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Fighting for fitness

Salomons, Henri Martijn

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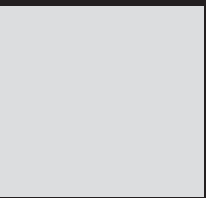
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Why fight? Socially dominant jackdaws *Corvus monedula*, have low fitness

Simon Verhulst
H. Martijn Salomons

Summary

Social dominance is intuitively assumed to be associated with higher fitness, because social dominance implies better access to resources. We found that, in a colony of jackdaws, the dominant males consistently produced fewer fledglings, which had lower chances of survival to 1 year of age. Laying date and clutch size were independent of dominance, but females that mated with dominant males were in poorer condition and laid smaller eggs. Parental survival was independent of social dominance, and the frequency of extra-pair fertilizations in jackdaws is negligible. Dominance was a stable trait of individuals, and not a state that all individuals eventually attained. We conclude that, in this colony, dominant jackdaws had lower fitness. To our knowledge, this is the first example of such a pattern in a free-living species. We hypothesize that the high density of our colony resulted in high testosterone titres, which suppressed paternal care of mate and offspring to the extent that it outweighed the benefits of higher resource access.

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Introduction

Social groups are usually structured in the sense that some individuals are consistently more successful at obtaining resources when there is a conflict (Allee 1952; Drews 1993). Because socially dominant individuals, by definition, have priority of access to resources, it is generally assumed that these individuals also attain the highest reproductive success. The fitness advantage to socially dominant individuals is crucial in understanding the existence of dominance hierarchies; if dominants did not benefit investment in acquiring and maintaining social dominance would be wasted (Pusey & Packer 1997). Such investments are, for example, costly signals used in agonistic interactions (Zahavi & Zahavi 1997) and harmful side-effects of high androgen levels (Folstad & Karter 1992; Frank et al. 1995; Packer et al. 1995; Buchanan et al. 2001), and that agonistic interactions consume time and energy and increase the risk of an injury. Such costs could potentially outweigh the benefits of having priority of access to resources, resulting in neutral or even negative effects of social dominance on fitness (Rohwer & Ewald 1981; Ellis 1995). Many studies of primates have reported positive or neutral effects of dominance on reproductive success (reviewed in Ellis 1995), but this relation has been little studied in other taxa reviews in (reviews in Ellis 1995; Piper 1997; Koivula 1999). Negative effects of dominance on indicators of reproductive success have also been found, but only in captive animals (Ellis 1995). However, the greater access to resources ensured by being dominant is unlikely to yield a fitness advantage when resources are abundant, as is usually the case in captivity. For this reason, and because free-living individuals face a multitude of trade-offs and behavioural options that are absent in captivity, the fitness consequences of dominance can be assessed only in free-living animals.

We studied the life history consequences of social dominance in a colony of free-living jack-

daws. Jackdaws spend much of their time in groups that have a strong linear dominance hierarchy, in the sense that jackdaws rarely lose a conflict with an individual with lower social status (Tamm 1977; Röell 1978; Wechsler 1988). They are facultative colonial during breeding, and colonies can be found in buildings as well as under more natural conditions, for example, in rabbit warrens (Röell 1978; Vogel 2002). We determined social dominance by observing interactions over an artificial food source. The outcome of a conflict can be state dependent; hungrier birds may, for example, win more conflicts over food (Andersson & Ahlund 1991; Cristol 1992). However, jackdaws that were successful in interactions over food also had primary access to available nest boxes and succeeded in defending more nest boxes during winter (Röell 1978). This information, together with the observation that the hierarchy is highly stable over successive years, indicates that dominance in competition over food reflects resource-holding potential (Parker 1974), rather than some transient effect of state. There are two previous studies of the relation between social dominance and reproductive success in jackdaw colonies. Henderson & Hart (1995) showed that dominant pairs produced more fledglings. In contrast, Röell (1978) reported evidence suggesting that dominant pairs had fewer fledglings; neither study compared parental survival. However, Röell assessed dominance in June, during or after chick production, and he suggested that high dominance was the consequence of being without chicks (Röell observed temporary rank shifts in the breeding season that were subsequently reversed in autumn). Furthermore, Röell presented only the cumulative fledgling production of eight males over 5 years. These males were selected from a much larger sample, because they were present in all 5 years of the study, and these males may therefore constitute a biased sample of the population. Data on fledgling quality were not available, and low fledgling production might have been

