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Developmental stability in the Eurasian Otter (*Lutra lutra*) in Denmark

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Fluctuating asymmetry (FA) as expressed in metric and meristic skull traits was analysed in a sample of 172 otters collected in Denmark between 1861 and 1994. Tissue levels of organochlorine pesticide residues and PCBs were determined and the correlation between contaminant concentration and FA was tested. A significant correlation was found between FA in different traits and the year of collection, but there was no significant correlation between FA and the concentration of contaminants. These results suggest that factors other than pesticides have affected the developmental stability of skulls in the Danish otter population. Among these, a population bottleneck following habitat fragmentation is discussed as a possible cause.

1. Introduction

The otter (*Lutra lutra*), once a widespread species in Denmark, is today 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 believed to be responsible for the decline of otter populations both in Denmark and over much of lowland Europe (Mason & Macdonald 1986, Mason 1989). Additional threats to the remaining otter population in Denmark are traffic mortality, wetland destruction and human disturbance (see Madsen 1996 for a review).

Fluctuating asymmetry (FA) occurs when an individual is unable to undergo identical development on both sides of a bilaterally symmetrical trait (Van Valen 1962, Palmer & Strobeck 1986). FA tends to become elevated under stress (Leary & Allendorf 1989). Stress factors known to raise FA include various chemicals, including pesticides (Valentine & Soulé 1973), polluted habitats (Weiner & Rago 1987), extreme temperatures (Parsons 1962, Siegel & Doyle 1975, Sciulli *et al*. 1979), audiogenic stress (Sciulli *et al*. 1979), and food deficiency either in terms of quality or quantity (Parsons 1990). Also severe restrictions in the availability of nutrients to females during pregnancy causes asymmetry in the skeletal traits of offspring (Sciulli *et al.* 1979). Furthermore, directional selection, homozygosity, inbreeding and mutations, are also thought to be associated with elevated levels of FA (see Parsons 1992 for review). For example, Clarke and McKenzie (1987) demonstrated that homozygous individuals were often developmentally less stable than their heterozygous counterparts (but see also Britten 1996 for a different view).

Three groups of stressing factors could have affected the dynamics of otter populations in Denmark, and have influenced their degree of developmental stability: (1) contamination of habitats by pesticides, (2) population decline with subsequent erosion of genetic diversity and increasing rate of inbreeding, (3) strong sexual selection which can differentially affect developmental stability in both sexes (males have a larger body size than females, Moors 1980), can result in sexual dimorphism.

Persistent pollutants, which accumulate in living tissues, are a particular problem in fresh water habitats of otters because there are many sources of contamination. Rainfall washes atmospheric pollutants and chemicals applied to land into waterbodies. Many industries discharge effluents into rivers, directly or indirectly. Small amounts of persistent pollutants in effluents may become quickly concentrated in the biota. PCBs were not identified as environmental contaminants until 1966 (Jensen 1972), though they had been in industrial use for at least 35 years before that, and have since been proved to be widespread in the ecosystem. Of pesticides, the chlorinated hydrocarbons dissolve readily in animal fats and hence accumulate in tissues. When these fats are mobilised during periods of stress, such as food shortage or reproduction, large amounts of pesticides may be released into the blood stream.

The otter population in Denmark declined sharply starting from an estimated size of more than 1 500 individuals in 1961 to only 200 in 1980 (Schimmer 1981), and increased thereafter again to 400 animals censused in 1991. This decline was probably an effect of pesticide contamination (Mason & Madsen 1993). The reproductive biology of otters suggests that the ratio of the effective population size N_e to the observed population size N is on average 0.11 (see Frankham 1995 for review). Therefore, the population bottleneck during the 80s should have been N_e about 20 individuals for at least 5 generations. During this period, the Danish otter population may have lost rare alleles and possibly became less heterozygous. The estimates of low effective population sizes are also supported by very low genetic variability found in the mitochondrial DNA control region (D-loop) (N. Mucci, C. Pertoldi, A. B. Madsen, V. Loeschcke and E. Randi unpubl.).

