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Dominance and survival of dippers *Cinclus cinclus*

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Abstract Survival of dippers *Cinclus cinclus* in the wild was studied in relation to their dominance. Dominance was assessed amongst groups of temporary captives in a laboratory arena. Adults tended to be more dominant than juveniles, and within age classes males generally dominated females. Dominant individuals also sang more. Logistic regression was used to examine survival in the wild in relation to dominance and other factors. Annual survival of juvenile males was negatively related to dominance during the previous autumn. No significant effects of dominance on winter or annual survival were found amongst females or adult males. Dominance effects on overwinter survival approached significance for adult females, however, and were significant for both winter and annual survival when the data from adult females and juvenile males were combined. None of the other factors considered, which included body size, song frequency and year, had a significant effect on overwinter or annual survival. We concluded that dominance either had no influence on survival, or had a negative effect particularly on dippers of intermediate status. We were unable to show if dominance had a direct effect, however, or acted indirectly on survival via an unidentified factor we did not examine.

Key words Dominance · Body size · Life-history strategy · Survival · *Cinclus cinclus*

Introduction

Attributes commonly associated with dominance include body size, age, sex, weapons and coloration (Clutton-Brock et al. 1982; Jarvi and Bakken 1984; Enoksson 1988; Hogstad 1989; Richner 1989; Wagner and Gauthreaux 1990; Keys and Rothstein 1991). Dominance often allows individuals to gain priority of access to resources such as territories (Kaufmann 1983; Arcese and Smith 1985), food (Ens and Goss-Custard 1984; Hogstad 1988; Wiley 1991), water (Wrangham 1981) and mates (Komers and Dhindsa 1989). It therefore seems likely to confer a net fitness benefit and so affect lifetime reproductive success positively.

Many studies of dominance have been carried out in captivity because this facilitates experiments and observations. Results have nevertheless been used to interpret behaviour in the wild, principally within a context of short-term benefits (Cristol et al. 1990; Belthoff and Gauthreaux 1991; Sandell and Smith 1991). Fewer studies have attempted to integrate dominance status assessed in either the field or laboratory with subsequent life-history events in wild populations. Kikkawa (1980) found a positive link between dominance and survival in silvereyes *Zosterops lateralis,* and comparable results were obtained for song sparrows *Zonotrichia melodia* (Arcese and Smith 1985), tits (*Parus* spp.) (Hogstad 1989; Ekman 1990) and other birds (Newton 1989). Amongst mammals, reproductive success can be higher amongst dominants, including male savanna baboons *Papio cynocephalus* (Bulger 1993), female gelada baboons *Theropithecus gelada* (Dunbar and Dunbar 1977) and red deer *Cervus elaphus* stags (Clutton-Brock et al. 1982). However, these patterns are not universal; for example, dominance does not enhance survival in acorn woodpeckers *Melanerpes formicivorus* (Stanback 1994) and its relationship with reproductive success in primates can be inconsistent (Robinson 1982). Therefore, the relationship between dominance and lifetime reproductive success, or its

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components, can often be obscure (Clutton-Brock 1988).

Site residency or familiarity can have a marked effect on dominance (Davies 1978; Krebs 1982; Choe 1994) and this might confound attempts to explore the fitness consequences of dominance. Great tits *Parus major* resident in an aviary prior to assessment were largely dominant over non-residents regardless of age, whereas in the wild, adult great tits normally dominate juveniles (Sandell and Smith 1991). Similarly, young dark-eyed juncos *Junco hyemalis* were dominant over adults if they were prior residents in an aviary, thus reversing the general trend for juveniles to be subordinate (Cristol et al. 1990; Wiley 1990). Resident advantage is not universal, however, since amongst wintering white-throated sparrows *Zonotrichia albicollis* length of time in an area did not affect status (Piper and Wiley 1989). Nevertheless, the common occurrence of resident advantage suggests that assessments of status are best made in a neutral setting.

Accordingly, in this study of dippers *Cinclus cinclus* we separated assessments of dominance from site-related factors by measuring dominance in a laboratory arena, and then examined the relationship between dominance and survival. We focused on the following two questions. First, how does dominance status in dippers relate to sex, age, song and body size? Second, is dominance status assessed in the laboratory related to subsequent survival in the wild?

