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The role of age, sex, subspecies, body size and fuel load in determining the social status of a migratory passerine during the non-breeding period

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The social status is seen determined by sex and/or age, body size and body condition. However, knowing which of these factors play a more relevant role to determine social dominance is often difficult since studies of competition under field conditions are commonly affected by several confounding factors that cannot be controlled or are even unknown. We studied experimentally which factors determine the dominance in captive Northern Wheatears, *Oenanthe oenanthe* during the non-breeding season, i.e., autumn and winter. We subjected two individuals at a time to experimental conditions with food provided at a feeder; these individuals differed in sex, age, body size, fuel load and subspecies. Social status appeared to be determined by age and sex during the autumn migration period, but not in winter. In particular, adults and males displaced first-year birds and females from the feeding site. Other traits such as body size, fuel load and subspecies, did not have significant effects on the social status.

1. Introduction

The social status can determine priority access to resources, such as food (Snow & Snow 1984, Carpenter *et al.* 1993, Ekman & Lilliendahl 1993, Polo & Bautista 2002), mate (Møller 1990, Veiga 1996) or shelters (Cuadrado 1997), having therefore direct consequences on life history aspects like survival or reproduction (Johnston & Fleischer 1981, Piper & Wiley 1990). Knowing which factors cause a bird to be dominant over others is hence of great interest.

Commonly, social status is determined by sex and/or age (Moore *et al.* 2003), body size and body condition (e.g., fuel load; Lindström *et al.* 1990). Thus, males, adults and larger birds are often dominant over females, first-year-birds and small birds (Snow & Snow 1984, Lundberg 1985, Lindström *et al.* 1990, Moore *et al.* 2003). The fuel load of an individual can also determine its dominance status independently of its sex, age or body size. Migrants must commonly accumulate large loads of fuel for the next flight bout. It is expected that birds with lower fuel reserves may be dominant over those with more fuel (Lindström *et al.* 1990), because lean ones could have more motivation to feed (Cristol 1992, Yong & Moore 1997). The social status can also vary between seasons (Lindström *et al.* 1990). For instance, the individual age-associated difference in social status between adults and first-year-birds should be expected to disappear as first-year-birds get older. During or in preparation for the spring migration period, males could be dominant over females (Yong *et al.* 1998, Dierschke *et al.* 2005) because males are forced to arrive in their breeding areas ahead of females (Rubolini *et al.* 2004). Moreover, dominance structure can be depend on context (Cristol *et al.* 1990, Jonart *et al.* 2007). For instance, birds occupying a territory first may be dominant over later-arriving individuals (Cristol *et al.* 1990, Tobias 1997).

Studies of competition under field conditions are commonly affected by several confounding factors that cannot be controlled or are even unknown. We, therefore, studied which factors determine the dominance in captive Northern Wheatears (*Oenanthe oenanthe*) during the non-breeding season.

2. Material and methods

2.1. The model species

The Northern Wheatear is a common, widespread songbird breeding in most of the Holarctic region and wintering in tropical Africa (Cramp 1988). Wheatears defend territories across the whole annual cycle and, therefore, they have strong social hierarchies determining priority access to a territory (Conder 1989). Thus, the Northern Wheatear is a good model species with which to analyse factors that determine social dominance. A common assumption is that males and large individuals are dominant over females and small birds, whereas 'other factors', such as fuel load, would have a minor effect on their social status (Dierschke *et al.* 2005). It is unknown, however, whether other factors could significantly affect the dominance structure. Hence, we studied this issue under laboratory-like, controlled conditions.

2.2. Data and experimental design

All the studied individuals (n = 22) were born in captivity from ancestors taken as chicks from *O. o. leucorhoa*, *O. o. oenanthe* and *O. o. seebohmi* subspecies when they were 5-10 days old; for further details, see Maggini and Bairlein (2010). All these were either pure *O. o. oenanthe* or hybrids of *O. o. oenanthe* with one of the other subspecies. The data used in this study were obtained from two sets of experiments carried out during the non-breeding period (autumn: 29 Sep.–24 Oct. 2009; winter: 20 Jan.–11 Mar. 2010).

