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Phenotypic correlates of dominance in carrion crows and their effects on access to food

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Abstract. The role of age, sex and body size as determinants of dominance status was studied in a winter flock of individually marked carrion crows, *Corvus corone corone*, and their importance in gaining access to a clumped food source assessed. Sex, age and body size determined, in decreasing order of importance, the outcome of agonistic encounters between individuals. Males won over females, adults over juveniles, and within the same age–sex classes, the large birds over the small ones. Males had access to clumped food for a higher proportion of time than females, and large individuals for a higher proportion than small individuals. Juvenile males, however, had as much access to the food as adult males, achieving this through shorter and more frequent feeding bouts. Thus the determinants of dominance, as assessed from the dyadic interactions, did not strictly correspond to the determinants of food access. The rank order of age, sex and body size as determinants of dominance is important, since different orders determine which members of a population will be subordinate. If subordination has consequences for survival, access to resources, dispersal and other life-history parameters, this order is important in predicting which individuals will survive, breed, disperse or migrate.

The dominance structure within a population of animals has important consequences for many parameters of an individual's life. Studies on birds have shown that dominant group members have access to preferred feeding sites (Ekman & Askenmo 1984) and that they exclude subordinates from a food patch or force them to feed at sites that are more exposed to predators (Schneider 1984). Dominance behaviour can be a driving force for distribution between habitats (Fretwell & Lucas 1969) and dispersal. Dominant individuals enjoy higher survival rates than subordinates in many bird species (e.g. Fretwell 1969; Knapton & Krebs 1974; Smith 1976; Kikkawa 1980; Baker et al. 1981; Arcese & Smith 1985) and have higher reproductive success than subordinates, as is impressively demonstrated in polygynous birds (Wiley 1973) and mammals (LeBoeuf & Peterson 1969; Clutton-Brock et al. 1982).

Phenotypic correlates of dominance often include sex, age and body size. Males often dominate females (Wilson 1975), adults dominate juveniles (Goss-Custard et al. 1982; Enoksson 1988) and within the same sex and age group the bigger individuals dominate the smaller ones (e.g. Searcy 1979; Clutton-Brock et al. 1982). Only a few studies have controlled for the close association of sex, age and body size, and few have attempted to establish the ranking of these three factors as determinants of dominance. Bird studies that do consider two or three of these factors show that their order of importance in determining the dominance status of an individual varies from one species to another (Baker & Fox 1978; Fugle et al. 1984; Greig et al. 1985). If subordination has consequences for survival, dispersal and other life-history parameters, this order is important in predicting which members of a population will survive, breed, disperse or migrate.

A field study on carrion crows, *Corvus corone corone* (Richner 1989a) showed that fledglings in an urban habitat were much smaller than their parents in tarsus length, which represents a measure of permanent character that is highly correlated with other measures of linear body size, e.g. bill length and wing length. In contrast, fledglings from a rural habitat were of similar size to their parents. Since dominance status influences several life-history parameters as outlined above, a principal question in evaluating the fitness consequences of undersized offspring is that of the importance of body size in carrion crows as a determinant of dominance status. A correlation between body size and dominance cannot be assumed a priori, as several studies that control for the effects of sex and age showed no such correla-

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tion for other bird species (e.g. Glase 1973; Davies & Lundberg 1984; Fugle et al. 1984; Arcese & Smith 1985).

Some evidence for body-size-related dominance in carrion crows in the wild comes from Charles' (1972) study, which reported, for six tagged adult males, a positive correlation between body weight or a bill measure and the proportion of encounters won against flock members of unknown age, sex and body size. In two studies on small groups of captive crows (Charles 1972; Richner et al., in press) the males dominated the females, and within the same sex class the bigger birds dominated the smaller ones. Information on the phenotypic correlates of dominance from a larger sample of free-living carrion crows has been lacking.

In the present study data were collected from a winter flock of over 100 individuals, of which more than 60 were marked and of known age, sex and body size. The aims were (1) to investigate, and (2) to establish the hierarchical order of, the phenotypic correlates of dominance, and (3) to investigate the relation between phenotype-correlated dominance and access to food.

MATERIALS AND METHODS

Study Area and Population

The study area was in Lausanne, on lake Geneva in south-western Switzerland. It comprises 0·9 km^2 of parkland habitat with small oak and beech woods, short-cut lawns and alleys. It is mainly a recreational area, bordered on one side by the lake and on the other by a highway. Between 33 and 35 territory-holding carrion crow pairs breed regularly in the park, their territories covering almost the entire area year round, leaving only a small undefended area of 0·05 km^2 which is used by a non-breeding flock of 80-130 birds. Some birds stay in the non-breeding flock for years, others are more transient. The birds feed on the filtrates of a water treatment plant and on leftovers brought by people. These food sources are typically clumped, e.g. bread, a carcass of a chicken, a heap of filtrates, and much fighting between individual crows occurs over these food items.

