The Auk 118(2):553–556, 2001

Sexual Size Dimorphism and Positive Assortative Mating in Alpine Choughs (*Pyrrhocorax graculus*)

ANNE DELESTRADE[1]
Centre de Recherches sur les Ecosystèmes d'Altitude, 400 route du Tour, Montroc, 74400 Chamonix, France

ABSTRACT.—The degree of sexual size dimorphism in a number of different morphological characters was examined in a social corvid, the Alpine Chough, using measurements taken on 178 males and 144 females. A small amount of size dimorphism appeared in all morphological characters, and weight was the most dimorphic character. To identify if Alpine Choughs mate assortatively, measurements of mates were compared in 76 pairs. A positive assortative mating was found on tarsus length, and a small positive trend is suggested between body condition of partners, but that needs to be confirmed with a larger sample size.

The Alpine Chough (*Pyrrhocorax graculus*), is a social corvid living in large flocks in high mountain areas in the Palearctic (Goodwin 1986). Like all corvids, Alpine Choughs appear sexually monomorphic and the two sexes are indistinguishable in size. However, that species has not been well studied and morphometric data on sexed birds are lacking. Measurements of Alpine Choughs have only been reported from museum collections of skins (Cramp and Perrins 1994). Thus, the first aim of this study is to report the first large data set of live Alpine Choughs of known sex and to identify the degree of sexual size-dimorphism with several body measurements. The second aim is to identify whether Alpine Choughs mate assortatively. Assortative mating, defined as nonrandom mating with respect to some phenotypic character, may be indicative of active mate choice. Most cases of size-assortative mating have been observed in species that are highly sexually dimorphic in size, such as raptors (Newton and Wyllie 1996, Olsen et al. 1998), waders (Hedenström 1987), or geese (Cooke and Davies 1983). Very few examples of size-assortative mating have been reported in passerines. Even with corvids, which are thought to form life-long, monogamous pair bonds, very few studies have looked at morphology of mates (Pinyon Jays *Gymnorhinus cyanocephalus*; Marzluff and Balda 1988).

Methods.—This study is part of a long-term program on social behavior of Alpine Choughs carried out in the Northern French Alps (Chamonix Valley, Haute-Savoie) (Delestrade and Stoyanov 1995, Delestrade 1999). Nine-hundred-ninety-five Alpine Choughs were caught between January 1988 and September 2000 by canon net or clap net; nestlings were caught at the nest. All birds were color-banded, and the following measurements were taken: body weight, wing length, tail length, tarsus length, bill length from the nostrils to the tip of the bill, bill depth, and bill width at the point of contact with feathers. Wing and tail length were measured with a ruler (±1 mm), tarsus and bill were measured with callipers (±0.1 mm), and each specimen was weighed using a 500 g Pesola spring balance (±1 g). All body measurements were taken in all months of the year, but wing and tail lengths of molting Alpine Choughs (from July to September) were excluded. I removed seasonal variation in weight by using standardized residuals in three seasons (winter, December–February; spring, March–May; and summer, July–September).

Different age classes could be distinguished by the color of their legs (black for yearlings vs. orange for adults). Most birds (75%) are caught as adults (i.e. older than one year, but unknown age). Only the age of birds caught as yearlings (22% of banded birds) or nestlings (3%) could be determined. Pairing and sex were determined by observations of behavior—males feed their mates during the breeding season. During capture, 114 adults were caught several times, which are a good sample of birds with repeated measures. The sex of 30 of those adults was unknown and was determined using a discriminant function analysis, performed on five variables (wing, tail and tarsus lengths, bill nostril, and bill width). I correctly classified 93% of 250 adults of known sex using this method (A. Delestrade unpubl. data). I calculated repeatability of morphometric data on successive measurements for birds caught two to four times over the same year in order to examine time or age effects (Lessells and Boag 1987). Because of small sample size, I combined data on both sexes by analysing residual values for each sex. All measurements were repeatable within a year (Table 1). I used a principal components analysis (PCA) to combine the six morphological measurements (wing, tail and tarsus lengths, and bill measurements) and extract first principal component (PC1) as a multivariate index of overall body size for each mate. An index of body condition of each mate was also calculated as the residuals of a regression of weight, corrected by season, on the index of overall body size (PC1). Be-

[1] E-mail: crea@crea_chamonix.org

TABLE 1. Repeatability and analysis of variance of measurements taken on adult Alpine Choughs. Successive measurements were taken over a single year. Weight is corrected for season effect for each sex.

Variables	*F* ratio	df	*P*	Repeatability
Weight	8.9	20 and 46	<0.001	0.78
Wing	14.6	16 and 39	<0.001	0.85
Tail	21.4	17 and 41	<0.001	0.90
Tarsus	4.9	20 and 47	<0.001	0.59
Bill nostril	7.3	20 and 47	<0.001	0.69
Bill width	7.8	20 and 47	<0.001	0.71
Bill depth	4.9	20 and 47	<0.001	0.58

cause confidence intervals give more information than the significance test (Yoccoz 1991), I calculated confidence intervals at 95% of Pearson product moment correlation coefficient, using the Fisher transformation.

