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Variation of skull morphometry of Eurasian otters (*Lutra lutra*) in Denmark and Germany

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The distance between opistokranion and zygomatic process of frontal bone (*A*), the condylobasal length (*X*), and the total length of the mandible (*M*) were measured in skulls of the Eurasian otter collected in Denmark and in the east of Germany (Lausitz). The Danish population showed a strong reduction in size of the traits in males, and an increase with time in the variances of the traits in females, whereas in the Lausitzian population, no significant changes in the same traits over the same time period were observed. The skulls were also investigated for fluctuating asymmetry (FA) and a negative correlation was found between the size of a skull and FA in the males from both populations, whereas no correlations were found in the females.

1. Introduction

Spatial and temporal variations in habitat quality and population density can affect adult body size and skull traits in species (Klein 1964, Lowe 1972, Holbrook 1982). Morphometrical differences between local populations distributed over the species range may be of a genetic origin, and affect growth rates and development stability (Manning 1971, Huson & Page 1980, Atchley *et al.* 1981).

There are several hypotheses which can explain the relation between ecological factors and size variability. Among them, the "niche variation hypothesis" (Van Valen 1965) suggests that morphological variation is related to the number of competing species, as a niche width can increase in absence of competitors, determining an increase in morphometrical variance (Grant 1967, Rothstein 1973). Moreover, in species with sexual dimorphism, different evolutionary forces are acting on each sex, and the optimum size of males and females may result from different selective pressures (Erlinge 1979, Moors 1980). Finally, variation in fluctuating asymmetry (FA) of traits may be related to the individual's body size. If larger body signals generally good health, body size will be negatively correlated with the FA (see reviews in Møller & Pomiankowski 1993, Møller & Swad-

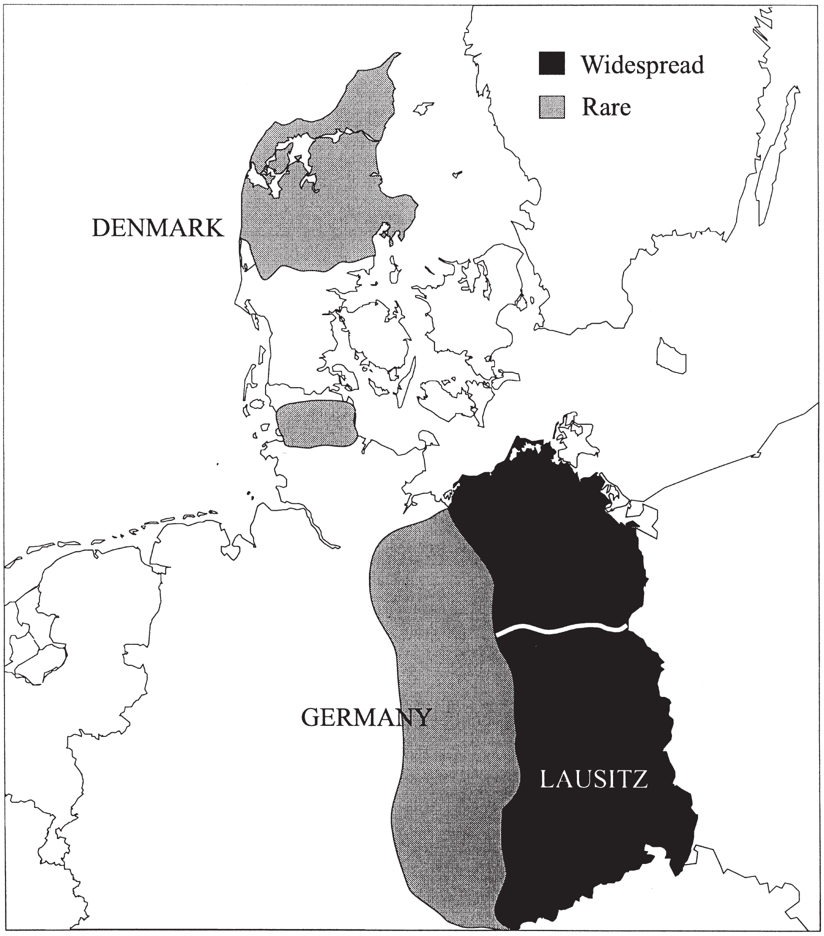

Fig. 1. The distribution of the otter in Denmark and in Germany (according to Macdonald & Mason 1994, and Hammershøj *et al.* 1996).

dle 1997). The above hypotheses could be tested by analysing temporal series of morphometric measurements in species which have experienced environmental or genetic stress.