Factors considered to influence the social status were wing length, tarsus length, body mass, fuel load (over lean body mass), age and sex. Wing and tarsus length were used to assess body size (Senar & Pascual 1997, Dierschke *et al.* 2005), and body mass and fuel load were used to assess body condition. Fuel load (FL) was calculated as

$$FL = (BM–LBM)/LBM \qquad (1)$$

where BM is actual body mass, and LBM is lean body mass. LBM was calculated for each individual (i) as

$$LBM_i = 22.7 \times 0.28(97.0–WL_i) \qquad (2)$$

where WL_i is wing length in mm (Dierschke *et al.* 2005).

Prior to the experimental day, each bird was kept in an individual cage of 0.40 (height) ×0.50×0.35 m^3 in a room at 20 ºC ± 2 ºC and at a controlled photoperiod of 12L:12D (local light time: 08:30–20:30). All first-year birds were born in 2009 (n = 8), and all adults were born in 2008 (n = 12), except one that was born in 2006 and another one in 2007. Prior to the experiment all birds had experienced a social contact. Wheatears were provided food and given water *ad libitum*. The experiments were carried out in two experimental aviaries, each of 3.00 (height) ×1.55×2.35 m, placed in a room at 20 ºC ± 2 ºC.

Wheatears were paired for the experiment, and each pair was determined by trying to maximize the difference in social rank between the two members, either in terms of age (adult *versus* first-year), sex (male *versus* female), body size or body mass (n = 24 pairs) (Table 1). As we worked with 22 birds in total, some birds were used more than once. However, pseudoreplication was not an issue because a given individual could behave as a dominant in one pair but as a subordinate in another pair. Each pair remained in the aviary for a period of one day (from 09:00 to 20:00), when Wheatears were given water and food (mealworms) *ad libitum*. Food was offered in a single

Table 1. Characteristics of each experimental pair (AD = adult; FY = first-year bird; M = male; F = female; *o* = *oenanthe* subspecies; *l* = *leucorhoa*; *s* = *seebohmi*). For each pair, we show which bird was dominant during the autumn and winter experiments. In winter, it was not possible to determine the dominance structure in 9 pairs; these are shown as "Null". Depending on their characteristics pairs were used for different statistics. Pairs where both birds belonged to the same age, sex and subspecies were used in paired *t*-tests to compare whether the biometry and fuel load differed in relation to social status. Pairs differing in age, sex or subspecies were used to test for the effect of each variable on social status, respectively.

Pair	Ind. 1	Ind. 2	Dominant bird (autumn)	Dominant bird (winter)	Paired *t* test (biometry)	Contingency tables		
						Age	Sex	Origin
Differing in age, not in sex								
	ADM*l*	FYM*o*	ADM*l*	ADM*l*		+		+
	ADM*o*	FYM*o*	ADM*o*	Null	+	+		
	ADM*l*	FYM*s*	ADM*l*	Null		+		+
	ADF*l*	FYF*o*	ADF*l*	FYF*o*		+		+
Differing in sex, not in age								
	ADM*o*	ADF*l*	ADM*o*	ADM*o*			+	+
	ADM*l*	ADF*l*	ADM*l*	ADM*l*	+		+	
	ADM*l*	ADF*l*	ADM*l*	ADF*l*	+		+	
	ADM*l*	ADF*o*	ADM*l*	Null			+	+
	ADM*o*	ADF*o*	ADM*o*	Null	+		+	
	FYM*s*	FYF*o*	FYM*s*	FYM*s*	+		+	+
	FYM*o*	FYF*o*	FYM*o*	Null	+		+	
Differing in age and sex								
	ADM*l*	FYF*s*	ADM*l*	ADM*l*		+	+	+
	ADF*l*	FYM*o*	ADF*l*	ADF*l*		+	+	+
	ADF*l*	FYM*s*	ADF*l*	ADF*l*		+	+	+
	ADF*l*	FYM*s*	FYM*s*	ADF*l*		+	+	+
	ADF*o*	FYM*s*	ADF*o*	FYM*s*	+	+	+	+
	ADF*l*	FYM*s*	FYM*s*	Null		+	+	+
	ADF*l*	FYM*o*	FYM*o*	Null		+	+	+
Similar age and sex								
	ADM^1*o*	ADM^2*l*	ADM^1*o*	ADM^2*l*				+
	ADM^1*o*	ADM^2*l*	ADM^1*o*	Null				+
	ADF^1*o*	ADF^2*l*	ADF^1*o*	ADF^1*o*				+
	ADF^1*l*	ADF^2*l*	ADF^1*l*	Null	+			
	FYM^1*o*	FYM^2*o*	FYM^1*o*	FYM^1*o*	+			
	FYM^1*s*	FYM^2*s*	FYM^1*s*	FYM^2*s*	+			

