

Sexual Size Dimorphism in the Skull of Norwegian Lynx

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Wiig Ø. Andersen T., 1986: Sexual size dimorphism in the skull of Norwegian lynx. Acta theriol., 31, 12: 147—155 [With 2 Tables & 2 Figs.]

Sexual size dimorphism in 16 skull dimensions of Norwegian lynx *Lynx lynx* (Linnaeus, 1758) aged between 17 and 60 months was studied. The measurements were adjusted for ontogenetic variation by regression to the mean age of the total sample (33.9 months). In 15 of the 16 measurements, the males were significantly larger than the females ($p < 0.01$), whereas the postorbital constriction was significantly wider in the females ($p < 0.025$). The multivariate separation between the sexes was highly significant ($p < 0.001$). The degree of the sexual size dimorphism was 6—7% in most of the dimensions measured, ranging from 4% (condyl breadth) to 10% (mandible height); the postorbital constriction was 2% narrower in the males. The sexual dimorphism was found to be functionally related to the feeding apparatus.

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1. INTRODUCTION

Sexual size dimorphism is common among vertebrates, males usually being the larger sex (Selander, 1966; Schoener, 1967; Ralls, 1976, 1977; Andersson & Norberg, 1981; Smith, 1982). Traditionally such dimorphism is believed to be caused by sexual selection as described by Darwin (1859). Recently the extreme dimorphism in *Mustelidae* (e.g. Erlinge, 1979; Moors, 1980; Wiig, 1986) and *Pinnipedia* (e.g. Stirling, 1975), and the reversed dimorphism in predatory birds (e.g. Andersson & Norberg, 1981; Smith, 1982) has attracted particular interest and new theories have been proposed, ascribing the sexual dimorphism to divergent selection pressures on males and females.

In the present study we examine the sexual size dimorphism in adult lynx, *Lynx lynx* (Linnaeus, 1758), based on a collection of Norwegian skulls. The data have been processed by univariate as well as multivariate methods.

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2. MATERIAL AND METHODS

2.1. Material

The present study is based on the skulls of 130 Norwegian lynx (74 males and 56 females), aged between 17 and 60 months. The specimens were hunted during the ten-year period 1960 to 1969, mostly in the four northern counties Sør-Trøndelag, Nord-Trøndelag, Nordland and Troms, but a few individuals from the southern parts of Norway are also included.

Until recently The Norwegian Ministry of Agriculture payed a bounty on lynx provided the hunters sent the carcasses to The Norwegian Game Research (DVF Viltforskningen). According to Kvam (1979, 1983) each specimen was sexed by dissection and aged from incremental annuli in the cementum of the canine tooth root using the method described by Reimers and Nordby (1968).

On each specimen the following sixteen measurements (Fig. 1) were taken by calliper and recorded to the nearest 0.1 mm (Andersen & Wiig, 1984): mandible

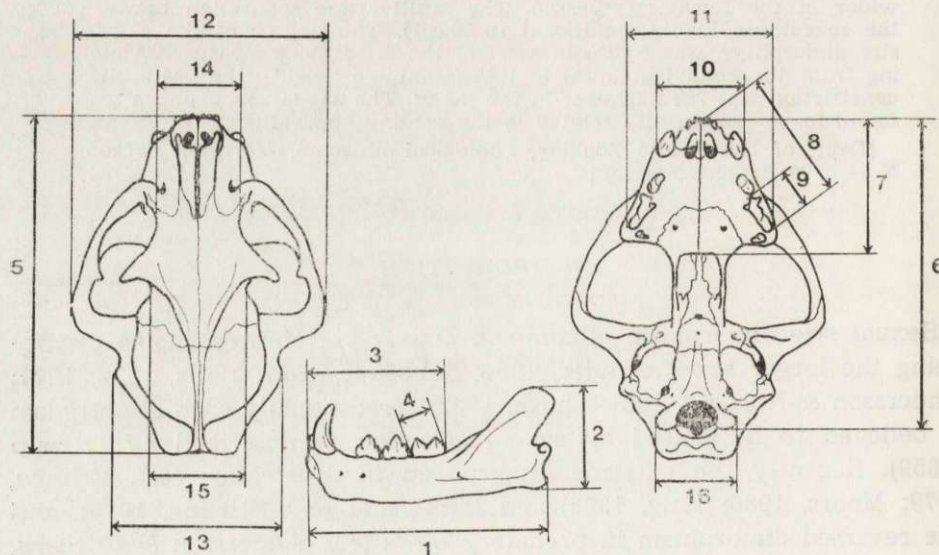


Fig. 1. Skull dimensions of Norwegian lynx: 1-mandible length, 2-mandible height, 3-mandible dental length, 4-M₁ length, 5-profile length, 6-condylobasal length, 7-palatal length, 8-dental length, 9-P⁴ length, 10-rostrum breadth, 11-dental breadth, 12-zygomatic breadth, 13-mastoid breadth, 14-interorbital constriction, 15-postorbital constriction, 16-condyl breadth.