The Eurasian otter provides an interesting example. The species has declined in many European countries (Macdonald & Mason 1994), and in optimal habitat conditions it has virtually no ecological overlap or potential interspecific competition with other species (Chanin 1991), and therefore, the degree of sexual dimorphism should not depend on interspecific interactions. However, in suboptimal habitats, with a possibility of food shortage, we can suspect a dietary overlap with the smaller American mink (*Mustela vison*), which has been accidentally released from Danish mink farms since the beginning of the 1940s (Andersen 1981).

In Denmark, the otter was widespread, but now it is largely restricted to the Limfjord area in the northern part of Jutland (Fig. 1), with isolated population fragments in the surrounding region (Hammershøj *et al.* 1996). Toxic chemicals are likely to have been responsible for the decline of the otter population in Denmark, and large parts of lowland Europe (Mason & Macdonald 1986, Mason 1989). Today, the additional threat is mortality caused by traffic, wetland destruction, and human disturbance (see Madsen 1996 for review). The otter population in Denmark declined sharply from more than 1 500 animals in 1961 to only 200 individuals in 1980 (Schimmer 1981), and increased thereafter again to 400 animals censused in 1991. The reproductive biology of polygynous mammals like the Eurasian otter suggests that the ratio of the genetically effective to the observed population sizes is low (see Frankham 1995 for review). Assumptions of a small effective population size are also supported by a very low genetic variability found in the mitochondrial DNA control region (N. Mucci, C. Pertoldi, A. B. Madsen, V.

Loeschcke & E. Randi unpubl.), and by the increasing with time levels of fluctuating asymmetry in skulls (Pertoldi *et al.* 1997). Therefore, we can consider the Danish otter population to be endangered as compared to, for example, the population living in Lausitz (eastern Germany).

In this paper, we aim to estimate the variation in size of different skull traits of two populations of the European otter. We test for variation in length and its variance in different periods of collection, to see whether the presumed bottleneck in the Danish population, and the concomitant increased habitat fragmentation in the Danish territory, have influenced the otters' developmental stability. The same test was made for the Lausitzian population (Fig. 1) which presumably has not experienced bottlenecks and does not live in a fragmented habitat (Macdonald & Mason 1994).

2. Material and methods

2.1. Measurements

We measured three traits in 94 Danish and 44 Lausitzian skulls of adult Eurasian otters *Lutra lutra* collected in 1861–1959 (13 specimens at the Zoological Museum in Copenhagen, Denmark), in 1959–1961 (34 specimens at the Natural History Museum in Aarhus, Denmark), in 1979–1993 (47 specimens at the National Environmental Research Institute in Kalø, Denmark), and in 1955–1996 (44 specimens at the Staatliches Museum für Naturkunde in Görlitz, Germany). The traits, measured with a digital calliper to the nearest 0.1 mm, were the distance between opistokranion and zygomatic process of a frontal bone (A), the condylobasal length (X), and the total length of a mandible (M; Infradentale-Goniocaudale), (illustration given in Pertoldi *et al.* 1997). Because traits A and M are bilateral, and in a previous investigation (Pertoldi *et al.* 1997) they showed a significant fluctuating asymmetry, they were measured on both sides of the skulls. Unfortunately, trait A was not measured in the Lausitzian skulls.

Asymmetry was estimated as the difference in length between each bilateral pair of traits (right side [r] – left side [l]). Fluctuating asymetry (FA) was calculated as the absolute value of asymmetry (Palmer & Strobeck 1986).

$$\mathrm{FA} = |r - l| \quad (1)$$

In a previous investigation of the skulls of the Danish otters, the overall repeatability of the FA was estimated to be 97% or greater, so that the measurement error should have accounted for no more than 3% of the total variation (for details see Pertoldi *et al.* 1997). To estimate possible errors in measuring the condylobasal length, we had chosen ten skulls at random, and measured each of them ten times. Coefficient of variation (CV, %) with Haldane's (1955) correction for small sample size, was calculated for the mean condylobasal length (X) of each skull. The average CV was 0.1%.