Methods

Capture and measurements

Samples of five dippers (exceptionally four) from a colour-ringed population in central Scotland (56°10′N, 3°40′W) were caught at roosts on 27 nights. On each night, birds were caught at widely scattered sites to avoid bringing together individuals in regular contact during daytime. Nine, eight and ten dominance assessment sessions were conducted each autumn, between 26 October and 30 November 1989, 24 October and 16 November 1990, 25 September and 25 October 1991. Totals of 36, 37 and 48 different individuals were involved each year, respectively, with a few appearing twice (see below). The birds were immediately weighed and measured to give body mass, wing-length, tarsus, keel-length and head plus bill length. These size measures are closely correlated (Newton 1989). They allowed birds to be reliably sexed, whereas ringing history and plumage criteria (Svensson 1992) were used to distinguish adults (> 1 year) from juveniles (< 1 year). The standard time of capture (2000–2300 hours) ensured that the birds involved in our experiments were in a comparable energetic state (Cristol 1992; Witter 1993). Birds were held in cloth bags until dawn at the prevailing outside ambient temperature.

Dominance assessments

The dominance assessment arena, a matt grey fibreglass tank measuring 95 × 95 cm and 37 cm high, was half-filled with water and contained an up-ended brick which served as a perch just large enough for a single dipper. The rapidly circulating water simulated stream-flow and smothered most extraneous sounds. It came to within 3 cm of the top of the brick, which resembled a typical dipper perch in the wild. The arena was in a cool, lit room and topped with plastic mesh with concealed observation points at each corner.

At the start of each session, at dawn, birds were released singly into the arena for 5 min to allow them to become accustomed to their surroundings. In all cases they chose to stand on the perch, alert or preening, and make occasional forays around the arena. For all dominance trials, two dippers were released into the arena simultaneously for 3 min (T_{total}); this time was occasionally extended by up to two minutes when no dominant was evident. During each trial, two concealed observers recorded the birds' behaviour and interactions as they disputed tenancy of the favoured brick perch. Dominants gained access to the perch, whereas subordinates were displaced and obliged to swim. The number of songs produced by each bird (SONG) was also noted, but calls were ignored since they were difficult to ascribe to individuals. Interactions were classed as "non-contact" (NI) or "contact" (CI): the latter involved physical contact, whereas in non-contact interactions the aggressor chased or veered away from an opponent without physical contact being made. Winners of interactions almost always returned to the brick perch. At the end of each trial, one bird was judged the "qualitative" dominant and the other the subordinate; in virtually all instances the qualitative dominant was the individual commanding the perch at the end of the trial. Exceptionally, however, dominants spontaneously abandoned the perch near the end of a trial to seek an escape. Sex and age classes were mixed in our dominance assessments because we aimed to reflect circumstances in the dipper's natural habitat, where interactions occur between all classes. Typically, each bird was matched against four others in each session, with all five birds therefore engaging in a total of ten trials per session. No individual was involved in consecutive trials, hence there was a minimum 5-minute inter-trial interval during which birds were retained in cloth bags. No food was provided. After the assessments, birds were released at their capture sites, within about 2 h of dawn, thereby entailing only a small loss of potential feeding time (Bryant and Tatner 1988). We consider our assessments unlikely to have had any significant effect on subsequent survival (see below).

Dominance status in the test arena during each session was quantified from the observations described above using the following four measures; they were closely correlated (Bryant and Newton 1994) (Table 1):

1. %TIME: percentage of time in the arena during each session spent occupying the favoured brick perch (= $T_{\text{perch}}/T_{\text{total}}$ %)
2. %WIN: percentage of interactions won during each session, with non-contact and contact interactions combined (= $\text{NI}_{\text{won}} + \text{CI}_{\text{won}}/\text{NI}_{\text{total}} + \text{CI}_{\text{total}}$ %)
3. %QWIN: percentage of the four trials (TR) in each session where a bird was judged the qualitative winner (= $\text{TR}_{\text{won}}/\text{TR}_{\text{total}}$ %)
4. %CWIN: percentage of an individual's wins during each session achieved through physical contact (= $\text{CI}_{\text{won}}/\text{NI}_{\text{total}} + \text{CI}_{\text{total}}$ %)

Ten birds which appeared twice within the same year, mainly during 1989, showed consistent dominance rankings. The correlation coefficients for the four (arcsine transformed) dominance measures on the two occasions were: %TIME, $r = 0.36$, NS; %WIN, $r = 0.49$, NS; %QWIN, $r = 0.74$, $P < 0.05$; %CWIN, $r = 0.72$, $P < 0.05$. The analogous correlation for SONG in this sample was $r_s = 0.91$, $P < 0.01$. The consistency for %QWIN and %CWIN suggested they would be more reliable measures of status, and so they are given greater emphasis below. Further details of dominance assessments are given by Bryant and Newton (1994).