length, mandible height, mandible dental length, M₁ length, profile length, condylobasal length, palatal length, dental length, P⁴ length, rostrum breadth, dental breadth, zygomatic breadth, mastoid breadth, interorbital constriction, postorbital constriction, and condyl breadth.

2.2. Statistical analyses

It is often claimed that growth in mammals is more or less deterministic, *i.e.* that no further growth takes place in adult specimens (*e.g.* Bryden, 1972). In lynx, however, the growth of the skull continues at a slow rate in older specimens as well (Andersen & Wiig, 1984). Therefore, the ontogenetic variation had to be adjusted for prior to the analysis of sexual size dimorphism.

A conventional way of achieving such an adjustment is to calculate the value expected if the independent variable (age) is equal to its mean and the observation retains its observed deviation from the predicted value based on a estimated regression line (Sokal & Rohlf, 1981; Wiig & Lie, 1984). This was achieved by regressing the measurements against age via an analysis of covariance (ANCOVA), as suggested by Thorpe (1976) and Thorpe and Leamy (1983). The analysis requires a linear relation between the dependent variable and the covariate, which is fulfilled in specimens between 17 and 60 months of age (Andersen & Wiig, 1984).

The age adjusted data were then subjected to univariate (ANOVA) and multivariate (canonical) analyses (BMDP7M, Dixon, 1981). The latter analysis calculates the significance of the dimorphism based on Mahalanobis' distance (D^2) (Mahalanobis, 1936), which considers differences in means, variances, and covariances of characters among groups (Gould & Johnston, 1972). The components of the standardized canonical vectors can be used to indicate the characters which contribute most to the separation between sexes.

The distance between the two sexes was calculated from the formula:

$$D^2 = d' \cdot V^{-1} \cdot d$$

where d is the vector of differences between the two means and V^{-1} the pooled variance-covariance matrix (Hope, 1968). This distance statistic is most useful in morphometric studies because the values are weighted by the inverse of the variance-covariance matrix, thereby eliminating the effects of correlation among characters. The distance based on only one measurement is

$$D^2 = \frac{(X_1 - X_2)^2}{S^2}$$

where X_1 and X_2 are the means of the measurements within each sex and S^2 the pooled within group variance.

3. RESULTS

All measurements were adjusted to the age of 33.19 months, which is the mean age of the total sample. Table 1 summarizes basic age-adjusted statistics and the results of the ANOVA between the sexes. In 15 of the 16 dimensions the males were highly significantly larger than the females ($F > 8.2$, $df = 1, 128$, $p < 0.01$), whereas the postorbital constriction was wider in the females than in the males ($F > 5.35$, $df = 1, 128$, $p < 0.025$). The degree of the sexual size dimorphism in the former dimensions ranged from 4% (condyl breadth) to 10% (mandible height), but was mostly 6–7%.

The dimensions which discriminated best between the sexes were mandible length, mandible height, profile length, and condylobasal length ($D^2 > 4.00$ for all), Table 1.

The multivariate separation between the sexes based on Mahalanobis' distance was highly significant ($D^2 = 6.05$, $F = 10.64$, $df = 16, 113$, $p < 0.001$). In a two group analysis this multivariate test corresponds to the

Table 1

Means and standard deviations of 16 mandible and skull dimensions of 74 males and 56 females Norwegian lynx aged between 17 and 60 months. The dimensions of each individual are adjusted by regression to the age of 33.9 months, which is the mean age of the total sample. The ratio between adjusted male and female means (R) and the Mahalanobis' distance (D^2) are also given together with the results of ANOVA between the sexes, and the standardized canonical coefficients.