We estimated the age of the animals whose skulls were used in our research using the methods described by Pertoldi *et al.* (1997).

2.2. Statistical analysis

In all the analysis, sexes were treated separately. Spearman's rank correlation coefficients (r_s) were calculated for the condylobasal (X), and mandible lengths (M) versus total body length (from nose to tail), and versus body weight of the Danish adult otters. These correlations were computed to test if the skull traits are good indicators of the adult body mass. A linear regression analysis and a Spearman test for traits X and M versus the year of collection of the otters' skull were used. The years of the skulls' collection were grouped in two periods: 1960–1961 and 1981–1994 for the Danish males, 1959–1964 and 1982–1993 for the Danish females, 1955–1985 and 1986–1996 for the Lausitzian males, 1968–1986 and 1987–1996 for the Lausitzian females. Means and variances of traits X and M were calculated, and an F-test (Fowler & Cohen 1990) was employed to compare the variances between both periods of collection. For traits which variances did not differ significantly, we conducted a two way t-test to test for significant differences between the means.

A Mann-Whitney U-test was used to test if the median of the distribution of traits X and M increased or decreased, and consequently, if the degree of dimorphism varied in the two periods. The average degree of sexual dimorphism was measured for the skull length (X) and calculated as follows: $\mathrm{SD} = [\mathrm{mean}_{\mathrm{males}} - \mathrm{mean}_{\mathrm{females}}]/\mathrm{mean}_{\mathrm{females}} \times 100\ (\%)$ (Rossolimo & Pavlinov 1974).

A linear regression analysis and a Spearman rank correlation test were used to test if the fluctuating asymmetry of traits A and M was correlated with X, A and M. When calculating these relations we used largest size per pair to avoid autocorrelation effects (Sullivan *et al.* 1993).

3. Results

In a population of the Danish male otters, positive correlations (Spearman test) between the condylobasal length (X) and mandible length (M) of an otter's skull versus the weight and length of an animal before necropsy were found (Table 1). However, the correlations in females were weaker than those found in males, and the correlation between the skull mandible length and an animal body weight in females was not significant (Table 1). Significant negative correlations (linear regression analysis and Spearman test) between the year of collection of the skulls and traits X and M in the Danish males were found. No such correlations were detected in Danish females and in Lausitzian males and females (Table 2).

In the Danish males and Lausitzian males and females, no significant differences in variances (F-test) of traits X and M between the two periods of collection were found (Table 3). A significant increase in variance of the Danish female skull traits was recorded in the second period of collection (Table 3). In the Danish males, we found a significant reduction in the means of the traits in the second period. In the Lausitzian males and females, we did not find a significant change in the means of the traits in the second period of collection (Table 3). The average degree of sexual dimorphism in trait X of the Danish population was 9.5% in the first period and 6.1% in the second period, hence, a reduction of 3.4%.

In the Danish males, significant differences ($p < 0.05$) in the medians of the traits between the two periods were found (Mann-Whitney U-test, trait X: $U = 112.5^*$, $n_1 = 15$, $n_2 = 25$, trait M: $U = 76.5^*$, $n_1 = 13$, $n_2 = 22$), (lower value of the median in the second period), which was in concordance with the result obtained with the parametric t-test (Table 3). No significant differences in the medians of the Danish female traits or in the Lausitzian male and female traits between the collection periods were found.

A negative correlation (linear regression analysis and Spearman test) between traits A and M and the degree of FA in the males, and a general positive correlation between some traits and the degree of FA in the females were found (Table 4).