FA tends to be higher in sexually selected characters than non-sexually selected traits (Møller 1992, Manning & Chamberlain 1993). However, it is not known whether nutrient deficiency, or any of the other factors listed above, cause any differential effect on FA in characters subjected to sexual selection as compared with ordinary morphologically traits.

In this paper, we aim to estimate FA in metric and meristic skull traits in Eurasian otters collected in Denmark from 1861 until 1994. FA will be correlated with morphometric variability, the period of sample collection, demographic trends of the Danish otter population, and levels of pesticide and PCB contaminants in tissues.

2. Material and methods

We used skulls of Eurasian otters (*Lutra lutra*) from the Zoological Museum, Copenhagen (skulls from 1861 until 1959), the Natural History Museum, Aarhus (1959–1961) and the National Environmental Research Institute, Kalø (DMU) (1979–1993). Animals from DMU (only animals from DMU were age-determined) were considered as juveniles (less than about 5 months old) if tooth replacement was incomplete, subadults (5–18 months) if the epiphyseal closure of humerus and femur at their proximal and distal ends was not finished, or as adults (older than about 18 months). In males, the length of the baculum was also used in age determination (Van Bree *et al.* 1966). Skull growth in otters is complete by the third year of life (Chanin 1991), and further changes, except senility changes in the skull will not affect the skull measurements.

All skulls, until 1961 originated from different parts of Denmark (Jutland, and the isles of Zealand and Funen). After that date, no more otters were found on the isles (Fig. 1).

A total of 172 skulls were examined. Four characters of the skulls A, B, C and M, and the Dental foramen (which are small openings for nerves and blood vessels) of the lower jaws were counted (Fig. 2). Trait A is the distance between the opistokranion and zygomatic process of frontal bone, trait B is the shortest distance between the zygomatic process of frontal bone and frontal process of zygomatic bone, trait C is the shortest distance between the jugular foramen