Results.—I measured 322 adults (i.e. older than one year) of which I determined by observation the sex of 178 males and 144 females. Significant differences occurred between sexes for all measurements (all *t*-tests $P < 0.001$, Table 2). Thus, in adult Alpine Choughs, all measurements of males are on average larger than those of females (Table 2). The dimorphism index was between 87 and 95% for all measurements (Table 2). The greatest difference between sexes was in weight (13% greater in males), which was also the most variable measure within each sex (CV = 7.2 or 8.5). All other measurements were between 4.5 and 7% greater in males.

To avoid pseudoreplication, measurements of mates were compared in 76 pairs using only the first mate. In 10% of pairs, males were mated with females bigger than themselves. Index of overall body size was not correlated between male and female mates (Table 3). In contrast, I found a significant positive correlation in male and female tarsus length in paired birds (Fig. 1, $r = 0.4$, $n = 76$, $P < 0.001$; Table 3). That result suggests that Alpine Choughs were assortatively mated by tarsus length. I found no significant relationship in body condition of mates, even if a small positive trend is suggested (Table 3). Because mates were not all measured at the same time, I performed a separate analysis using only partners measured the same year. In that case, with small sample size, small positive trends for both tarsus length and body condition are suggested, although the relationship was not significant (for both $r = 0.37$, $n = 27$, $P = 0.06$, confidence interval: $0 < r < 0.64$).

Assortative mating by tarsus length could result from an assortative mating by age if tarsus length increased with age. To determine whether tarsus length increased with age for adult Alpine Choughs, I examined variation in tarsus length of 71 adult males and 42 adult females that were measured two times within a few months to 10 years interval. No significant increase in tarsus length was detected in adults with time (for males: $r = -0.005$, $n = 71$, $P = 0.97$, confidence interval: $-0.23 < r < 0.22$; for females: $r = 0.17$, $n = 42$, $P = 0.21$, confidence interval: $-0.13 < r < 0.44$). To confirm that tarsus length did not increase over time, I analysed repeatability of tarsus lengths taken on the same individual within a minimum interval of three years. Tarsus length and all other measurements, except bill depth, were repeatable after three years (Table 4).

The effect of birth year on tarsus length of yearlings (i.e. birds for which birth year is known) was analysed to detect a possible influence of rearing

TABLE 2. Measurements of adult male and female Alpine Choughs captured in Chamonix Valley. Dimorphism index = (mean females/mean males) × 100.

Variables	Sex	*n*	Range	Mean	SD	CV	Dimorphism index
Weight (g)	F	144	160–254	197	16.8	8.5	87.2
	M	176	194–277	226	16.2	7.2	
Wing (mm)	F	141	242–279	256.1	6.9	2.7	94.5
	M	172	253–285	271.1	6.0	2.2	
Tail (mm)	F	137	153–187	168.2	5.8	3.5	94.5
	M	174	160–200	177.9	6.5	3.7	
Tarsus (mm)	F	132	40–47.5	43.5	1.4	3.3	95.4
	M	157	40.8–50.4	45.6	1.6	3.4	
Bill nostril (mm)	F	143	19.1–23.9	21.1	1.0	4.6	93.0
	M	167	18.8–29	22.7	1.1	4.8	
Bill width (mm)	F	133	10.5–13.8	12.3	0.7	5.6	94.6
	M	155	10.9–14.8	13	0.7	5.1	
Bill depth (mm)	F	143	8.8–12.3	10.6	0.7	6.5	95.5
	M	176	9.7–12.7	11.1	0.6	5.2	

TABLE 3. Correlations between measurements, overall body size (PC1), and body condition of mates. The confidence interval of Pearson product moment correlation coefficient was calculated using Fisher transformation.

Variables	*r*	*n*	Confidence interval		*P*
			r lower	*r* upper	
Wing	0.02	80	−0.2	0.24	0.86
Tail	0.09	79	−0.13	0.3	0.45
Tarsus	0.4	76	0.2	0.57	0.0004
Bill nostril	0.05	78	−0.17	0.26	0.68
Bill width	0.006	76	−0.22	0.23	0.96
Bill depth	0.05	78	−0.17	0.27	0.68
Body size	−0.003	74	−0.23	0.22	0.98
Body condition	0.21	73	−0.02	0.41	0.08

conditions. No effect of birth year was detected on mean tarsus length of yearlings measured in winter (ANOVA, $F = 1.6$, df = 8 and 72, $P = 0.14$), but sexes were unknown and thus combined for this analysis.