Survival

All rivers in the study area were checked repeatedly for survivors in the spring (March–May) and autumn (September–November) following the dominance assessments. Survivors were determined from sightings of colour-ringed birds, or from catching marked birds at roosts or with mist nets on the river. Although a small number of dippers may have dispersed to rivers outside the study area or escaped detection within it, previous work (Newton 1989) has shown that the numbers involved are likely to be small and have little effect on recorded survival rates. This is consistent with the survival rates presented here being similar to those derived in a concurrent population study (J. Logie and D.M. Bryant unpublished work) which used the program SURGE to derive survival estimates (Lebreton et al. 1992). This situation arises from several favourable factors: dippers are relatively easy to find since they are wholly confined to rivers and are conspicuous in their habits; they are resident and normally disperse only a short distance (Galbraith and Tyler 1982; Newton 1989; Tyler et al. 1990); natal dispersal is largely completed by the time dominance assessments started in late September (Newton 1989); the area searched for survivors was more extensive than the area from which birds were drawn; the population was monitored year round and fidelity to roosts meant that survivors could normally be found at or near their site of capture. Hence, while strictly we deal with "local" survival, we consider this to be equivalent to "true" survival for the birds handled for this study. Further, we tested if the dominance trials affected subsequent survival by comparing "assessed" and "non-assessed" individuals. Over the 3 years there was no significant difference in survival to the spring census (assessed birds, 69% survived, $n = 121$; non-assessed birds, 59% survived, $n = 206$, $\chi^2 = 2.64$, $P > 0.1$), whereas survival to the following autumn was apparently higher amongst assessed birds (assessed birds, 54% survived; non-assessed birds, 40% survived: $\chi^2 = 5.61$, $P < 0.05$). Since birds assessed for dominance came wholly from catches at roosts, and dippers are generally faithful to roosts, they apparently had a greater chance of being recaptured than birds caught in other ways. Therefore, the chance that our laboratory trials had an adverse effect on survival was slight.

Data analysis

An initial consideration was the independence of dominance assessments given that a few individuals necessarily appeared in more than one trial. This occurred because we held the number of birds in each trial at five but on some nights could not find enough new individuals during our searches at roosts. To avoid pseudoreplication, therefore, only the first dominance assessment from each year was used for each individual. Birds which appeared in successive years mostly shifted from the juvenile to the adult category, with associated changes in status, and so were necessarily analysed separately. The few adults which appeared in successive years were also treated as independent for the purpose of our analyses because their competitors in the arena always differed and their circumstances on the rivers also changed. We considered whether the quality of opponents within each session had an effect on measured dominance status; an individual facing generally low-ranked opponents, for example, might be expected to gain a higher dominance rating than one facing only high-ranked individuals. In practice, however, our sessions comprised quasi-random samples across sex and age classes: 96% of sessions ($n = 27$) contained more than one age/sex class and in some cases all four. Furthermore, there was much overlap in dominance between categories (Table 1). No systematic effect of opposition status on dominance measures was detected. For example, none of the dominance measures was correlated with the number (or proportion) of males in each trial: r_s was > 0.1 in all cases (A.V. Newton, S. Newton and D.M. Bryant, unpublished work). Furthermore, a small sample of birds showed consistent dominance measures during successive trials with different opponents (see above). We therefore employ our dominance measures in an unweighted form. This will induce variability within our data but will not bias the results. Furthermore, it avoids the circularity inherent in deriving any weighting factors from the same sample of birds. Statistical analyses were carried out using SPSS Version 4.0 (SPSS 1990). All parametric tests involving proportions were carried out after arcsine transformation. Means ± standard deviations are given unless otherwise stated.

