

Assortative Mating and Sexual Size Dimorphism in Black-legged Kittiwakes

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Abstract.—We examined several morphological characters of adult Black-legged Kittiwakes (*Rissa tridactyla*) breeding in Brittany, France, near the southern limit of the species' range. Males were significantly larger than females in body mass, head length, wing and tarsus, and the French population differed highly significantly in size from previously studied populations in England and Alaska. There was a strong pattern of assortative mating on tarsus length ($r_{16} = 0.87$) which was also correlated with arrival date in both sexes. After removing the variance produced by arrival date, assortative mating remained significant, suggesting that it may have been produced via sexual selection. Received 28 November 2003 accepted 15 April 2004.

Key words.—Black-legged Kittiwake, *Rissa tridactyla*, assortative mating, sexual dimorphism, Brittany.

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Kittiwakes are well-studied colonial seabirds with sexually monomorphic plumage (Cramp 1983). Morphological measurements and sexual size dimorphism have been reported for several populations (Coulson *et al.* 1983; Cramp 1983; Jodice *et al.* 2000) but regional variation in body size has not been examined. Additionally, no study has examined whether assortative mating by a morphological variable occurs, although Coulson and Thomas (Coulson and Thomas 1983) have reported assortative mating by age. Assortative mating by size is widespread in birds and has been reported to occur in such features as wing (Olsen *et al.* 1998; Wagner and Morton 1997), bill (Coulter 1986; Forero *et al.* 2001; Wagner 1999), tail (Regosin and Pruett-Jones 2001) and tarsus (Delestrade 2001). Assortative mating may have important evolutionary consequences (Crow and Felsenstein 1968; Johnstone 1997) and may arise from active mate choice, intra-sexual competition, mating constraints or differential mate availability (Crespi 1989). Assortative mating may provide information on the processes underlying pair formation, a topic of considerable interest, especially for researchers of species with long-term pair bonds and high levels of biparental care.

Our primary aim is to report a pattern of assortative mating on a morphological char-

acter in kittiwakes and to examine the possible reasons for its occurrence. Our second aim is to report morphological data on a population breeding near the southern limit of the species' range and to compare body size and sexual size dimorphism with that from two other published studies.

METHODS

Kittiwakes have been intensively banded at Cap-Sizun in Brittany, France (48°50'N, 4°35'W) since 1979 (Cam *et al.* 1998; Danchin and Monnat 1992). While color-ringing the chicks from mid-June to the end of July, we captured and marked unringed adult birds and also recaptured some adults of known age. Adults were captured using a metal hook fixed to a pole to draw in adults by hooking the birds under their lower mandible. The sex of captured individuals was determined by subsequent observations of copulation and courtship feeding (Helfenstein *et al.* 2003b). Measurements were collected on 221 birds of known sex (97 males and 124 females) and dial calipers were used to measure head-plus-bill length (Coulson *et al.* 1983) and tarsus length (± 0.1 mm) and a stop-ended ruler for flattened wing length (± 1 mm). We also weighed each individual (± 5 g) using a Pesola spring balance. A body condition index was estimated using the residuals of the regression of the body mass against tarsus length and wing length. We captured some individuals several times in different years and morphometric data were collected at each capture. Repeatability of morphometric data and body condition between years and within individuals can be estimated from an ANOVA with individual identity as a factor (Falconer and Mackay 1996; Lessells and Boag 1987). For analyses other than repeatability, when the same individual had several records of the same morphological trait, we used the first record of this measurement.

Arrival date at the breeding area may reflect an individual's health and its ability to forage and to sustain migratory flights (Both and Visser 2001; Møller 1994; Potti 1998); arrival date may therefore co-vary with morphological traits. Kittiwakes do not strictly migrate but are pelagic sea birds that travel long distances to locate food in cold-water upwellings (Cramp 1983). Their flying abilities may also determine their foraging ability and thus body condition, and be reflected in their arrival date at the breeding ground (Helfenstein *et al.* 2003b). We defined arrival date as the first day on which a kittiwake was re-sighted in the study area in any year (Helfenstein *et al.* 2003b). As most of the individuals we measured were previously non-banded unknown-age adults, arrival date was not available for the year of measurement. However, as soon as birds have bred at least once in the study area, this parameter is very repeatable within an individual from year to year (Lessells and Boag 1987; repeatability = 0.29, $F_{1,485} = 3.86$, $N_e = 6.89$, $P < 0.0001$), even in early years (birds up to five years old: repeatability = 0.48, $F_{1,172} = 1.43$, $N_e = 3.01$, $P = 0.003$). We therefore used the date an individual arrived the following year as a surrogate for this variable.