compensated by producing high-quality fledglings. However, finding a species where the fitness consequences of social dominance depend on the ecological or social setting to the extent that dominance even results in low fitness would offer a valuable tool to study the costs and benefits of dominance and increase our understanding of the evolution of dominance and social structures. We therefore studied the association between dominance and reproductive success in the same colony as did Röell, but we determined social dominance before the breeding season, and we also measured parental survival and offspring quality in relation to social dominance.

Methods

Study Population

We studied free-living jackdaws in the colony at the Zoological Laboratory in Haren, The Netherlands, a semi-urban environment. The colony was established in 1965 and enlarged to 36 nest boxes in 1996 when the study was resumed. Data on dominance and reproduction reported in this study were collected in 1998 and 2000, and survival was measured up to 2003. The study was carried out under license from the Ethical Committee for animal experiments of the University of Groningen.

Nest boxes were checked daily, starting in the first week of April, until the clutch was complete. To determine from which egg a chick had hatched (for another study), we moved clutches to an incubator 1–2 days before the estimated hatching date (temperature 37.7°C, RH 75%). Clutches were exchanged for hard-boiled quail eggs, which birds readily accepted. Length and width of the eggs were measured (± 0.1 mm), and egg volume (V , in cm^3) was estimated using the formula: $V = (\pi * A^2 * L * K) / 6$, where A is width, L is length and, for jackdaws, the constant, K , is 0.00096 (Soler 1988). Eggs in the incubator were checked at least every 2 h during the daylight period. Eggs that

did not hatch were dissected to check for presence of an embryo. Hatching success of eggs with an embryo was 95.7% ($N = 211$, years combined). Hatchlings were weighed, individually marked by clipping the tip of one or two nails and returned to their nests. An equal number of quail eggs was subsequently removed from the nest.

We checked the survival of the chicks in the nest every 5 days (day 1 = hatch date of the first egg). At days 10, 20 and 30, we also weighed the chicks and measured tarsus and wing length (days 20 and 30). At day 30, shortly before fledging, the chicks were ringed.

Breeding birds were individually marked with colour rings and a metal numbered ring. Birds were caught in a large baited cage or in their nest box using trap doors. Early in the nestling period (day 5), a sample of adults was captured in 1998, and most breeding birds were captured in 2000. Biometric characteristics (tarsus and wing length, mass) were measured, a small blood sample (~60 ml) was taken for DNA from the brachial vein, and most birds were released within 20 min.

To estimate survival and identify nest box owners, we regularly observed colour-ringed birds from mid-February. Whenever possible, other colour-ringed jackdaws visiting the colony and the surrounding areas were also identified. Resighting probability is the product of the probability that a bird is still alive and the probability that a living individual is seen, and survival analysis usually requires estimating both these parameters using capture-recapture analysis. However, the probability of observing individuals known to be alive was high (91–100% over the study years 1998–2003 for both sexes, except for 1999, when fieldwork intensity was low). We therefore used the Kaplan–Meijer test to compare survival between dominant and subordinate birds. Resighting probability of an individual was independent of the fate of its partner in all years ($0.34 < P < 0.99$).

Dominance

Agonistic interactions were recorded during March and the first half of April of 1998 and 2000, until the first egg in the colony was laid. Conflicts are resolved in different ways, either through displacement, threat or fights, and these were all scored to obtain a rank order (Röell 1978). To stage conflicts, we offered food in small pits (diameter 10 cm, one in 1998, two in 2000) approximately 10 m from the nearest nest box. The pits were 30 m apart. At these pits, only one jackdaw or a jackdaw pair could eat at a time. The feeding pits were filled only preceding an observation period. We used only interactions at the feeding pit in which both participants were ringed to calculate social rank ($-X \pm SD = 80.0 \pm 58.2$ interactions / male, $N = 42$ males).