small feeder, so that only one bird of the pair was able to use the feeder at a time. Wheatears were weighed at 09:00 and 20:00; wing length (± 0.5 mm) and tarsus length (± 0.1 mm) were measured as well. Dominance status was determined in relation to the change in weight between morning (09:00) and evening (20:00). Wheatears that gained mass at the end of the day were considered dominant, as they were clearly able to use the feeder, while birds losing mass at the end of the day were considered subordinates. In pairs in which both birds lost or gained mass (winter trials; for details, see Table 1) it was not possible to determine the social status; hence such pairs were removed from the analyses. After the experiment the Wheatears were returned to their individual cages.

We detected aggressive interactions in the aviary but none was severe. They consisted of displays, intimidating calls and flights, but not direct aggressions (J. Arizaga, pers. obs.). Thus, it was not necessary to intervene in case of severe aggression. Most aggressions took place at or near the feeder and, therefore, the subordinate was able to escape if attacked.

2.4. Statistical analyses

To test whether body size and fuel load differed in relation to social status, paired *t* tests were used (i.e., each pair was considered an experimental unit; data followed the normal distribution; K-S test, $p > 0.05$). We obtained a variable that summarized structural size with a Principal Component Analysis (PCA) on body-size measurements (wing length, tarsus length; each bird considered once). This PCA resulted in the component 1 (PC1) with an eigenvalue of 1.373 (for PC2 was 0.627), explaining 68.7% of the variance and having positive, high factor loadings for both variables (wing length, 0.829; tarsus length, 0.829). Thus, the PC1 was used here to assess the structural size. The PC1 did not differ between age and sex classes (ANOVA: age, $F_{1,21} = 1.250$, $p = 0.278$; sex, $F_{1,21} = 0.289$, $p = 0.597$; age×sex, $F_{1,21} = 1.152$, $p = 0.297$), but it did between the subspecies ($F_{1,21} = 8.950$, $p = 0.002$), with *leucorhoa* being larger (0.82 ± 0.18) than the other two subspecies (*oenanthe*: –0.53 ± 0.34; *seebohmi*: –0.65 ± 0.17). Pairs formed either by a single subspecies or by *oenanthe* and *seebohmi* hybrids were hence considered in the analyses (Table 1).

Fuel load did not differ between age and sex (age, $F_{1,21} = 0.001$, $p = 0.975$; sex, $F_{1,21} = 1.735$, $p = 0.204$; age×sex, $F_{1,21} = 0.084$, $p = 0.776$; data from autumn trials; each bird considered once, data on one of the trials were considered in birds used twice or more) nor in relation to the subspecies ($F_{1,21} = 0.434$, $p = 0.654$). Thus, in this case we included all pairs for statistical comparisons.

Comparisons of sex, age and subspecies-related frequencies between individuals of different social status were done with contingency tables. With this goal, pairs where the two members had the same or different sex but different age ($n = 11$) were used to test for differences between age classes, and pairs where the two members had the same or different age but different sex ($n = 14$) were used to test for differences between sex classes. Pairs where the two birds belonged to a different subspecies ($n = 16$) were used to test for differences between subspecies (see for further details Table 1).