Table 1. The Spearman rank correlation coefficient (r_s) calculated for traits X and M versus the body weight, and length of the Danish otters; n = sample size

Traits	Body weight	Body length
X (♂)	0.75 ($n = 35$)***	0.84 ($n = 38$)***
M (♂)	0.47 ($n = 23$)*	0.69 ($n = 24$)**
X (♀)	0.41 ($n = 25$)*	0.75 ($n = 25$)***
M (♀)	n.s. ($n = 23$)	0.49 ($n = 31$)**

* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$

4. Discussion

The strong correlation between traits X and M (condylobasal length and mandible length) and the body weight and length found in the males otters, indicates that the size of a head is a good estimator of the body size of a male. Hence, we can suspect that the head is used for interspecific and intraspecific signals in threat behaviour as was demonstrated in amphibians (Shine 1979), snakes (Shine 1994), and salmon (Quinn and Foote 1994). A large head may enhance male's mating success, either because males with large heads will more often win a male-male combat for access to females or because they have a possibility to maintain the best territory (Moors 1980, Lynch & Hayden 1995). Some authors (Dayan & Simberloff 1994) suggested that selection acts directly on the trophic apparati, while skull and body sizes may also be affected by other, perhaps autecological, factors. The reasons for the lower degree of correlation or lack of correlation found between body weight of a female and the mandible length (M), could have different explanations. The first one, which supports the hypothesis that the head is involved in signalling the dominance status in males, is that there is no intrasexual competition between females and that the males usually tolerate the presence of females within their home range. Therefore, the dominance status should not

Table 2. The linear regressions (r) and the Spearman test (r_s) between trait X, M and the year of the skulls' collection; n = sample size.

Country		r	r_s
Denmark			
	X (♂)	– 0.41 ($n = 44$)**	– 0.36 ($n = 44$)*
	M (♂)	– 0.38 ($n = 37$)*	– 0.33 ($n = 37$)*
	X (♀)	n.s. ($n = 49$)	n.s. ($n = 49$)
	M (♀)	n.s. ($n = 36$)	n.s. ($n = 36$)
Germany (Lausitz)			
	X (♂)	n.s. (n = 27)	n.s. ($n = 27$)
	M (♂)	n.s. ($n = 26$)	n.s. ($n = 26$)
	X (♀)	n.s. ($n = 16$)	n.s. ($n = 16$)
	M (♀)	n.s. ($n = 17$)	n.s. ($n = 17$)

* = $p < 0.05$, ** = $p < 0.01$

Table 3. Comparison of traits X and M in the skulls collected in two periods. For traits which variances did not differ significantly, we conducted a two ways t-test to test for significant differences between the means.

Traits	Variance	n	Mean (mm)	Variance	n	Mean (mm)	F-test		t-test	
							p	F	p	df
	Denmark males									
	Period (1960–1961)			Period (1981–1994)						
X	13.30	15	119.2	12.4	25	116.5	n.s.	1.07	*	38
M	5.60	13	75.6	5.00	22	73.7	n.s.	1.12	*	33
	Denmark females									
	Period (1959–1964)			Period (1982–1993)						
X	5.50	19	108.9	12.28	22	109.8	*	2.22	–	–
M	1.30	17	69.1	6.89	17	68.5	**	4.99	–	–
	Lausitzian males									
	Period (1955–1985)			Period (1986–1996)						
X	14.71	7	117.3	16.64	20	119.0	n.s.	1.13	n.s.	25
M	4.24	6	75.9	8.52	20	76.2	n.s.	2.02	n.s.	24
	Lausitzian females									
	Period (1968–1986)			Period (1987–1996)						
X	1.44	6	109.4	2.76	10	110.7	n.s.	1.92	n.s.	25
M	0.93	6	69.2	2.43	11	69.5	n.s.	2.61	n.s.	24

* = $p < 0.05$, ** = $p < 0.01$

Table 4. The linear regressions (r) and the Spearman tests (r_s) between traits X, A, M and FA of these traits; n = sample sizes.