The success in agonistic interactions (R) of bird J was calculated following Henderson & Hart (1995): $R = (\text{no. of interactions won by } J / \text{no. of interactions lost by } J) * (\text{no. of individuals supplanted by } J / \text{no. of individuals that supplanted } J)$. This equation takes both the proportion of interactions won and the proportion of individual birds supplanted into account; other methods to assign rank yielded almost identical results. Based on the success score (R), a rank number was assigned to each bird. We then scaled rank between 0 and 1 (most and least dominant male, respectively), because the number of birds in the hierarchy differed slightly between years.

Male jackdaws are dominant over females, and the females' success in conflicts is highly dependent on the rank and proximity of her partner (Lorenz 1931; Röell 1978; Wechsler 1988). Consequently, we cannot determine female rank independently and instead used the rank of the male to characterize the rank of the pair.

Statistical Analysis

A number of individuals bred in the colony in both 1998 and 2000, and different breeding attempts from the same individuals cannot be considered independent samples. Data were

therefore analyzed with a repeated measures hierarchical linear model to avoid pseudo-replication, using the program MLwiN (version 1.10, Rabash et al. 2000). Statistical significance of variables was assessed from the increase in deviance (ΔDev) when the variable was removed from the model. The change in deviance is asymptotically distributed as χ^2 with corresponding change in degrees of freedom (Snijders & Bosker 1999). Unless stated otherwise, data from both years (1998 and 2000) were combined in the analysis. Separate regressions (calculated using SPSS 9.0) are also shown in Table 6.1 for comparison between years.

Results

The hierarchy

Birds present in both 1998 and 2000 had very similar ranks in the 2 years ($F_{1,7} = 12.5$, $P = 0.01$; Figure 6.1). Despite becoming 2 years older, males did not acquire higher dominance between 1998 and 2000 (mean difference = -0.03 , paired t -test: $t_8 = -0.41$, $P = 0.7$). The rank of birds determined at both feeding pits separately was highly correlated (Pearson: $r_{12} = 0.90$, $P < 0.001$; data from 2000), indicating that rank was not site dependent on the scale of the colony.

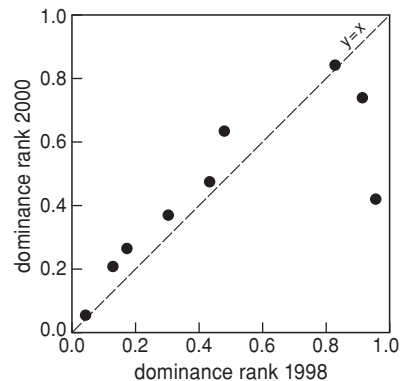


Figure 6.1. Dominance rank of jackdaws in 1998 and 2 years later. Low rank indicates high dominance. Line indicates equal values ($y = x$).

Observations at the two feeding pits were therefore combined. The constancy of dominance rank in space and time shows that our method yields highly repeatable estimates of rank.

Reproduction

Rank was not correlated with laying date of the first egg or clutch size (Table 6.1). However, more dominant pairs produced smaller eggs (Figure 6.2) and smaller hatchlings (Table 6.1). Nestling mortality was higher in nests of dominant pairs, especially in 1998. This resulted in fewer fledglings produced by dominant birds (Figure 6.3A). Furthermore, chicks of dominant pairs fledged with lower mass (Figure 6.3B) and smaller size (Table 6.1). Too few fledglings were observed in later years to test directly whether dominant birds produced fewer surviving offspring, and we therefore verified whether fledging mass predicted survival prospects. For fledglings in 1996–2002, we compared fledging mass between fledglings found dead within a few weeks of fledging ($X \pm SD$ mass at fledging = 155.0 ± 36.3 g, $N = 35$), fledglings whose fate was unknown (194.8 ± 31.3 g, $N = 107$) and fledglings seen alive the next year or later (212.2 ± 20.3 g, $N = 24$). Using hierarchical linear models (with year and parents as hierarchical levels), we found that fledglings