Finally, we used stepwise logistic regressions to test which of the collected variables (structural size, fuel load, age, sex and subspecies) was the strongest determinant of social status for the Northern Wheatear. All pairs were used for that. – All statistics were done using SPSS 18.0 software; mean values ± SE are given.

3. Results

3.1. Autumn season

Structural size and fuel load did not differ in relation to social status (paired-*t* test from Table 2). Adults tended to be dominant over first-year birds (72.7%; contingency tables: $\chi^2_1 = 4.545$, $p = 0.033$, $n = 22$, relative to 11 pairs in total with birds differing in age). Moreover, males were found to be dominant more often than females (78.6%; $\chi^2_1 = 9.143$, $p = 0.007$, $n = 28$; 14 pairs with birds differing in sex). Subspecies did not have a detectable effect on social status ($\chi^2_2 = 0.234$, $p = 0.999$, $n = 32$).

Stepwise logistic regression on all pairs revealed that age and sex had a significant effect on the dominance structure (parameters: constant, $B = –0.582 ± 0.508$, Wald = 1.312, $p = 0.252$; age, $B = –2.073 ± 0.877$, Wald = 5.592, $p = 0.018$; sex, $B =$

Table 2. Paired *t*-test checking for body size and fuel load-related differences in relation to social status during autumn and winter; means are given ± SE. The structural size was assessed with the component one (PC1) obtained in a PCA on wing and tarsus length.

Variable	Dominant	Subordinate	*n*	*t* test	*p*
Autumn					
Structural size	0.15 ± 0.29	–0.21 ± 0.32	10	1.232	0.249
Fuel load	0.49 ± 0.03	0.40 ± 0.03	24	1.875	0.074
Winter					
Structural size	–0.24 ± 0.30	0.27 ± 0.43	6	2.115	0.088
Fuel load	0.50 ± 0.03	0.40 ± 0.04	15	1.987	0.067

+2.451 ± 0.878, Wald = 7.799, p = 0.005; 68.9% of Wheatears were correctly classified, i.e., were classified by the equation as dominant when they were dominant in reality, and subordinate when they were subordinate in reality). The rest of variables (subspecies, structural size, fuel load and interactions between subspecies, age and sex) remained out of the regression.

3.2. Winter season

In winter, the social status could be determined only for 15 out of the 24 pairs used during autumn. In the remaining pairs, both individuals similarly lost or gained weight, and in these cases it was not possible to infer dominance. Forty percent of the pairs with determined dominance changed their social status between autumn and winter. In particular, in six out of the 15 pairs the previously dominant bird became subordinate in winter. In the remaining 9 pairs, the birds that were dominant in autumn remained dominant in winter too. This dominance change was not, however, significant (χ^2_1 = 1.200, p = 0.466).

Neither structural size nor fuel load differed significantly between dominant and subordinate Wheatears, although fuel load tended to be slightly higher among dominant birds, as was the case in autumn too (Table 2). In winter, social status was not determined by age (χ^2_1 = 2.571, p = 0.286; n = 14), sex (χ^2_1 = 0.222, p = 0.637; n = 18) or origin (χ^2_2 = 1.700, p = 0.550; n = 22). The stepwise logistic regression, carried out with the data from winter trials, resulted in non-significant results, thus agreeing with the t test and contingency analyses obtained earlier.

4. Discussion

In autumn, age and sex, but not subspecies, structural size or fuel load, appeared to predict the dominance status of a Wheatear individual. In ca. 70% of all pairs, adults were dominant over first-year birds, and in ca. 80% of pairs, males were dominant over females. Similarly, Dierschke *et al.* (2005) observed that males under wild conditions were dominant over females during the spring migration period. Therefore, our results support the hypothesis that adult birds and males have a higher social status (Moore *et al.* 2003) and, therefore, they are able to expel first-year birds and females (i.e., subordinates) from a preferred territory. This finding also agrees with the idea that social status has direct consequences on access to resources during migration (Moore *et al.* 2003, Dierschke *et al.* 2005). No significant differences were detected in winter, which might partially be due to the lower sample size, although a seasonally associated change in relative weight of factors shaping the social structure cannot be rejected. Thus, as first-year birds gain experience from autumn to winter, it is reasonable that age did not affect the social status in winter.