Between 1985 and 1988 over 500 carrion crows were caught using a trap beside a water treatment plant. It was a large cage trap measuring 4 × 4 × 2 m, similar in design to the one described by Rowley (1968). All birds were sexed by laparoscopy, described elsewhere (Richner 1989b). Juveniles were distinguished from older birds by inspection of the arrangement of pigmentation bands. In juveniles the pigmentation bands on wing or tail feathers form continuous lines, whereas in adults these bands are staggered (Svensson 1984). Most birds caught in the trap were juveniles, but the two sexes were caught in equal numbers. Many birds entered the trap repeatedly or even entered the unbaited trap. All birds were individually wing-tagged and colour-ringed.

Tarsus length, body weight, wing length and bill dimensions (length from bill tip to skull, height and gape) were measured. Tarsus length was taken as the distance between the intertarsal joints bent at right angles, since it is a more repeatable tarsus measure than the one taken on the true tarsus. Tarsus length correlates highly with all other measures of body size, and was used to represent overall body size. Since tarsus length might vary over time, as shown for a few other species (Woolfenden 1978; Smith et al. 1986), this possibility was checked (Richner 1989a): tarsus length remained constant for birds that were caught repeatedly over periods of up to 3 years, and for birds measured as fledglings and recaptured 1–2 years later. Weight, wing length and bill dimensions all showed much greater variation over time. In addition, for body weight and bill dimensions it would be impossible to distinguish between cause and effect of dominance. That is, a higher body weight or a longer bill can be the cause of dominance, or may be a consequence of it.

Assessment of Dominance and Access to Food

The feeding experiments for the present study were carried out between January and March 1988, with the non-breeding winter flock described above. Dominance was assessed from direct observation of marked birds fighting over a food item. For each observation session I provided a piece of frozen ground beef of approximately 2 kg. As it slowly unfroze the crows could continuously hack off the meat from the surface, and one such piece allowed for an observation period of approximately 1 h. A bird was recorded as dominant over another bird if it successfully displaced the other from the food source as the result of an interaction between the two. Access time to the clumped food source was assessed by the focal animal sampling method (Martin & Bateson 1986): of the marked

Table I. The number of interactions won in agonistic encounters with respect to age and sex

Interaction	Winner	W≤L	W>L	Total	χ^2 total
(a) Effect of sex					
Between males and females	Males	20 *	79 **	99 **	75·0
	Females	8	1	9	
Between males and females within same age class	Males	9 *	38 **	47 **	38·7
	Females	2	1	3	
(b) Effect of age					
Between adults and juveniles	Adults	75 **	113 **	188 **	145·0
	Juveniles	6	10	16	
Between adults and juveniles within same sex class	Adults	39 **	94 **	133 **	96·3
	Juveniles	5	9	14	

W≤L denotes interactions where the winner was smaller than or the same size as the loser, W > L denotes interactions where the winner was bigger than the loser.
* $P<0·05$; ** $P<0·001$.

birds at the food patch one was randomly chosen on the basis of its record number in the data file, and then followed by telescope for 5 min. Interactions with other marked individuals and the beginning and end of each feeding bout were recorded on tape and later analysed. Total feeding time of all recordings of the same individual were summed and the percentage of time spent feeding calculated as (total feeding time/total observation time) × 100. Feeding bout duration from all sessions on the same individual were averaged to give the mean bout duration.

Statistical Procedures

The percentages of time spent feeding were arcsine-transformed and checked for homogeneity of variances, normality and independence of means on the variances before they were submitted to an analysis of variance. One birds was excluded from the analysis since it was observed hopping on one leg for several days, which may have given him a strong disadvantage in the struggle for access to the food patch. The mean feeding bout durations were log-transformed before analysis of variance. All significance values throughout the paper are two-tailed.

RESULTS

Phenotypic Correlates of Dominance

Effect of sex on dominance

In 91% of all interactions between individuals of different sex the males won against the females (Table Ia). Excluding a possible age-effect by analysing interactions between birds of different sex within the same age-class shows that 92% of all agonistic encounters between males and females ended with a male win. Males won against females significantly more often than vice versa even when the female bird was of equal size or bigger than the male: in 21 interactions with the female being of equal size or bigger than the male, the female won only once, the male 20 times ($P<0·001$).