Discussion.—This study reports for the first time morphometric data of sexed Alpine Choughs. Results show a slight but significant sexual dimorphism. On average, males were bigger than females in all measurements (from 4.5 to 13% depending on measurements). That seems to be a general character in corvids (see Cramps and Perrins 1994). When comparing both species of the genus *Pyrrhocorax*, the Alpine Chough, which is the smallest species, seems to have a lesser degree sexual size dimorphism than the Chough (*P. pyrrhocorax*), especially for weight: males are 13% heavier than females in Alpine Choughs (this study) versus 16% in Choughs (Tella and Torre 1993).

To my knowledge, this is the first report of positive assortative mating based on tarsus length in birds. Assortative mating by age has often been observed in birds (Coulson and Thomas 1983, Black and Owen 1995). One possible explanation for assortative mating by tarsus length in Alpine Choughs is that they paired by age, and tarsus length increases with age in adults. However, no increase in tarsus length was found between successive measurements taken on same adults, suggesting that is not the cause of the relationship. In the same way, no increase in tarsus length has been found with age in closely related species, the Chough (Blanco et al. 1996, Blanco and Tella 1999) or the Carrion Crow (*Corvus corone*) (Richner 1989a). Another explanation for assortative mating by size has been suggested by Cooke et al. (1995). Similarity of tarsus length within pairs may be related to differential rearing conditions of different cohorts, differentially affecting tarsus length. In this case, an assortative mating by tarsus length could be a byproduct of long-term pair-bonding and the greater availability of same-age birds at the onset of pairing. In constrast with results obtained on fledgling Carrion Crows (Richner 1989b), no effect of birth year was found on tarsus length of yearling Alpine Choughs. But that has to be confirmed because sexes were unknown here and that may mask potential variations with birth year if sex ratios in yearlings vary between years.

Active mate choice is another explanation for assortative mating by tarsus length. An interesting result is that other size characters were not correlated

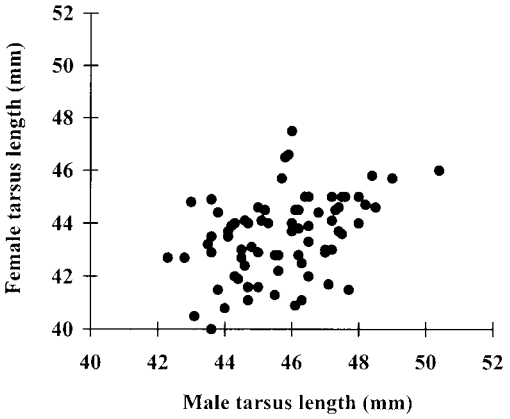

FIG. 1. Relationship between tarsus length of mates ($r = 0.4$, $n = 76$, $P < 0.001$).

TABLE 4. Repeatability and analysis of variance of successive measurements on adults taken within an interval of minimum three years. Data of both sexes were combined. Analyses were performed by using residuals for each sex.

Variables	*F* ratio	df	*P*	Repeatability
Wing	12.3	41 and 83	<0.001	0.90
Tail	4.04	46 and 93	<0.001	0.60
Tarsus	18.8	47 and 95	<0.001	0.90
Bill nostril	4.07	47 and 95	<0.001	0.61
Bill width	2.33	45 and 91	0.003	0.40
Bill depth	1.8	47 and 95	0.02	0.29

between mates. Thus, assortative mating was not related to overall body size, but to a particular trait. There was no significant relationship between body condition of partners although a small positive trend is suggested. That has to be confirmed with a larger sample size of partners measured at the same time. However, potential correlations of body condition could simply result from males feeding females or from similar access to food due to similar social rank of mates.

The Alpine Chough has a yellow bill and red legs contrasting with black plumage, characters that distinguish it among the crow family. Tarsus color turns black to red between yearling and adult, which suggests that the appearance of the tarsus could be involved in signal of status. Tarsus length may be related to dominance (Richner 1989a), and size-related dominance interactions could play a role in mating patterns. Furthermore, tarsus length is a measurement invariable with time (age, season, or body condition). Thus, tarsus length could be a good phenotypic character involved in status signaling and in mate choice. Although mating is nonrandom in terms of tarsus length, there is no evidence that birds are actually choosing on the basis of size. Future studies should consider tarsus length as a factor in male competitive interactions and mate preferences of both sexes.

Acknowledgments.—I am very grateful to all the following people: G. Jarry, P. Perret, and all people who participated in the capture operations for their much appreciated efficiency; C.R.B.P.O. for permitting bird banding; V. Bretagnolle and N. G. Yoccoz for statistical advices; J. L. Dickinson and three anonymous referees for improving the previous version; and C. Watt for improving the English of this paper.

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Received 2 February 2000, accepted 27 November 2000.
Associate Editor: J. Dickinson