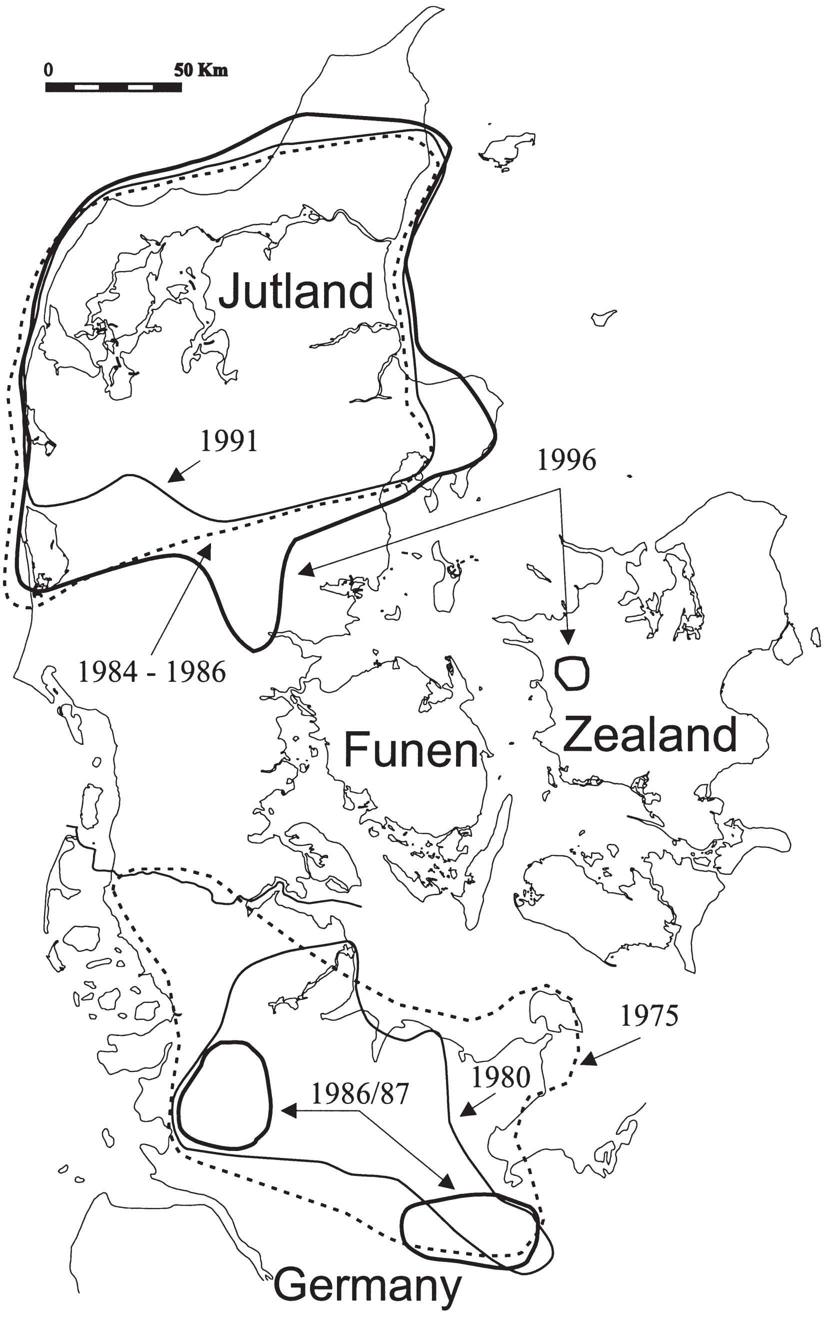
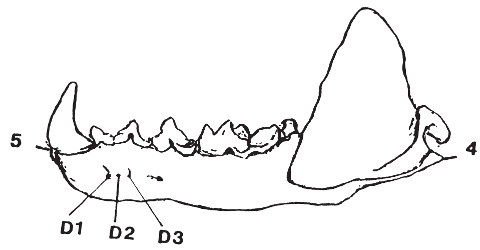


Fig. 1. The distribution of the otter in Denmark in 1996, 1991, between 1984 and 1986, and between 1960 and 1980.

and staphylion and trait M is the total length of the jaw: infradentale-goniocaudale. The traits chosen (Fig. 2a–c) appeared to show a high level of fluctuating asymmetry.

The traits A, B, C and M were measured with a digital calliper to the nearest 0.1 mm. The magnitude of asymmetry was estimated from the difference in length between each bilateral pair as right minus left ($r - l$). FA was calculated as the absolute value of asymmetry and as the variance of ($r - l$) (Palmer & Strobeck 1986). To reduce the measurement error, all measurements were replicated 3 times (at an interval of 3 hours), and the median of the 3 measures was chosen. The overall repeatability (r_l; see Zar 1984) of the size measurement was estimated to be around 97% ($0.968 < r_l < 0.982$, $p < 0.001$), so that the measurement error should have accounted for no more than 3% of the total variation in even the least repeatable character. No measurements were attempted on broken or worn parts of the skulls, therefore, for some skulls we have missing values. The difference in number between sides of the bilateral pair of foramina was used to estimate the magnitude of a

c



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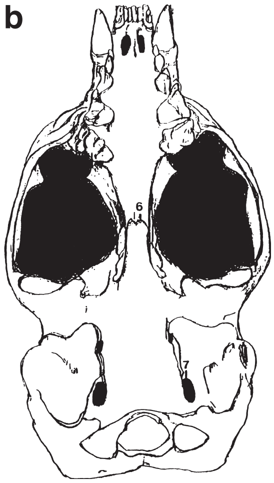

Fig. 2. View of an otter's skull. — a: Lateral view of an otter's skull. Trait A: distance between points 1 and 2 (distance between the opistokranion and zygomatic process of frontal bone). Trait B: distance between points 2 and 3 (shortest distance between the zygomatic process of frontal bone and frontal process of zygomatic bone). Trait M: distance between points 4 and 5 (total length of the jaw: infradentale-goniocaudale). — b: Ventral view of an otter's skull. Trait C: distance between points 6 and 7 (shortest distance between jugular foramen and staphylion). — c: Lower jaw of an otter's skull. Dental foramen: D1, D2, D3.