Results

Comparison of dominance between sex and age classes

During autumn 1989–1991, 27 dominance assessment sessions involving 131 birds were completed. Excluding 10 birds that appeared twice within the same year left results for 35 adult males, 37 adult females, 22 juvenile males and 27 juvenile females (Table 1). Assessed birds made up about half the study population in each year. A similar pattern emerged amongst all four measures of dominance (%TIME, %WIN, %QWIN, %CWIN) and their component measures (Table 1). Adult males were more dominant than other age/sex classes, for example, winning 80% of their trials (%QWIN). Adult females tended to dominate juvenile males, which in turn were dominant over juvenile females, which won only 34% of their trials (Table 1).

Differences in status between age and sex classes were analysed by two-way ANOVA. Results for the four

Table 1 Dominance measures and behaviour of dippers interacting in mixed age/sex groups in a laboratory arena. Means (± SD) and medians (range) are given for each variable as appropriate. See Methods for definitions of variable symbols

Variables	Adult males		Adult females		Juvenile males		Juvenile females		All	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
$NI_{tot}+CI_{tot}$	28.3	11.3	37.6	10.7	35.0	9.2	36.3	12.2	34.2	11.5
$NI_{won}+CI_{won}$	19.1	12.5	20.1	12.8	15.6	9.3	11.1	11.0	17.0	12.1
CI_{won}	9.1	6.6	7.4	6.1	7.0	5.0	4.7	5.2	7.2	6.0
TR_{won}	2.3	1.4	2.2	1.4	1.9	1.2	1.2	1.1	1.9	1.3
%TIME	63	40	59	35	50	31	33	27	53	36
%WIN	74	50	64	44	48	28	31	33	57	44
%QWIN	80	58	73	57	57	42	34	36	63	53
%CWIN	31	21	21	16	20	15	12	11	21	18
SONG	7.0(0–28)		3.0(0–20)		0.5(0–5)		0(0–9)		1.0(0–28)	
n	35		37		22		27		121	

Table 2 Analysis of variance for dominance measure of dippers with age and sex as factors: two-way ANOVA for four (arcsine transformed) dominance measures. Since results were similar, only those for %CWIN are shown in detail under **a**. The significance of *F*-values from the two-way ANOVA for the other dominance measures is given under **b**

	Dependent variable	Source of variation	SS	*df*	*F*	*P*
a	%CWIN (arcsine)	Age	0.267	1	9.707	0.002
		Sex	0.272	1	9.859	0.002
		Age × sex	0.002	1	0.076	0.783
		Explained	0.561	3		
		Total	3.784	120		
b	%TIME (arcsine)	Age **,	Sex *,	Age × Sex NS		
	%WIN (arcsine)	Age **,	Sex *,	Age × Sex NS		
	%QWIN (arcsine)	Age **,	Sex *,	Age × Sex NS		

$*P \leqslant 0.05$, $**P \leqslant 0.01$, NS not significant

measures of dominance were very similar, so three are presented in summary with only %CWIN shown in detail (Table 2). In each case age and sex showed a significant association with dominance measures, with age more significant than sex, except for %CWIN where they were the same, while the interaction term (age × sex) was non-significant in all cases. Clearly, the predominant trend amongst non-breeding passerine birds for males to dominate females, and adults to dominate juveniles, also applied to our sample of dippers in the laboratory arena, and occurred even though prior-residency effects were eliminated.

Song, body size and dominance

In the arena, males sang more than females (Kruskal-Wallis ANOVA, $\chi^2 = 4.37$, $P < 0.05$), and adults more than juveniles (K-W ANOVA $\chi^2 = 37.06$, $P < 0.001$). SONG was also closely linked to dominance measures within all age/sex classes. For example, correlation coefficients were as follows: SONG in males with %QWIN: $r_{\mathrm{ad}} = 0.65$ ($P < 0.001$, $n = 35$), $r_{\mathrm{juv}} = 0.55$ ($P < 0.01$, $n = 22$), and with %CWIN: $r_{\mathrm{ad}} = 0.51$ ($P < 0.01$), $r_{\mathrm{juv}} = 0.65$ ($P < 0.001$). SONG in females with %QWIN: $r_{\mathrm{ad}} = 0.62$ ($P < 0.01$, $n = 37$), $r_{\mathrm{juv}} = 0.44$ ($P < 0.05$, $n = 27$), and with %CWIN: $r_{\mathrm{ad}} = 0.54$ ($P < 0.01$), $r_{\mathrm{juv}} = 0.37$ ($P < 0.1$). Body mass and size measures differed significantly between the sexes but not between age classes (Table 3). Significant correlations for mass and four body size measures with dominance were relatively few (Table 3). Only head plus bill length was positively correlated with dominance for more than a single age/sex class: namely adult ($P < 0.001$) and juvenile ($P < 0.05$) females. After Bonferroni adjustment of critical probabilities (to $P = 0.0025$), body mass and head plus bill alone remained significant. Overall, body size correlations with dominance were weaker than for SONG and, in contrast, were often inconsistent between age/sex classes. For example, amongst juvenile males, head plus bill length was negatively correlated with %TIME (Table 3).