The social status shifted from autumn to winter in 40% of pairs. This finding supports the idea that the social rank is flexible and depends on subjective elements, such as an individual's motivation to defend a resource at a certain moment or its personality (Kurvers *et al.* 2010), and also the actual timing of the internal circannual rhythm (Maggini & Bairlein 2010). Although Wheatears in captivity show circannual rhythms similar to wild birds, individual variation is still found, especially during the spring migration period (Maggini & Bairlein 2010). Such variation is likely to result in Wheatears having variation in their motivation to feed, independent of sex, age or body size. Our observation that dominant birds were found to carry slightly more fuel than subordinates supports this hypothesis; dominant birds were probably in the stage of migratory hyperphagia (Bairlein 1985), thus out-competing others at the feeder.

Structural body size did not affect the social status; hence larger birds were not systematically dominant over smaller ones. This result is opposite to results of two studies carried out with Bluethroats and Wheatears in the wild (Lindström *et al.* 1990, Dierschke *et al.* 2005). In these two cases, however, body size was assessed using only wing length, which is positively correlated with age in both species (Cramp 1988). This methodological difference may explain the discrepancy.

During winter (migratory stopover in early spring), males were found to start and win most aggressive encounters, and to be territorial more often, than females. Nevertheless, their fuelling rates did not significantly differ from females, apparently because females compensated by having a higher intake rate when they accessed to food (Dierschke *et al.* 2005). In our experiment, sex did not appear to play a significant role on social status in winter, but it did in autumn. Although males were found to be dominant in ca. 80% of cases, females reached a higher social position in 20% of cases. We suggest that females were able to successfully expel males under the present experimental conditions with just one feeder. This might be different from the wild with more feeding opportunities. It is also possible that, in the field, there is a bias for competitive interactions between juvenile females and old males.

In conclusion, social status in the Northern Wheatear was found to be determined by age and sex during the autumn migration period, but not in winter. In particular, adults and males displaced first-year birds and females from the experimental feeding site. Other traits such as body size, fuel load and subspecies, did not show detectable effects on the social status.

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Iän, sukupuolen, alalajin, ruumiinkoon ja ruumiinkunnon merkitys muuttavan varpuslinnun sosiaaliselle asemalle talviaikana

Sosiaalisen aseman voivat määritellä sukupuoli ja/tai ikä, fyysinen koko tai ruumiinkunto. Kilpailututkimuksissa on kuitenkin usein jopa mahdotonta päätellä, mikä näistä kulloinkin on sosiaalisen aseman tärkein määrittelijä. Tämä johtuu siitä, että kenttäoloissa kilpailututkimuksien tuloksiin vaikuttaa kerrallaan useita tekijöitä, joita on vaikea kontrolloida. Tutkimme kokeellisesti, mitkä tekijät vaikuttavat tarhattujen kivitaskujen (*Oenanthe oenanthe*) dominanssiin pesimäkauden ulkopuolella (syksy ja talvi). Altistimme kaksi yksilöä kerrallaan ruokintakokeeseen; yksilöt erosivat toisistaan sukupuolen, iän, ruumiinkoon, ruumiinkunnon ja alalajin suhteen. Sosiaalisen aseman määräsivät ensisijaisesti ikä ja sukupuoli syksyllä, mutteivät merkittävästi talvella. Aikuiset ja koiraat häätivät nuoret ja naaraat ruokinta-automaatilta. Muut parametrit, kuten ruumiinkoko, ruumiinkunto ja alalaji, eivät merkittävästi vaikuttaneet soaiaaliseen asemaan.

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