FA. The numbers were counted macroscopically, each pair of foramina was counted 3 times and when we found incongruence we excluded the measurement. However, it is worth noting that meristic characters will only become asymmetric once stress reaches a threshold level (Swain 1987).

Departures from normality of $(l - r)$ for each trait, were tested with a Kolmogorov-Smirnov test (Sokal & Rohlf 1981). The hypothesis that the mean of left minus right character values equals zero was tested in a one sample *t*-test.

Differences between age groups and periods of skull collection were compared with an *F*-test (Fowler & Cohen 1990). For this purpose, we considered all adult and subadult female otters between 1980 and 1993 and male otters between 1980 and 1994.

A linear and polynomial regression analysis (year of collection versus absolute value of asymmetry) were conducted for each trait. The periods of collection were divided in 3 periods (1, 2 and 3): for males, the three periods were 1926 to 1939, 1960 to 1961 and 1980 to 1994; for females, they were 1932 to 1942, 1959 to 1962 and 1980 to 1993; the variance of $(r - l)$ and the median of FA for each trait A, B and C were calculated.

A Mann-Whitney *U*-test was used to test if the median of FA for traits A, B and C increased through the three periods, and if the median for these traits and dental foramen was different between the two sexes (only periods 2 and 3) and an *F*-test was conducted to see if the variance of $(r - l)$ increased during the 3 periods of collection.

Tissues of otters found dead in Denmark between 1980 and 1990 were analysed for organochlorine pesticide residues and PCBs (Lindane, Dieldrin, pp-DDE, op-DDD, op-DDT, PCBs and pp-DDE/op-DDT). In this period (1980–1990), an average annual decline of 7% per year for PCBs and of 6% for DDE were found (Mason & Madsen 1993).

A Spearman correlation coefficient was used for correlations between the concentration of contaminants in the otter's tissues and the absolute FA of its skull. A Spearman correlation coefficient was performed to test a possible correlation between the condylobasal length (skull length and weight, and length from nose to tail) of the otter before necropsy.

3. Results

There was no evidence of directional asymmetry or antisymmetry and all deviations from normal distributions were not significant (Kolmogorov Smirnov test: $0.089 < p < 0.47$, $125 < n < 150$), and no significant deviations from zero as the mean of the trait $(l - r)$ distributions were found (one sample *t*-test: $0.062 < p < 0.312$, $67 < d.f. < 75$).

All the traits were tested for independence of overall traits with a Spearman rank correlation test, and no significant correlation was found for males, although for females the trait A was correlated with traits B and C (A and B: $r_s = 0.29$, $n = 49$, $p = 0.044$, between traits A and C: $r_s = 0.31$, $n = 52$, $p = 0.026$).

No significant differences of FA between the two age groups (adults and subadults) of the same sex were found (Table 1) and, therefore, the two age groups were pooled in the following regression analyses (Table 1).

No correlation was found at the 0.01 level between overall length of the traits (A, B, C and M) and the degree of FA in these traits (males: $-0.02 < r_s < 0.17$, *d.f.* = 61–73, $0.09 < p < 0.96$, females: $-0.05 < r_s < 0.24$, *d.f.* = 50–65, $0.06 < p < 0.74$).

A strong positive correlation (Spearman test) was found in both sexes between the condylobasal length of the skull, and its weight and length before necropsy, indicating that skull length is a good indicator of the body mass of an otter: females $r_s = 0.41$, $n = 25$, $p = 0.046$, males $r_s = 0.75$, $n = 35$, $p = 0.0001$; "body length–condylobasal length": females $r_s = 0.75$, $n = 25$, $p = 0.0002$, males $r_s = 0.84$, $n = 38$, $p = 0.0001$.