Survival

Overwinter (autumn release to spring census) and annual survival (autumn release to subsequent autumn census) rates did not differ significantly between the 3 years studied (Table 4). Overwinter survival was 63–75%, with 1991–1992 slightly lower than the other 2 years. Annual survival was 50–65%, although in this case with 1990–1991 rather higher than the other 2 years (Table 4). Survival of juveniles (63% overwinter, 45% annual) was lower than for adults (respectively 74% and 63%) but samples were too small to usefully test the significance of this difference in survival rate (Graves 1991). While the same qualification also applies, differences between sexes were smaller (overwinter and annual respectively: males 70% and 54%, females 69% and 56%). Since dominance-survival relationships could be confounded by age and sex differences in survival, however, it was necessary to establish the significance of this heterogeneity. An

Table 3 Body mass and body size measures of dippers observed in the arena. All differences in mass and body size between sexes were significant, whereas none of the differences between age classes were significant (Student *t*-tests, $P < 0.05$). Significant Pearson product-moment correlation coefficients for mass and size with dominance measures are identified. See text for discussion of Bonferroni probabilities

	Adult males		Adult females		Juvenile males		Juvenile females	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Body mass (*m*, g)	68.7	3.9	57.6	3.1	66.9	2.8	55.5	3.2
Winglength (*w*, mm)	98.3	1.8	90.4	1.7	97.1	1.8	89.3	1.8
Keel (*k*, mm)	32.0	1.4	28.2	1.0	32.0	1.0	27.9	0.8
Tarsus (*t*, mm)	29.7	1.0	28.1	0.9	29.5	1.1	28.0	0.8
Head plus bill (*h*, mm)	47.7	0.9	45.7	1.1	47.3	0.5	45.8	0.8
% TIME	*t**		*h***		−*h**			
% WIN	*k**,*t**		*m**, *h***					
% QWIN	*k**, *t**		*h****				*h**	
% CWIN	*k**		*m***, *h****					
n	35		37		22		27	

$*P \leqslant 0.05$, $**P \leqslant 0.01$, $***P \leqslant 0.001$

Table 4 Percentage survival of dippers assessed for dominance during 1989–1991. Overwinter (*OW*), denotes survival overwinter to breeding; annual (*AN*), survival over a full year, autumn to autumn. Sample sizes are in parentheses. Survival rates amongst assessed individuals did not differ between years (overwinter, $\chi^2_2 = 0.56$, N.S., annual, $\chi^2_2 = 0.90$, N.S.), sexes (overwinter, $\chi^2_1 = 0.00$, N.S., annual, $\chi^2_1 = 0.01$, N.S.) or age classes (overwinter, $\chi^2_1 = 0.58$, N.S., annual, $\chi^2_1 = 0.27$, N.S)

Year		Adult males	Adult females	Juvenile males	Juvenile females	All
1989–1990	OW	83 (12)	80 (10)	75 (8)	50 (6)	75 (36)
	AN	67 (12)	60 (10)	50 (8)	17 (6)	53 (36)
1990–1991	OW	83 (12)	83 (12)	25 (4)	67 (9)	73 (37)
	AN	67 (12)	83 (12)	25 (4)	56 (9)	65 (37)
1991–1992	OW	54 (11)	60 (15)	70 (10)	67 (12)	63 (48)
	AN	45 (11)	53 (15)	50 (10)	50 (12)	50 (48)
1989–1992	OW	74 (35)	73 (37)	64 (22)	63 (27)	69 (121)
	AN	60 (35)	65 (37)	45 (22)	44 (27)	55 (121)