Effect of age on dominance

In 92% of all interactions between birds of different age classes the adults won against the juveniles (Table Ib). Excluding the effect of sex by analysing interactions between birds of different age within the same sex-class shows that adults won 90% of all interactions against juveniles. Adults won against juveniles significantly more often than vice versa even when the juvenile bird was of equal size or bigger than the adult: in 85 interactions with

Table II. The number of interactions, within the same age–sex group, won in agonistic encounters with respect to body size

Interaction	W≤L		W>L	χ^2
Within juvenile males	9	*	26	8·3
Within adult males	39	**	101	27·5
Within juvenile females	4	NS	4	
Within adult females	0	0		

W≤L denotes interactions where the winner was smaller than or the same size as the loser, W>L denotes interactions where the winner was bigger than the loser. * $P<0·01$; ** $P<0·001$.

Table III. Percentage of time spent feeding (re-transformed arcsine values), and mean feeding bout duration (s) with respect to age and sex; sample sizes (N) refer to individually marked birds

	% Time spent feeding	95% confidence limits	N	Feeding bout duration	SD	N
Males						
Adults	20·3	15·6–25·5	32	16·7	6·43	26
Juveniles	18·3	7·0–34·4	8	9·7	3·48	7
Females						
Adults	7·6	4·2–14·9	3	6·7	4·15	3
Juveniles	5·3	2·6–9·1	14	6·1	1·76	9

the juvenile being of equal size or bigger than the adult, the juvenile won 10 times, the adult 75 times ($P<0·001$).

Effect of size on dominance

To assess the effect of body size on the outcome of agonistic encounters, the tarsus lengths of the two opponents were compared within the same age and sex class (Table II). Thirty-five interactions occurred between juvenile males, 26 of them won by the bigger bird. Out of 140 interactions between adult males, 101 were won by the bigger bird. Thus, for males within the same age class, the bigger bird won an encounter significantly more often than the smaller bird. Females could not be compared since juvenile females interacted only eight times with each other and adult females were never observed interacting with other adult females.

The order of importance of the determinants of dominance

Dominance, measured in terms of the oucome of agonistic encounters between two individuals, correlated with sex, age and body size. The fact that males won against females independently of body size and age shows that sex is the strongest determinant of dominance in carrion crows. Within the same sex class the adults won against juveniles independently of body size and, thus, age is the next best predictor of dominance status. Finally, within the same age–sex class the bigger males won against the smaller ones. These results show that sex ranks highest as a determinant of dominance, followed by age, then by body size.

Table IV. Analysis of variance of the percentage of time spent feeding

Source	F	df	P
Covariate:			
Body size (tarsus length)	20·15	1	<0·001
Factors:			
Age (juvenile/adult)	0·19	1	0·66
Sex (male/female)	6·32	1	0·015
Factor interactions:			
Age × Sex	0·43	1	0·51

Food Access in Relation to Age, Sex and Size

Percentage feeding time

Body size and sex of an individual significantly affected the total amount of time that it had access to the food patch (Tables III, IV). Whether a bird was an adult or a juvenile, however, was not important. The results of an analysis of variance (Table IV) on the arcsine transformed percentages of time spent feeding showed that it correlated significantly with body size ($r=0·49$, N=57, $P<0·001$). When the median of observed body sizes is used to partition the males into two size classes, the analysis shows that the average percentage of time spent feeding for big males (tarsus ≥67 mm) was 27·9% (95% confidence limits= 21·2–35·4%), whereas the average for small males (tarsus <67 mm) was 14·3% (95% confidence limits=9·9–19·5%; t-test, $t=3·34$, N=40, $P=0·002$).

When the effects of body size and age are

Table V. Analysis of variance of duration of feeding bouts

Source	*F*	*df*	*P*
Covariate:			
Body size (tarsus length)	89·50	1	<0·001
Factors:			
Age (juvenile/adult)	7·92	1	0·008
Sex (male/female)	11·87	1	0·001
Factor interactions:			
Age × Sex	2·76	1	0·105

controlled for, the sex of an individual proved an important determinant of percentage of time spent feeding. Percentage of time spent feeding for males was on average three times higher than for females (Table III). When the effects of body size and sex are controlled for, the age is not a significant factor in determining percentage of time spent feeding (Table IV). Sex and body size explain 37% of total variation in the percentage of time spent feeding at the patch.

Duration of feeding bouts

The mean duration of feeding bouts (Table III) was significantly affected by an individual's body size, sex and age. In an analysis of variance on the log-transformed mean feeding bout durations (Table V) body size correlates significantly ($r=0{\cdot}73$, $N=44$, $P<0{\cdot}001$) with bout duration. Bigger birds show longer feeding intervals than smaller birds. Further, when the effects of body size and age are controlled for, feeding bout duration is significantly affected by sex, and when the effects of body size and sex are controlled for, feeding bout duration is significantly affected by age (Table V). Adults have longer feeding bouts than juveniles, and males have longer feeding bouts than females (Table III). Age, sex and body size account for 75·1% of total variation in mean duration of feeding bouts.