No significant correlation (Spearman test) was found between the degree of asymmetry and contaminant concentration at the level of $p < 0.01$, indicating that factors other than contaminants have contributed to the levels of FA (Table 2).

Table 1. Comparison of fluctuating asymmetry variance of left–right-hand size measurements of skull characters (traits: A, B, C and M) in adults and subadults.

Traits	Adults (81–94) Variance	*n*	Subadults (80–93) Variance	*n*	*F*	*p*
Males						
A	0.67	23	0.50	22	1.34	*n.s.*
B	0.50	20	0.35	23	1.43	*n.s.*
C	0.36	27	0.30	28	1.20	*n.s.*
M	0.30	23	0.26	31	1.15	*n.s.*
Dental foramen	0.90	7	1.72	17	1.90	*n.s.*
Females						
A	0.70	21	0.42	10	1.70	*n.s.*
B	0.29	14	0.15	8	1.90	*n.s.*
C	0.29	18	0.28	19	1.10	*n.s.*
M	0.16	17	0.12	19	1.30	*n.s.*
Dental foramen	2.17	6	1.61	10	1.40	*n.s.*

Table 2. Spearman rank correlation coefficients and corresponding test values p and r_s for testing correlations between the absolute value of FA in the traits: A, B, C and M, and the concentration of 6 contaminants. (Contaminants: Lindane, Dieldrin, pp-DDE, op-DDD, op-DDT, PCBs and the ratio of pp-DDE/DDT).

Traits			
Males			
A	$15 < d.f. < 18$	$(0.21 < r_s < 0.20)$	$0.38 < p < 0.83$
B	$15 < d.f. < 17$	$(-0.12 < r_s < 0.27)$	$0.26 < p < 0.88$
C	$19 < d.f. < 22$	$(-0.49 < r_s < 0.18)$	0.02[1)] $< p < 0.42$
M	$15 < d.f. < 19$	$(-0.03 < r_s < 0.43)$	$0.06 < p < 0.93$
Females			
A	$8 < d.f. < 14$	$(-0.53 < r_s < 0.23)$	$0.13 < p < 0.84$
B	$6 < d.f. < 10$	$(-0.62 < r_s < -0.05)$	0.05[1)] $< p < 0.91$
C	$10 < d.f. < 20$	$(-0.57 < r_s < 0.09)$	$0.07 < p < 0.97$
M	$6 < d.f. < 16$	$(-0.57 < r_s < 0.01)$	0.02[1)] $< p < 0.97$

[1)] Significance disappears if one extreme value is removed.