For measurements of three out of four traits there were no effects between the measurement taken by the five field workers (ANOVAs with observer as a factor; wing length: $F_{4,215} = 0.70$, n.s.; body mass: $F_{4,211} = 1.68$, n.s.; head-plus-bill: $F_{1,58} = 0.97$, n.s.). However, there was an effect on tarsus length ($F_{4,193} = 10.7$, $P < 0.0001$). The residuals of ANOVAs modeling the effect of the observer's identity on tarsus length were therefore used for subsequent analyses on tarsus length.

RESULTS

Except for body condition, morphometric data were repeatable (Lessells and Boag 1987) between years in the same individual (Table 1). Because of insufficient data, the repeatability of head-plus-bill length was not estimated. Males and females were significantly different in all four morphological traits ($t > 4.1$, $P < 0.0001$) (Table 2). Males were on average 5.3% larger than females (wing length: 2.8%; tarsus length: 3.5%; head-plus-bill length: 4.5%; body mass: 10.2%). Kittiwakes in France (latitude 48.5°N) differed significantly in all measured size variables from those in England (55°N) and Alaska (59°N) and those two

populations differed from each other (all $P < 0.0001$). The degree of sexual size dimorphism was very similar between populations (Table 2). We also examined body size traits within individuals and found only two correlations out of six to be significant: tarsus length and body mass, and head-plus-bill length and body mass (Table 3).

Pairs showed a strong pattern of assortative mating on tarsus length (Fig. 1), but not on any other measurement (wing length, body mass and body condition; all $r < 0.28$, n.s.). Assortative mating by tarsus length may be a byproduct of assortative mating by age if tarsus length increases with age. However, there was no relationship between tarsus length and age ($r_{17} = 0.02$, n.s.) or with the number of years elapsed between the first and second captures of the same individuals ($r_{15} = 0.002$, n.s.). Arrival date (i.e., the first day of the season that an individual was first sighted in the breeding areas) was positively correlated with tarsus length both in males ($r_{74} = 0.33$, $P < 0.005$) and in females ($r_{104} = 0.29$, $P < 0.005$) indicating that individuals with long tarsi arrived later. As tarsus length does not vary with age, the relationship between arrival date and tarsus length is unlikely to be mediated by age, even if older birds are known to arrive earlier at the breeding area than younger birds. Kittiwakes were also paired assortatively by their arrival dates (i.e., early arriving females were paired to early arriving males) ($r_{18} = 0.79$, $P < 0.0001$), however, assortative mating remained significant when using the residuals of tarsus length against arrival date ($r_{16} = 0.65$, $P < 0.005$).

DISCUSSION

Our main finding was a strong, positive correlation between the tarsus lengths of

Table 1. Repeatability of successive morphometric measurements taken in different years from the same individual kittiwakes

Variable	F ratio	df	P	Repeatability
Tarsus length	3.61	8,11	n.s.	0.54
Wing length	7.46	10,15	<0.001	0.74
Body mass	3.56	10,14	<0.02	0.53
Body condition	1.95	8,10	n.s.	0.31

Table 2. Comparison in morphological measurements of three kittiwake populations from Cap Sizun, France, North Shields, UK (from Cramp 1983), and Middleton Island, Alaska (from Jodice *et al.* 2000).

Morphometric trait	Females				Males				D.I. ^b
	Mean	SD	CV ^c	N	Mean	SD	CV ^c	N	
Cap Sizun									
Tarsus length (mm)	36.18	2.23	6.2	111	37.50	2.44	6.5	87	96.5
Wing length ^a (mm)	308.1	5.6	1.8	123	317.1	8.5	2.7	95	97.2
Head-plus-bill length (mm)	87.6	14.5	1.7	34	91.89	1.80	2.0	27	95.5
Body mass (g)	340.7	28.3	8.3	121	379.5	34.7	9.1	94	89.8
North Shields									
Tarsus length (mm)	—	—	—	—	—	—	—	—	—
Wing length ^a (mm)	302.6	6.7	2.2	21	312.1	4.7	1.5	24	97.0
Head-plus-bill length (mm)	85.80	1.70	2.0	21	91.40	1.50	1.6	24	93.9
Body mass (g)	365.5	24.2	6.6	21	410.0	28.0	6.8	24	89.1
Middleton Island									
Tarsus length (mm)	35.08	13.6	3.9	289	36.32	12.4	3.4	316	96.6
Wing length ^a (mm)	317.5	6.6	2.1	37	327.9	5.6	1.7	36	96.8
Head-plus-bill length (mm)	94.0	2.30	2.4	37	99.6	2.40	2.4	36	94.5
Body mass (g)	—	—	—	—	—	—	—	—	—