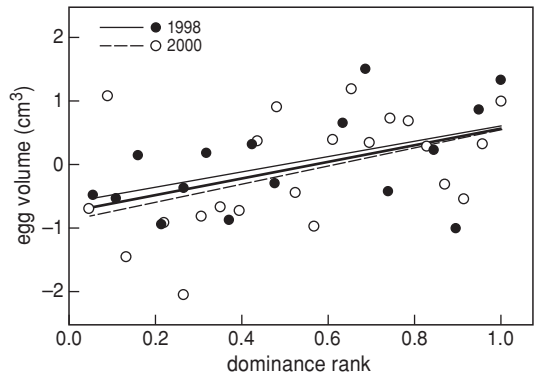


Figure 6.2. Egg volume in relation to parental dominance rank. Thin and dashed lines are regression lines for data from 1998 and 2000, respectively; bold line shows linear regression for data from both years combined. Data shown are differences between observed values and annual means. Low rank indicates high dominance.

that survived their first year weighed more than fledglings whose fate was unknown ($\Delta Dev_1 = 8.08$, $P < 0.005$), which in turn weighed more than fledglings found dead within a few weeks of fledging ($\Delta Dev_1 = 27.95$, $P < 0.001$). When this analysis was repeated using mean fledgling mass per brood as the independent variable, and either the proportion of fledglings

Table 4.1. Dominance rank and reproduction.

Dependent variables	1998			2000			Years combined		
	<i>r</i>	<i>N</i>	<i>P</i>	<i>r</i>	<i>N</i>	<i>P</i>	ΔDev	<i>N</i>	<i>P</i>
Laying date	-0.26	16	0.33	-0.17	22	0.45	1.81	38	0.18
Clutch size	0.21	16	0.44	0.22	22	0.33	1.70	38	0.19
Egg volume	0.49	16	0.056	0.46	22	0.03	9.24	38	0.002
Hatchling mass	0.55	14	0.04	0.36	22	0.10	7.12	36	0.008
Fledgling mass	0.72	9	0.03	0.63	18	0.005	14.02	27	<0.001
Fledgling tarsus length	0.42	9	0.27	0.39	18	0.11	3.71	27	0.054
Fledgling wing length	0.75	9	0.02	0.39	18	0.11	7.60	27	0.006
Number of fledglings	0.54	16	0.03	0.15	22	0.50	4.56	38	0.03

Results are calculated for each year separately, and years were combined using hierarchical linear models. All tests for years combined are with 1 df. Sample sizes for fledgling mass and size are lower because not all nests resulted in fledged young. Significant correlations are in bold.

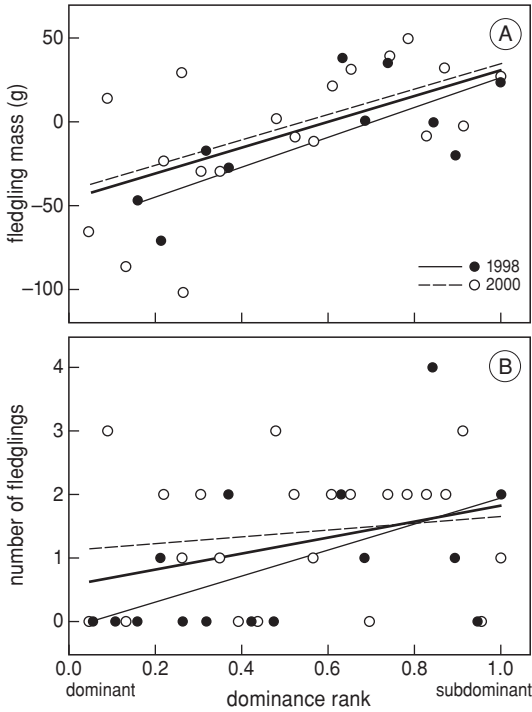


Figure 6.3. Dominance and reproductive success. (A) Fledgling mass (relative to annual mean). (B) Number of fledglings. Thin and dashed lines are regression lines for data from 1998 and 2000, respectively; bold line shows linear regression for data from both years combined. Low rank indicates high dominance.