analysis was carried out using SURGE (Lebreton et al. 1992) as part of a 10-year study of the population ecology of the dipper in the study area (J. Logie and D.M. Bryant, unpublished work). It demonstrated that overwinter survival rates did not differ between the sexes for the population as a whole (mean = 63.8, SE 3.1%). Annual survival of adults was 52.6, SE 3.0%. However, survival overwinter was significantly lower amongst juveniles of both sexes than amongst adults (males 47.0, SE 5.5%, $t = 2.66$, $P < 0.01$; females 50.1, SE 4.0%, $t = 2.71$, $P < 0.01$).

Dominance and survival

While survival tended to be higher amongst the more dominant adults and lower amongst the generally subordinate juveniles, their precise correspondence was unclear. Logistic regression was therefore used to examine the relationship between dominance and survival more fully. For this, survival was treated as a binary variable (0 died; 1 survived) (Myers 1990). Since dominance was related to both age and sex (Table 2), and survival differed between age classes (see above), however, it was necessary to segregate sex and age categories to explore these interrelationships in detail. Initially, all four dominance measures were entered for each age/sex, but the results were essentially the same so we only present results for %CWIN here. SONG, body mass and head plus bill, as measures of size (Table 3) and year were also entered using a forward stepwise procedure (Table 5). This allowed the importance of dominance and other related factors to be examined.

Table 5 Logistic regression models for survival of dippers in relation to dominance assessments. The probability that a dipper will die $P(y = 1) = \exp(u)/[1 + \exp(u)]$, where $u = A + B_1X_1 + \ldots B_{iN}X_{iN}$. A is a constant; B_1, B_N are coefficients for the first and *n*th variables respectively; X_1, X_{iN} are the first and ith independent variables included in the model using a forward stepwise procedure (see below), and $i = 1, 2, 3 \ldots, n$ (individuals)

Variable/constant	Coefficients	SE	*t*-ratio	Wald χ^2	*R*	*df*	*P*
Model 1 (Juvenile males, annual survival)							
X_1(%CWIN)	−11.824	5.254	2.25	5.064	32%	1	0.02
A	1.960	1.029	1.90	3.628	–	1	0.05
−2 log likelihood $\chi^2 = 22.25$ ($df = 20$, $P = 0.33$)							
Model χ^2 = 8.07 ($df = 1$, $P = < 0.01$)							
Other variables entered: X_2 body mass, X_3 head plus bill, X_4 SONG and X_5 year. All were non-significant ($P > 0.1$)							
Model 2 (Adult females, overwinter survival)							
X_1(%CWIN)	−4.512	2.492	1.81	3.279	17%	1	0.07
A	1.993	0.710	2.81	7.879	–	1	< 0.01
−2 log likelihood $\chi^2 = 39.69$ ($df = 35$, $P = 0.27$)							
Model χ^2 = 3.49 ($df = 1$, $P = 0.06$)							
Other variables entered: as for model 1. All were non-significant ($P > 0.1$)							
Model 3 (Adult females and juvenile males, overwinter survival)							
X_1 (%CWIN)	−3.785	1.950	1.94	3.770	16%	1	0.05
A	1.632	0.526	3.10	9.613	–	1	<0.01
−2 log likelihood $\chi^2 = 68.61$ ($df = 57$, $P = 0.14$)							
Model χ^2 = 3.97 ($df = 1$, $P = < 0.01$)							
Other variables entered: as for Model 1, but including age. All were non-significant ($P > 0.1$)							
Model 4 (Adult females and juvenile males, annual survival)							
X_1(%CWIN)	−4.381	1.971	2.22	4.942	19%	1	0.03
A	1.198	0.486	2.47	6.071	–	1	0.01
−2 log likelihood $\chi^2 = 74.87$ ($df = 57$, $P = 0.06$)							
Model χ^2 = 5.54 ($df = 1$, $P = 0.02$)							
Other variables entered: as for Model 3. All non-significant at $P > 0.1$							