DISCUSSION

Dominance has rarely been investigated in a way that dissociates the existing correlations between age and body size or sex and body size, despite the importance of the ranking order of the determinants of dominance for an individual's life-history parameters (e.g. survival, breeding, dispersal or migration). Some studies also use the differences in body size between males and females as a sexing criterion, weakening the confidence in the results. In addition, findings from aviary studies are often used to make predictions for the animals in the wild, though field studies may give a different ranking of the dominance determinants. For example, in a study on dark-eyed juncos, *Junco hyemalis*, in captivity, the wing length showed stronger correlation with dominance rank than sex, whereas in a free-living flock the wing length was not correlated with dominance (Baker & Fox 1978).

The important features of the present study are (1) the complete information of sex, age and body size for each individual, (2) the analysis of interactions between the tagged individuals only, which does not necessitate assumptions concerning the randomness of interactions with respect to age, sex and body size, (3) the use of a sexing method that does not rely on body size itself, and (4) the use of a measure of body size, tarsus length, that does not change with age or social status.

Carrion Crow Dominance Relationships

The motivating question for this study concerned the effect of body size on the dominance status of an individual and arose from a comparative study on the growth of carrion crow chicks. That study (Richner 1989a) showed that chicks in an urban habitat grow more slowly and reach lower final body size than chicks in an agricultural habitat, despite the fact that the parents, compared between the habitats, were of equal size. The present study thus suggests that the birds raised in the urban habitat will have a lower dominance status than the birds raised in the agricultural habitat. Is it disadvantageous to be a subordinate?

Although adults dominated juveniles within the area of clumped food distribution, the juveniles had equal access to food in terms of the percentage of time spent feeding. They achieved this by shorter but more frequent feeding bouts. The degree to which the patch is accessible to a subordinate probably depends on the momentary constellation of dominant birds at the patch. As this is very dynamic, it can give opportunities to subordinates to gain access to the patch, though for much shorter feeding bouts than dominants. As with the adult–juvenile dominance, the males almost invariably won in aggressive interactions with females.

The few females that tried to feed at the experimental patch could gain access to it for less than one-third of the time that males could. Feeding bouts were also much shorter.

Access to the clumped food source was strongly correlated with body size. Large males (tarsus ≥ 67 mm) had twice as much access to the food patch as small males (tarsus < 67 mm). As it is unlikely that a body size difference of 10% between small and large males results in a difference of metabolic needs in the order of 100%, large dominant males have higher net benefits at a clumped food source than small subordinates. For crows competing for clumped food it is disadvantageous to be small and hence subordinate.

Ranking of the Determinants of Dominance

This study shows that sex ranks highest as a determinant of dominance, followed by age, then by body size. These results differ from findings on other bird species, where age (white-crowned sparrow, *Zonotrichia leucophrys*: Fugle et al. 1984; herring gull, *Larus argentatus*: Greig et al. 1985) or body size (captive dark-eyed junco: Baker & Fox 1978) were more important than sex in determining the outcome of an agonistic encounter. Thus, for the carrion crow, we can expect a negative effect of dominance mainly on females; for the herring gull immatures will be most affected; whereas for the dark-eyed junco the target group to suffer from subordination would be the small individuals. Indeed Monaghan (1980) showed that immature herring gulls have a higher dispersal between feeding sites and explained this by adult–juvenile dominance.

The Meaning and Measurement of Dominance

It is interesting to note that the determinants of dominance as assessed from the dyadic interactions do not strictly correspond to the determinants of food access. That is, juvenile males are dominated in direct interactions with adult males, but in terms of food access they do equally well. This raises the question of what dominance actually means and how it should be measured. As pointed out by Gauthreaux (1978) in a review article on behavioural dominance, there are numerous and confusing behavioural definitions of social dominance. Wilson (1975, page 275) defined dominance as 'the assertion of one member of a group over another in acquiring access to a resource that adds to the genetic fitness of the dominant individual'. Gauthreaux (1978) proposed that measures of dominance must (1) indicate priority of access to a resource and (2) indicate that the observed priority is caused by the dominance behaviour of the participants rather than by some incidental factor. For studies that consider the ecological consequences of dominance, Wilson's (1975) measure is preferable since it includes the fitness term. However, applying Wilson's definition to the carrion crows would give the same ranking for adult and juvenile males, although it is obvious from the observations that adult males have priority of access. The adult males dominated the juvenile males, in the sense of Gauthreaux, but this dominance did not result in increased access to the resource and hence in possibly increased adult fitness. It further shows that the outcome of agonistic encounters, which is most often used as a measure of dominance, cannot without additional investigation be used as a meaningful predictor of ecological, behavioural or life-history consequences.

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