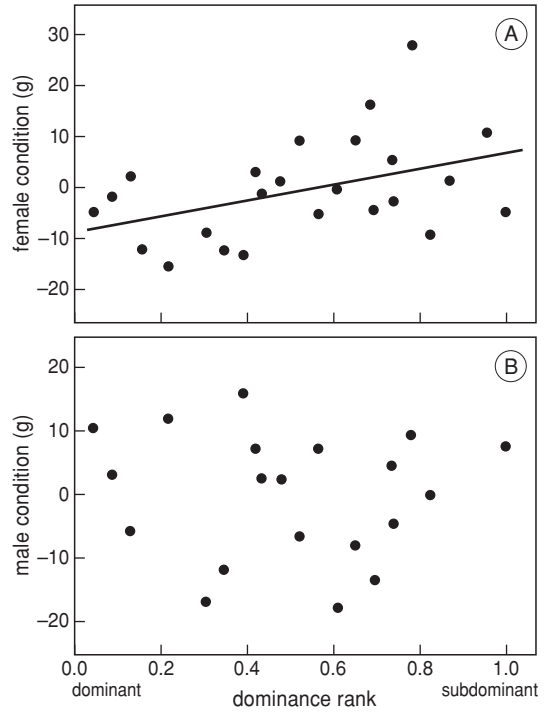


Figure 6.4. Social dominance and condition (residuals from regression of mass on tarsus) of (A) females and (B) males. Low rank indicates high dominance.

surviving or the proportion of fledglings found dead as the dependent variable, then the same result emerged (both $\Delta Dev_1 > 7.4$, $P < 0.01$).

Parental condition

Social dominance was independent of body size (length of tarsus and wing, males: $F_{1,18} < 1.1$, $P > 0.3$; females: $F_{1,22-21} < 0.2$, $P > 0.6$). Enlarging the sample size by including birds captured outside the 1998 or 2000 breeding seasons did not change this result. Condition (residuals from regression of mass on tarsus) was lower in females that mated with dominant males ($F_{1,20} = 6.28$, $P = 0.02$; Figure 6.4A), but male condition was independent of rank ($F_{1,15} = 0.85$, $P = 0.4$; Figure 6.4B). The relation

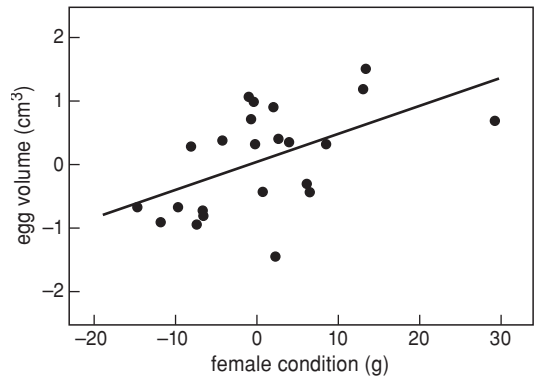


Figure 6.5. Egg volume in relation to female condition. Egg volume is deviation from annual mean egg volume, and female condition is the residual from a regression of mass on tarsus.

between dominance rank and condition differed significantly between the sexes (rank by sex interaction: $F_{1,36} = 4.20$, $P = 0.048$).

To check whether effects of female condition could explain lower reproductive success of dominant jackdaws, we included female condition in the model for egg volume and fledgling quality. Fledgling production was not correlated with female condition (data not shown), perhaps because most condition data were from 2000, and the effect of dominance on fledgling production was weak in that year (Table 6.1). The effect of social dominance on egg volume was mediated through condition of the female ($\Delta Dev_1 = 7.52$, $N = 23$, $P < 0.01$; Figure 6.5), because social dominance did not explain additional variation when female condition was taken into account ($\Delta Dev_1 = -1.8$, $P = 0.2$). Fledgling mass was correlated with egg volume, but there was also a significant effect of social dominance (Table 6.2). Thus, female condition and egg volume explained only part of the correlation between social dominance and fledgling quality.

