only were analysed, the percent of interactions won by blue tits from valley Mu was significantly related to the degree of difference in morphological measures between the birds. This held for field body mass ($F_{1,7} = 2.08$, $P = 0.038$, one-tailed), captive body mass ($F_{1,8} = 2.26$, $P = 0.038$, one-tailed), and wing length ($F_{1,9} = 1.95$, $P = 0.043$, one-tailed), but not for tarsus length ($F_{1,8} = 1.51$, $P = 0.08$, one-tailed).

In all four dyads combining juveniles with adults, juvenile blue tits from valley Mu dominated adult blue tits from valley Pi.

Discussion

Here we have shown that male Corsican blue tits from valley Mu are significantly heavier and somewhat larger than male blue tits from valley Pi, when measured in late autumn. We also found that birds from valley Pi gained significantly more weight in captivity, whereas no significant increase in body mass was observed in captive blue tits from valley Mu. This suggests that food is scarcer in valley Pi than in valley Mu during the autumn. Between-valley differences in food abundance have been reported during the reproductive period when the key prey for the raising of chicks is much more abundant in valley Mu than in valley Pi (Lambrechts et al. 1997, Blondel et al. 1999). This explains why blue tit chicks and breeding adults are significantly heavier and somewhat larger in valley Mu than in valley Pi (see Lambrechts et al. 1997, Blondel et al. 1999).

We showed that male blue tits from valley Mu dominate male blue tits from valley Pi in captivity where effects of site familiarity have been eliminated. Our experiments with food *ad libitum* apparently benefited subordinate males because the birds from valley Pi gained significantly more mass in captivity than the birds from valley Mu (see above). We also showed that social dominance is related to different body size or mass measures. The most simple explanation is that the between-valley differences in morphological traits contributed to the between-population differences in social dominance in the blue tits. Males from valley Mu were more likely to dominate males from valley Pi when the degree of difference in body size or mass was larger (see results). A field study of purple sandpipers *Calidris maritima* showed differences in bill length between Norwegian and Canadian populations, and a relationship between social dominance and bill length, perhaps indicating population effects on social dominance (Burton and Evans 2001). Another study demonstrated differences in social dominance between two subspecies of dark-eyed juncos *Junco hyemalis* in aviaries, after controlling for factors related to sex, body size and site familiarity (Wiedenmann and Rabenold 1987). The conventional view that dominant birds are older than subordinates (e.g. Sandell and Smith 1991, Piper 1997) does not hold for our blue tits because larger juveniles from valley Mu dominated smaller adults from valley Pi. Furthermore, trials in which birds were tested for the first time were carried out before the end of January, i.e. before the start of rapid gonad development (e.g. see Lebeurier and Rapine 1944, Lambrechts et al. 1996), excluding potential effects of reproductive endocrinological factors on social dominance (e.g. Colquhoun 1942, Schwabl et al. 1988). We therefore propose that between-population differences in developmental conditions related to food availability caused the differences in morphological traits and consequently the significant differences in social dominance between the two Corsican blue tit populations.

Can the aviary experiments tell us something about the field situation? Our common-garden experiments reveal that, as for reproductive traits (see above), the two blue tit populations from Corsica differ in their ability to dominate other individuals. The extrapolation of these results remains problematic as site familiarity may override the effects of phenotypic traits on social dominance in field conditions (e.g. Lambrechts and Dhondt 1988, Piper 1997). For instance, social dominance in relation to morphology or site familiarity may also differ between the sexes, perhaps causing sex-based differences in exchange between the two valleys. Evidently, detailed observations of the timing of movements between the valleys, studies of social dominance in females, experiments testing the importance of site familiarity, the genetic basis of morphological measures and their consequences for social dominance (e.g. Blondel et al. 1999), the genetic basis of social dominance (e.g. see Verbeek et al. 1996), and removal experiments in the two valleys (see also Marra 2000) may contribute to a better comprehension of the role of social dominance in the differentiation of natural populations.

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