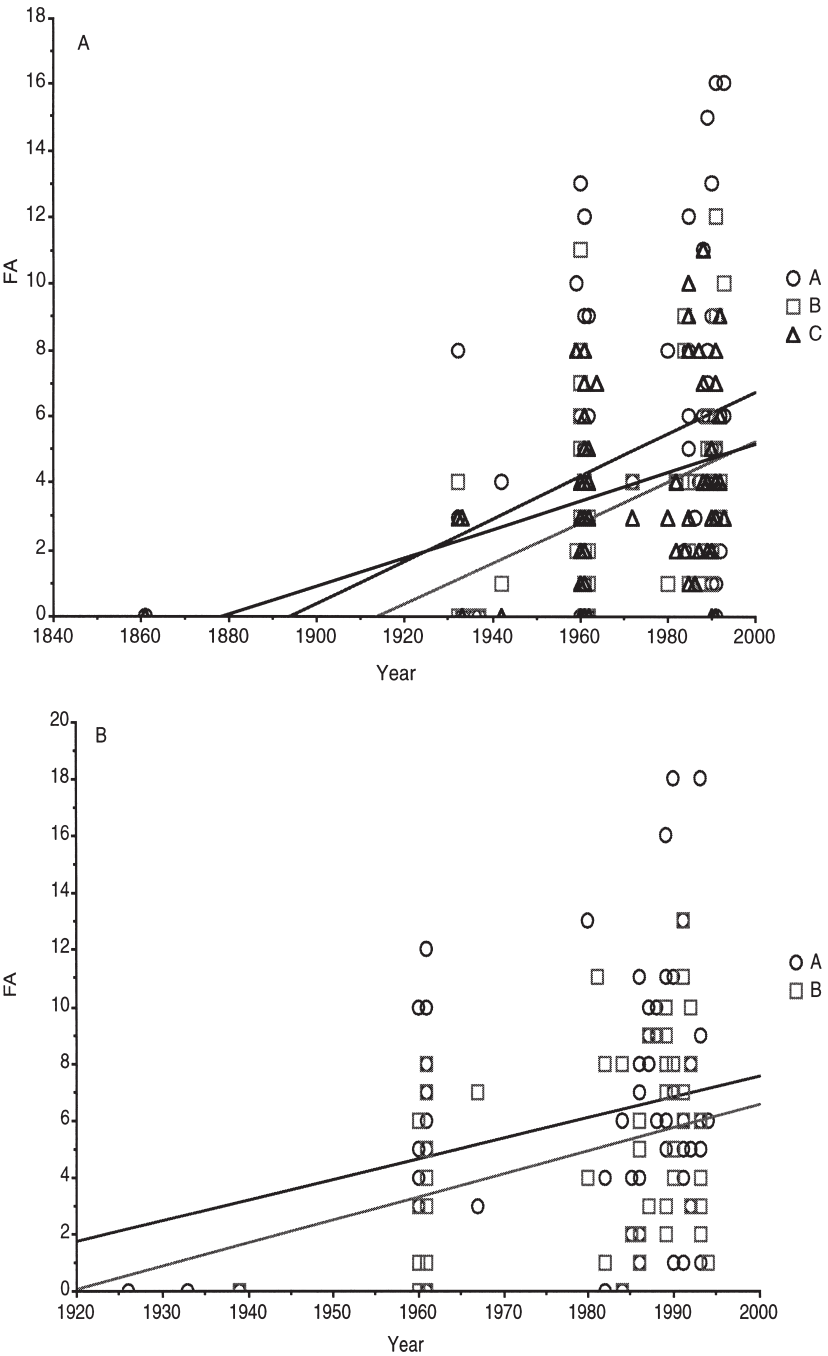

Fig. 3. Linear regression (females) of the absolute values of FA (1/10 mm) for traits A, B and C versus the year of skull collection. — A: Females. — B: Males (the trait C is not significant in the regression).

Significant correlations were found between the year of skull collection and the absolute values of FA (Fig. 3AB, Table 3). The relationship and its significance did not disappear when we removed the two skulls collected in 1861 from the regression analysis for females, but the significance of the correlation disappeared for trait A in males when we removed the 3 skulls collected before 1950 from the regression analysis. Significant differences in variance (*F*-test) of FA between the three different periods were found (Table 4).

Significant differences of the median of FA in the three periods were found (Mann-Whitney *U*-test, Table 5).

Significant differences were found between sexes in the median of FA for traits A and C in the periods two and three (males showed higher FA, see Mann-Whitney *U*-test, Table 6).

4. Discussion

PCBs dissolve readily in animal fats and hence accumulate in tissues. When these fats are mobilised during periods of stress, such as food shortage or periods of reproduction, large amounts of pesticide may be released into the blood stream (see Mason 1989 for review).

There was, however, no evidence for a relationship between asymmetry and pesticide concentration. The lack of correlation between contaminant concentration and FA could be due to different factors that could have confused relations. First, in mammals, females detoxicate

Table 3. Linear, 2nd and 3rd order polynomial regressions between the absolute value of FA in traits A, B and C and the year of skull collection. The numbers in parentheses are the sample sizes and the standard error for the regression coefficient, respectively.