Parental survival

Dominant jackdaws could compensate for lower annual reproductive output with a longer reproductive life span. We analyzed survival of jackdaws up to the breeding season of

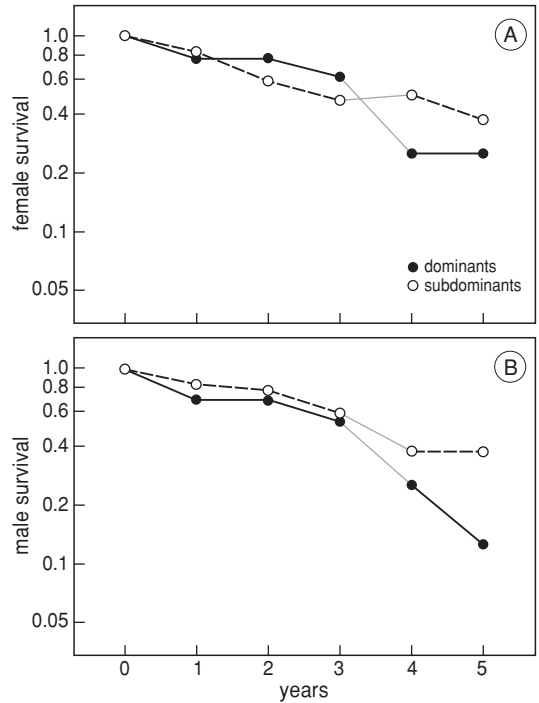


Figure 6.6. Parental survival in relation to social dominance in (A) females and (B) males. All birds were assigned to two groups of equal size on the basis of their rank. Y axis (log scale) shows proportion of birds still alive. Year = 0 denotes first year that rank was known (1998 or 2000). Broken line between years 3 and 4 is because the sample size is lower for years 4 and 5, with only birds that bred in 1998.

Table 4.2. Effects of dominance, egg volume and female condition on fledgling mass.

	ΔDev	Coefficient (SE)	Δdf	P
Null model	179.51			
Final model	158.46		15	
Constant		-39.55 (10.93)	+1	0.001
Dominance rank	+10.42	70.88 (18.87)	+1	0.001
Egg volume	+6.32	16.57 (6.02)	+1	0.012
Rejected term				
Female condition	-0.59		-1	0.44

Data (mean g per brood) were analysed using hierarchical linear models. Null model includes the constant only. Final model includes all significant parameters. Changes in deviance (ΔDev) and in degrees of freedom (Δdf) indicate the changes when parameters are dropped from the final model one at a time (or added to the final model for rejected terms). Female condition is the residual from a regression of mass on tarsus. $N = 18$ broods.

2003. Birds were assigned to two groups of equal size, which comprised the top and bottom 50% of the hierarchy. Data for both years were combined (first breeding season, either 1998 or 2000, was assigned 0, and each bird was used only once in the analysis). Survival was independent of rank in both sexes (females: log rank = 1.39, $N = 30$, $P = 0.24$; males: 0.38, $N = 30$, $P = 0.54$; Figure 6.6). Average survival rate was 72.7% for females ($N = 30$) and 70.8% for males ($N = 30$), in agreement with estimates on the basis of ring recoveries (69%; Dobson 1990).

Discussion

Social dominance was associated with low fledgling production and low fledgling quality (Figure 6.3). For example, the five least dominant males annually fledged 1.2 young of viable quality (fledging mass > 170 g), but the five most dominant males fledged only 0.5 viable young. This decrease was not compensated with greater longevity, because survival was independent of social dominance (Figure 6.6). In theory, males could also compensate for low success with their own partner by having extra-pair fertilizations, but jackdaws have an exceptionally strong pair bond (Lorenz 1931), and the frequency of extra-pair fertilizations is practically zero (Liebers & Peter 1999; Henderson et al. 2000). Dominance was a permanent trait of individuals, and not a state that all surviving individuals eventually attained. These findings led us to conclude that dominant jackdaws in our colony had lower fitness than did subdominants. To our knowledge, this is the first example of such a pattern in any free-living species.

Hypotheses that explain low fitness of dominant birds are based on one of two assumptions. Either it is assumed that there is a causal relation between dominance and reproductive success, or it is assumed that a third factor causes both high dominance and low reproductive success. One possible third variable is

senescence, when aging is associated with a decline in reproductive success and an increase in dominance. Although Henderson & Hart (1995) reported a correlation between age and dominance, we consider this explanation unlikely because dominance was independent of age in our colony, both in recent years (Figure 1; S. Verhulst & H. M. Salomons, unpublished data) and in the 1970s (Röell 1978), which may result from the near absence of breeding yearlings in our colony. We next consider hypotheses that assume a causal relation between dominance and reproductive success; although we acknowledge that we cannot rule out an unknown third factor.