Annual survival amongst juvenile males was negatively related to %CWIN as a measure of dominance (model 1, Table 5). None of the other factors was significant. %CWIN was also close to significance ($P = 0.07$) for survival of adult females to the spring census (model 2, Table 6) and again no other factor was significant ($P > 0.1$ in all cases). No factors were significant amongst adult males or juvenile females. In view of the effect of dominance on survival for juvenile males and adult females and the similarity in their status (Table 1), they were grouped for further analysis. Dominance was related to both overwinter and annual survival; at a significance level intermediate between that of models 1 and 2 (models 3 and 4, Table 5). While this analysis combines data from two different age/sex classes, we consider these to represent a coherent group characterised by an intermediate dominance status, contrasting with the generally dominant adult males and typically subordinate juvenile females (Table 1). Overall, of the five variables entered in each analysis, therefore, only %CWIN, the chosen measure of dominance, was found to be significantly related to subsequent survival.

Discussion

Assessments of dominance

The agonistic behaviour observed in the laboratory resembled that seen in the wild at the same season (Hewson 1967; Bryant and Tatner 1988; Newton 1989). Territorial activity amongst wild dippers in autumn involves all age and sex classes (Shaw 1979; Cramp 1988; D.M. Bryant, personal observations). Our assessments of dominance, in a sample which included approximately equal numbers of males and females, were therefore carried out in an appropriate social context at a suitable time of year.

Since our measures of dominance were closely correlated (Bryant and Newton 1994) they appear to describe similar features of individuals. %TIME nominally serves as a measure of resource-holding potential, because the brick perch was both the preferred and only resource available within the arena. %WINS and %QWIN both measured success in agonistic interactions, with the latter equivalent to a dominance rank. %CWIN similarly describes success in interactions but focuses on those involving contact between the participants. Møller (1987) maintained that contact interactions were more reliable measures of status, because they may imply a greater motivation or capacity for dominance amongst individuals with a high proportion of contact wins. This view would be consistent with %CWIN being more closely correlated with the basal metabolic rate of male dippers than other dominance measures (Bryant and Newton 1994). The emergence of this dominance measure as significant in both the metabolic and survival studies, therefore, suggests it may be a more pertinent dominance measure than others, although we had no *a priori* reason, or impression formed from observations of dippers in the laboratory arena, for anticipating this result.

Social status of dippers was related to both age and sex. The absence of strong associations between body mass or size and dominance in dippers is consistent with results from some other studies (Arcese and Smith 1985; Eden 1987). Age has been noted as most important in several small passerine species (Piper and Wiley 1989). Wagner and Gauthreaux (1990) considered sex to be more important than age in their migratory song sparrow population but in a resident population of the same species with year-round territoriality, age was the more important factor (Knapton and Krebs 1976; Smith et al. 1980). Studies of dominance in birds have mostly dealt with size-monomorphic species (Kikkawa 1980; Arcese and Smith 1985). This study shows that even when females are smaller than males, as in the dipper, this did not exclude them from dominating some males (Komers and Komers 1992), as well as other females. This reinforces the crucial role of age/sex differences in the dominance relations of dippers, and suggests that several factors, including plumage (Rohwer and Rohwer 1978) and physiology (Bryant and Newton 1994), as well as age or experience, sex and song production, are likely to interact to confer or maintain dominance. Failure to demonstrate an effect of SONG in this study, may relate in part to its close association with our measures of dominance. Since body mass and size were poor predictors of dominance, and they were anyway unrelated to subsequent survival within this sample, their proximate role in status determination is more appropriately dealt with elsewhere (A.V. Newton, S. Newton and D.M. Bryant in prep).

One question about our dominance assessments cannot be resolved. Would the same results have emerged if we had used a different experimental design to assess dominance? For example, an alternative approach could involve assessments within and then between age/sex classes rather than, as here, assessments amongst mixed classes. It could be argued that this would be more appropriate for examining dominance-survival relationships where the majority of dominance interactions in the field which had a survival implication involved the same sex (or age class). This is unlikely to be the case in dippers, however, since both sexes compete for, occupy and defend territories, necessarily involving interactions across as well as within age/sex categories (Robson 1956; Shaw 1979; D.M. Bryant, personal observations). Our mixed design was appropriate to this pattern of encounters in the wild, but leaves open whether alternative designs would yield analogous results, particularly for within-sex effects of dominance on survival.