Traits	Linear regression	2nd order	3rd order
Males			
A	0.26 (n = 65, *S.E.* = 0.003)*	*n.s.*	*n.s.*
B	0.34 (n = 62, *S.E.* = 0.003)**	0.35 (n = 62, *S.E.* = 2.682×10^{-4})*	*n.s.*
C	*n.s.*	0.31 (n = 75, *S.E.* = 1.672×10^{-4})*	*n.s.*
Females			
A	0.38 (n = 66, *S.E.* = 0.002)**	0.41 (n = 66, *S.E.* = 3.914×10^{-5})**	0.41 (n = 66, *S.E.* = 1.843×10^{-6})**
B	0.35 (n = 51, *S.E.* = 0.002)*	0.35 (n = 51, *S.E.* = 1.158×10^{-4})*	*n.s.*
C	0.32 (n = 65, *S.E.* = 0.002)**	0.32 (n = 65, *S.E.* = 3.202×10^{-5})*	*n.s.*

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

Table 4. *F*-test. Comparison of variance of the skull traits (A, B and C and dental foramen, named F) in the 3 periods (1, 2 and 3). The sign (+) or (–) indicate an increase or decrease in variance of the traits ($r - l$) with respect to the previous period. The numbers in parentheses are degrees of freedom and X indicates the absence of sufficent data.

	Period 1				Period 2			
	A	B	C	F	A	B	C	F
Males								
Period 2								
A	X							
B		X						
C			(+)*(2,17)					
F				(+) *n.s.* (2,13)				
Period 3								
A	X				(+) *n.s.* (16,45)			
B		X				(+)*(17,43)		
C			(+)*(3,55)				(–)*(17,55)[1]	
F				(+) *n.s.* (2,24)				(+) *n.s.* (13,24)
Females								
Period 2								
A	(+) *n.s.* (7,25)							
B		(+)*(6,22)						
C			(+) *n.s.* (6,19)					
F				(+) *n.s.* (6,16)				
Period 3								
A	(+)*(7,31)				(+) *n.s.* (25,31)			
B		(+)*(6,22)				(+) *n.s.* (22,22)		
C			(+)*(6,37)				(+)*(19,37)	
F				(+) *n.s.* (6,16)				(+)*(16,16)

[1] Significance disappears if one extreme value is removed, $p < 0.05$ = *

through nursing, where the organochlorines are transferred from mother to cub in the lipids of the milk (Tanabe *et al.* 1982). Thus, a female otter, after the nursing period, will have a lower concentration of PCBs, and developmental stability may thus not be related to pesticide concentrations. Hence, male and subadult otters may be more appropriate for this comparison, however, no significant correlations were found for these groups alone either.

The high correlation between the year of collection and FA may be explained by the increase in disturbing factors due to landscape fragmentation, pollution, human activity and agricultural practice. All these factors began to increase sharply at the beginning of the 1940s. A declining trend in population size prevailed throughout the 1970s. Populations of small size, for a number of generations, may lose a substantial proportion of genetic variation, and the genetic structure of the population will change, homozygosity will increase and inbreeding depression may become significant. The bottleneck around 1970–1980 may have resulted in increased FA in otter skulls. The N_e of about 20 individuals hypothesised in the 1970s, was probably even lower due to the

Table 5. Mann-Whitney *U*-test for testing if FAs of traits A, B and C are significantly higher in the later of the two periods compared. n_1 and n_2 are the sample sizes and *U* the test values. The values in parentheses are the mean and the standard error of FA of the earlier of the two periods compared.