In his extensive review, Ellis (1995) emphasized the variation in the fitness consequences of dominance, and proposed that dominance enhances reproductive success in particular when food availability is low. In agreement with this proposition, Henderson & Hart (1995) found in jackdaws that dominance had a stronger effect on fledgling production in years when overall success was low. Using simple optimality reasoning, this proposition can logically be extended to explain a negative association between dominance and reproductive success: when costs are associated with acquiring and maintaining dominance, and these costs are not compensated with increased resource access (because resources are abundant regardless of status), the net effect of dominance on reproductive success will be negative. However, there is no evidence that resources were abundant in our colony. One or more nestlings starved in almost every nest, and fledgling production was approximately equal in our colony and the colony studied by Henderson & Hart, where dominance enhanced reproductive success. Thus, high resource abundance (Ellis 1995) is unlikely to explain the negative association that we found between dominance and reproductive success.

Females paired with dominant males had poorer condition and produced smaller eggs, and this explained at least part of the effect of

dominance on reproductive success (Table 2). Dominant males could have partners in poor condition because high-quality females prefer subordinate males as partners, and low-quality females are 'making the best of a bad job' by pairing with a dominant male (Qvarnström & Forsgren 1998). Another possibility is that females suffer from having a dominant male as partner. These hypotheses are complementary, because if females suffer from having a dominant partner, this would explain why such males are less attractive. Dominant jackdaws do show more aggression towards their partner than do subordinate males (Röell 1978), and female preference of subordinate males to avoid intra-pair aggression has also been demonstrated experimentally in Japanese quail, *Coturnix coturnix japonica* (Ophir & Galef 2003). This evidence lends credibility to these hypotheses, but for a rigid test, mate choice experiments with jackdaws are required.

Henderson & Hart (1995) reported a positive effect of dominance on reproductive success, and a comparison of our colonies may provide further indications why dominance had a negative effect on reproductive success in our colony. Both colonies had approximately the same number of breeding pairs and comparable reproductive success, but nest boxes were approximately 8 m apart in their colony in the U.K. and only 1.5–3 m apart in our colony. This detail may have far-reaching consequences if closer proximity induces more interactions. It is well established that having close neighbours and more agonistic interactions results in higher testosterone titres in birds (Ball & Wingfield 1987; Wingfield et al. 1990; Beletsky et al. 1992). Testosterone suppresses paternal care (Hegner & Wingfield 1987; Ketterson & Nolan 1992) and could also explain higher intra-pair aggression. Data to compare aggression levels or testosterone between colonies are not available, but dominant jackdaws do participate more in agonistic interactions (Tamm 1977), including in our colony (effect of rank on number of interactions: $F_{1,36} = 17.65$, $P < 0.001$).

We consider a testosterone-based mechanism the most parsimonious explanation of our results, but further experiments, such as manipulation of colony density and measuring testosterone, are required to test this hypothesis. Such experiments may increase our understanding of the evolution of dominance and social structures. The question remains why males invest in acquiring dominance when they do not benefit. Apparently, the increase in resource access associated with being dominant is outweighed by other factors associated with dominance. This hypothesis suggests that the decision rule that jackdaws use in conflicts is maladaptive when it is assumed that birds could also 'choose' not to fight, at least in the specific circumstances (e.g. high density) of our colony. However, on a global scale, the decision rule may, on average, still be optimal, as illustrated by the positive association found between dominance and reproductive success in the colony studied by Henderson & Hart (Henderson & Hart 1995). Alternatively, the decision rule that jackdaws use in conflicts could be part of a genetically determined behavioural syndrome (as in great tits, *Parus major*: Verbeek et al. 1996; Drent et al. 2003) in the sense that variation in dominance reflects different behavioural syndromes. Variation between colonies in the fitness consequences of dominance could then contribute to the maintenance of genetic variation in behavioural syndromes.

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