Dominance and survival

In some studies, dominant individuals have been shown to have higher survival probabilities than subordinates. For example, Koivula and Orell (1988) and Ekman (1990) showed a relationship between social rank and survival in the willow tit *Parus montanus*. Dominant males survived better than subordinates, while females, although subordinate to males, gained survival benefits from the dominance of their mates. In other tit populations, adults may have priority of access to food resources and cover and thereby force juveniles to forage in more open situations where they become vulnerable to predation (Hogstad 1989). Dominance was also associated with higher fat levels in white-throated sparrows and such individuals showed higher return rates the following year (Piper and Wiley 1990). In contrast, the effect of dominance on survival of dippers was negative for juvenile males and was lacking amongst adult males and juvenile females. By combining data for the two intermediate status age/sex classes (juvenile males and adult females), we identified significant effects of dominance on both overwinter and annual survival. Why did the relationship between dominance and survival apparently differ between sex and age classes?

Sex and age differences did not arise just because classes where survival consequences were lacking are generally subordinate, because adult males generally dominated others and yet we found no effect on their survival. Alternatively, and more likely, adult male dominance may have been uniformly high, or not adequately discriminated by our assessment procedures. This would obscure any trend within this age/sex class. This interpretation implies a strengthening of the effect of dominance on survival if data for adult males were to be combined with that for juvenile males. Yet, in practice, this resulted in a loss of significance, encouraging rejection of this explanation. Nor does this interpretation get support from a lower variability of dominance measures amongst adult males compared to other age/sex classes, because variability in dominance was similar in all classes (Table 1).

Dominance may be crucial for the establishment of juveniles in a population, whether on territories or within a social hierarchy, and yet once established, site-related factors may take precedence over status (Dearborn and Wiley 1993). If this is the case, however, it could only apply to males, because the more dominant of the juvenile females apparently did not suffer survival costs related to their status. It may be that the opportunities for young females to oust opponents are so infrequent, since all other age/sex classes dominate them, that harassment by dominants is rare. In contrast, subordinate but not dominant adult females may gain survival advantages from common occupancy of a territory with an adult or previously established male (Davies and Houston 1981), which is, or could subsequently become, their mate (Ekman 1990). The overall effect of dominance on juvenile males remains unclear. One possibility is a trade-off between benefits for reproductive success against the reduced chance of survival, which may itself arise from the energetic or other costs of maintaining dominance (Bryant and Newton 1994).

This view of the survival costs of dominance principally affecting juvenile males and adult females, related to their intermediate status, is suggested by results from logistic regression analysis. Whether interactions in dippers conform to this pattern of behaviour in the wild, however, can only be resolved by integrating a study of the present type with a detailed study of the occurrence and consequences of dominance interactions within the wild population. Such a study should also examine the effects of dominance on reproduction, since some earlier studies have been equivocal regarding the benefits of dominance for breeding success (Kikkawa and Wilson 1983; Kikkawa and Catterall 1991).

Proof of survival benefits

Experimental confirmation of an effect of dominance on survival remains necessary because the dominance effects on survival identified here may have been confounded by habitat quality. Hence, dominance could simply facilitate territory acquisition, and it is this factor which subsequently moderates survival. Such experiments could draw on two approaches additional to those used in this study. First, manipulation of dominance status followed by comparison of survival between experimental and control groups: such manipulations might be achieved by removals (Hogstad 1980), introductions (Newton 1989), switching of individuals between populations, or by comparisons between groups with and without hormone implants (Nolan et al. 1992). Second, since our approach could not reveal any effect of site-specific factors on survival, site quality could in principle be manipulated or standardized between individuals before release. The specific role of dominance during the period immediately following status assessments might then be identified. Newton (1989) used an approach of this type with dippers. Newly independent juveniles were introduced to a novel river remote from their natal area, following assessments of their dominance in the laboratory arena. This showed dominance measures were correlated with "local survival" over a period of weeks, but too few remained for longer-term survival (i.e. overwinter or annual survival) to be investigated. It does demonstrate, however, that methods are available to separate the assessment of both dominance and survival from some of the effects of site-related factors, which can frustrate identification of causality in dominance-survival relationships (Ekman 1990).

Furthermore, it indicates that dominance indeed plays an important role in the survival prospects of some dippers over a range of time spans, even though the route by which it has an effect remains unresolved.

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