Country	Traits	FA	r	r_s
Denmark	A (♂)	FA (A)	n.s. ($n = 26$)	n.s. ($n = 23$)
	M (♂)	FA (M)	– 0.37 ($n = 30$)*	– 0.42 ($n = 30$)*
	X (♂)	FA (A)	– 0.41 ($n = 24$)*	– 0.51 ($n = 24$)*
	X (♂)	FA (M)	– 0.52 ($n = 28$)**	– 0.50 ($n = 28$)**
	A (♀)	FA (A)	0.28 ($n = 48$)*	0.37 ($n = 48$)*
	M (♀)	FA (M)	n.s. ($n = 36$)	n.s. ($n = 36$)
	X (♀)	FA (A)	n.s. ($n = 48$)	n.s. ($n = 48$)
	X (♀)	FA (M)	n.s. ($n = 35$)	n.s. ($n = 35$)
Germany (Lausitz)	M (♂)	FA (M)	– 0.57 ($n = 26$)**	n.s. ($n = 26$)
	X (♂)	FA (M)	– 0.54 ($n = 26$)**	n.s. ($n = 26$)
	M (♀)	FA (M)	0.60 ($n = 15$)*	0.65 (n =15)*
	X (♀)	FA (M)	0.66 ($n = 14$)*	0.75 ($n = 14$)**

* = $p < 0.05$, ** = $p < 0.01$

be important for females. The second explanation could be that the females used in our research were collected in different seasons, and that they represented different breeding status and therefore, that weight fluctuations could have confused the correlation.

The strong negative correlation found between the year of collection of the Danish male otters and the length of traits *X* and *M* (which means a shortening of the skull), may be explained by the general increase of stressing factors like pollution, human activity, food shortage in terms of quantity and quality, agricultural practice, habitat fragmentation, increased intrasexual competition, and their impact on the genetic structure of the population. The progressive reduction of suitable habitat and carrying capacity could have a particularly intense effect on otters which have a linear home range (Erlinge 1968, Kruuk 1995). All these factors will increase fragmentation effects that can be particularly intense if the costs associated with dispersal from one patch to another are high. That is the case in the Danish otter population, in which the number of otters killed by trafic increased with the increasing population and road network (see Madsen 1996 for review). The non-significant reduction in size of the skulls of the Lausitzian male otters indicates a more healthy and viable population, living in a more suitable habitat.

The reasons why we did not find a significant reduction in female skull traits in both the Lausitzian and Danish populations are different. Principally, the lower daily energy requirement of females, because of their smaller body size, smaller home range and the lack of intrasexual interaction (competition for mating, territory defending) (Moors 1980, Durbin 1996), will reduce the risk of starvation in periods of food shortage. These characteristics should lower the sensitivity to environmental fluctuations, particularly with regard to changes in food abundance. Another explanation could be the possibility that intermale competition (which is thought to have increased with the reduction of suitable habitats) may also affect female characteristics: if a large body confers major advantages on males and large mothers produce larger male offspring, intense competition between males may select for increased body size in females (Maynard Smith 1978). The increased morphological variance of skull traits *X* and *M* in the second period of collection with respect to the first one detected only in the Danish females, is probably due to some distinct causes. Some empirical studies indicate that higher phenotypic variability may be related to the reduction of the heterozygosity level (Eanes 1978, Mitton 1978, Leamy 1982, Mitton & Grant 1984). The low genetic variability in female otters could be the reason for the significant increase in phenotypical variance found in the second period (post bottleneck) as compared to the first period of collection. Also increased levels of stress may result in an increase of the phenotypic variance (e.g., Imasheva *et al.* 1997). The second reason could be the otters' increased niche width and diversification, as a degraded environment has a less structured ecosystem.

The discovered reduced sexual dimorphism in the skull length (*X*) (3.4%) between the Danish males and females (no significant reduction of the sexual size dimorphism were detected for the Lausitzian population) can influence the otter's diet. We should expect a significant increase in dietary overlap between sexes (intersexual competition) because of the reduction in size of the males which results in their reduced capacity to hunt bigger prey (Lynch & O'Sullivan, 1993). At the same time we should also expect an increase in an interspecific competition with smaller sympatric mustelid species like american mink, *Mustela vison*, especially in periods of food shortage as may happen during severe winters (Erlinge 1972).

The negative correlations between the skull traits (*A*, *M* and *X*) versus the level of FA found in males from both populations may be interpreted in the way that the big body size of a male otter is a good indicator of its general condition and its fitness (see reviews in Møller & Pomiankowski 1993, Møller & Swaddle 1997). The positive correlations between body size and FA found in females could then indicate the non-adaptive function of a big body size in females and the increased energetic cost associated with a bigger body size.

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