	Traits A	Traits B	Traits C
Males			
Periods 1–2	$U = 4.5^*$ (0, 0) $n_1 = 3$, $n_2 = 16$	*n.s.*	*n.s.*
Periods 2–3	*n.s.*	$U = 220.5^*$ (0.339, 0.061) $n_1 = 17$ $n_2 = 43$	$U = 283.5^*$ (0.659, 0.101) $n_1 = 17$ $n_2 = 55$
Periods 1–3	$U = 3^{**}$ (0.659, 0.069) $n_1 = 3$, $n_2 = 45$	*n.s.*	*n.s.*
Females			
Periods 1–2	*n.s.*	$U = 29^*$ (0.083, 0.065) $n_1 = 6$, $n_2 = 22$	*n.s.*
Periods 2–3	$U = 238^*$ (0.376, 0.089) $n_1 = 25$, $n_2 = 31$	*n.s.*	*n.s.*
Periods 1–3	$U = 40.5^*$ (0.639, 0.079) $n_1 = 7$, $n_2 = 31$	$U = 15^{**}$ (0.44, 0.069) $n_1 = 6$, $n_2 = 22$	$U = 49.5^*$ (0.46, 0.053) $n_1 = 6$, $n_2 = 37$

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

Table 6. Mann-Whitney *U*-test for testing the differences of FA in traits A, B and C and dental foramen between the two sexes. For this test, only two periods are considered (periods 1 and 2). n_1 and n_2 are the sample sizes and *U* the test values. An asterisk means a significantly higher degree of FA in males.

	Traits A	Traits B	Traits C	Dental foramen
Period 2	$U = 95^*$ $n_1 = 22$, $n_2 = 16$	*n.s.*	$U = 118^*$ $n_1 = 24$, $n_2 = 17$	*n.s.*
Period 3	$U = 231^*$ $n_1 = 22$, $n_2 = 45$	*n.s.*	*n.s.*	*n.s.*

$p < 0.05$ = *

effect that PCBs have on female fertility. Experiments with the closely related mink (*Mustela vison*) showed that pup mortality was severe when tissue concentrations of PCBs in their mother exceeded 50 mg kg^{-1} fat (Jensen *et al.* 1977). 18% of Danish otters had tissue concentrations exceeding 50 mg kg^{-1} and 21% had tissue PCB concentrations greater than 30 mg kg^{-1} (Mason & Madsen 1993).

Strong FAs, as in the skulls of otters, that are visible macroscopically, have been suggested to be the result of strong selective forces (Møller 1992). Probably, male and female otters are subject to different selective forces. In the Eurasian otter (like all mustelids), males are always the larger sex and until now there are two explanations for this size dimorphism (Moors 1980). The first hypothesis suggests that the dimorphism reduces intersexual competition for food by enabling each sex to exploit different prey. The second hypothesis takes into account the polygynous breeding systems of mustelids and that females alone raise their litters. It proposes that small females are favoured because they need less energy for daily maintenance. Because of this, they can channel more energy into reproduction than larger females. Larger males are favoured by sexual selection and the ability to exploit a wide range of prey, and for the enhanced dominance and mobility. Under these circumstances, dissimilar evolutionary forces would be acting on each sex and consequently the optimum size of each sex results from different selective pressures.

The only evidence for intrasexual selection favouring larger male mustelids comes from observations of fighting during the breeding season, and this is a common phenomenon among otters and other mustelids (Moors 1980). One factor that may help to promote fight avoidance is that resident and probably larger otters know their place in the social hierarchy. Nothing is known about the extent of epigamic selection in otters or its possible influence on the size of males. In mammals, male hierarchy positions appear to be strongly correlated with body size (Schaller 1967, Grant 1970, Erlinge 1977). If a larger body size gives a reproductive advantage to males and a smaller one gives an energetic advantage to females, body sizes are subject to selection with opposite directions between sexes. The intensity of selection may have increased with increased landscape fragmentation, because the decreasing number of suitable sites will increase the territorial behaviour due to the increased density of individuals in the suitable sites. Only the dominant male, with a large body size, may be able to defend a good territory. The length of skulls (condylobasal-length) was strongly correlated to weight. So probably the size of the skull reflects dominance of an individual, and the selective forces acting on this character may explain the relatively high level of FA found on the more recent otter skulls. Another interesting observation is the higher degree of FA found in males than in females, suggesting the potentially stronger effect of stress acting on males.

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