^aFlattened wing length only.^bDimorphism index: (female mean) × 100/male mean.^cCoefficient of variation: (SD × 100)/mean.

mates which remained constant after the variance produced by the covariate of arrival date was removed. As in other studies, it is difficult to determine the causes of assortative mating. It may be produced in kittiwakes by an additional covariate that we did not measure, or more interestingly, by active mate choice for partners of a favored size. It could be meaningful that assortative mating occurred by tarsus length but not by other variables, because tarsus is considered to be the best single measurement representing overall body size (Rising and Somers 1989). One possibility is that tarsus is an indicator of individual quality and larger kittiwakes choose large mates, leaving

smaller individuals to pair with smaller mates. One finding that contradicts this hypothesis is that kittiwakes with longer tarsi arrived to the breeding grounds later rather than earlier. An alternative explanation is that individuals prefer partners that are similar in size. This possibility is consistent with our finding in a behavioral study that among mates, a sexual conflict exists over copulation (Helfenstein *et al.* 2003a). Females often eject their mates' sperm immediately following copulation and this may reduce the ability of males to assure their paternity against the occurrence of occasional forced extra-pair copulations (Helfenstein *et al.* 2004). Males can

Table 3. Intra-individual correlations between morphological traits in males and female kittiwakes.

Morphological traits	Males			Females		
	r	N	P	r	N	P
Tarsus/wing	-0.11	86	n.s.	0.13	112	n.s.
Tarsus/head-plus-bill	0.11	27	n.s.	-0.12	34	n.s.
Tarsus/body mass	0.30	85	<0.0*	0.23	110	<0.02
Wing/head-plus-bill	0.12	27	n.s.	0.02	34	n.s.
Wing/body mass	0.03	93	n.s.	0.14	121	n.s.
Head-plus-bill/body mass	0.41	25	<0.05	0.45	33	<0.01

*P-value remains significant after sequential Bonferroni correction.

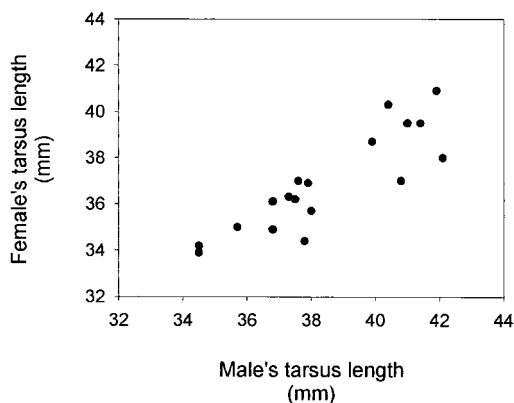


Figure 1. Female tarsus length plotted against male tarsus length in 18 pairs of Kittiwakes ($r_{16} = 0.87$, $b = 0.77$, $P < 0.0001$). The correlation remained significant ($r_{16} = 0.72$, $b = 0.68$, $P < 0.001$) when using the residuals of the ANOVA modeling observer effects on tarsus length (observer effect on males: $F_{1,16} = 4.02$, n.s.; females: $F_{1,16} = 1.47$, n.s.).

apparently prevent their mates from ejecting their sperm by remaining on the female's back, however females are more likely to force smaller males to dismount (Helfenstein *et al.* 2003a). Thus the conflict over sperm ejection could result in females preferring males that are not much larger than themselves. Similar reasoning was applied to Purple Martins (*Progne subis*) in which assortative mating by size was linked to the ability of females to obtain extra-pair copulations by overcoming their mates' guarding defenses (Wagner and Morton 1997; Wagner *et al.* 1996). These studies suggest that when searching for the causes of assortative mating in socially monogamous species, sexual conflict should be considered.

The existence of studies from varying sections of the wide breeding range of kittiwakes allowed us to make geographical comparisons of size and sexual dimorphism. Dimorphism was similar in all three locations but highly significant differences existed in morphological measurements between populations in France, England and Alaska. Perhaps surprisingly, there was no obvious latitudinal trend in that the southern French population had longer tarsi than the Alaskan population and was larger in wing and head length than in the more northern British population. The regional size differences

suggest the need for caution when applying discriminant function analyses (Jodice *et al.* 2000) between populations.

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