	Mean (Standard deviation)		R	D^2	ANOVA ¹		CVI
	Males	Females			F	P	
1. Mandible length	102.33 (3.45)	95.60 (2.98)	1.07	4.24	135.78	<0.001	0.001
2. Mandible height	46.76 (2.23)	42.35 (1.85)	1.10	4.49	143.99	<0.001	0.033
3. Mandible dental length	56.66 (1.73)	53.61 (1.59)	1.06	3.35	106.22	<0.001	0.009
4. M_1 length	15.63 (0.57)	14.76 (0.67)	1.06	2.04	64.31	<0.001	0.032
5. Profile length	153.11 (5.08)	143.04 (4.40)	1.07	4.41	140.39	<0.001	0.012
6. Condylobasal length	139.04 (4.43)	130.45 (3.75)	1.07	4.28	136.66	<0.001	0.003
7. Palatal length	58.92 (2.12)	55.30 (1.91)	1.07	3.17	101.71	<0.001	-0.034
8. Dental length	60.79 (1.95)	57.36 (1.69)	1.06	3.46	110.84	<0.001	-0.010
9. P^4 length	18.56 (0.68)	17.67 (0.75)	1.05	1.56	49.23	<0.001	0.019
10. Rostrum breadth	39.15 (1.43)	36.70 (1.31)	1.07	3.17	100.86	<0.001	0.003
11. Dental breadth	61.62 (1.75)	58.87 (1.70)	1.05	2.66	84.34	<0.001	-0.004
12. Zygomatic breadth	101.25 (3.72)	95.44 (3.11)	1.06	2.79	89.02	<0.001	0.000
13. Mastoid breadth	65.42 (1.96)	61.18 (1.69)	1.07	3.76	119.63	<0.001	-0.005
14. Interorbital constriction	33.12 (1.56)	31.01 (1.38)	1.07	1.99	63.79	<0.001	0.007
15. Postorbital constriction	37.84 (1.63)	38.55 (1.86)	0.98	0.17	5.35	<0.025	0.002
16. Condyl breadth	33.89 (1.05)	32.72 (0.95)	1.04	1.32	41.83	<0.001	0.031

¹ d.f. = 1,128.

MANOVA based on the approximation of a F -statistic to Wilke's lambda. The high level of significance did not mean, however, that the separation of the sexes was complete. The histogram of the canonical discriminant scores are shown in Fig. 2. These are the standard canonical scores for the variables, where the unit on the graph is one standard deviation of the canonical variable (Pimentel, 1981). Because the total distance between the means ($D=2.46$) (Fig. 2) was measured in standard deviation units, approximately 89% correct assignment of males and females to their respective groups was suspected according to the normal distribution. According to the classification matrix generated by

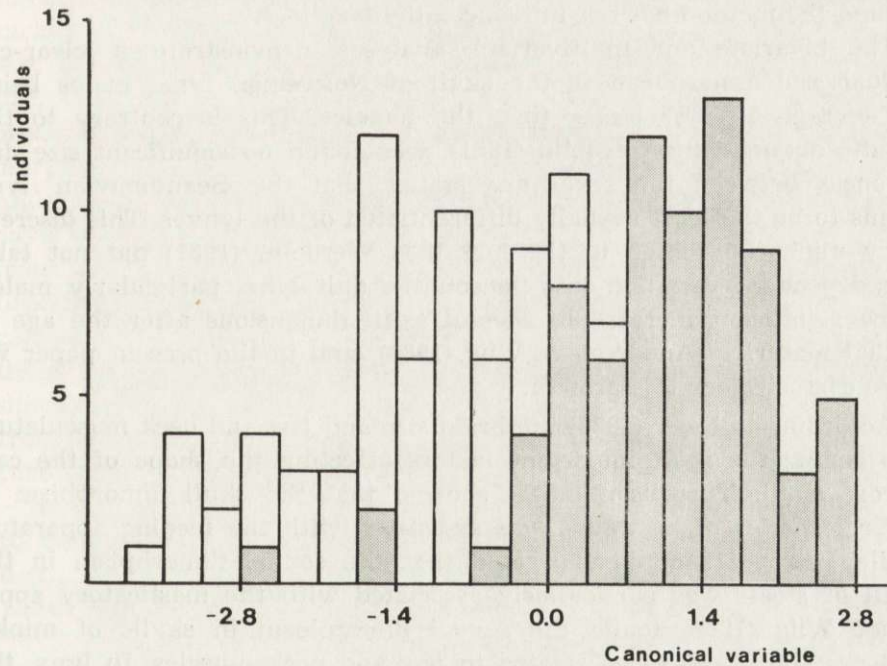


Fig. 2. Histogram of canonical score of male (shaded) and female Norwegian lynx aged between 17 and 60 months, based on 16 mandible and skull dimensions. Means of males=1.06, means of females=-1.40.

Table 2

Classification matrix of male and female lynx based on a discriminant analysis. Rows are actual groups and columns are predicted groups.

	Males	Females	% correct classified
Males	69	5	93.2
Females	7	49	87.5
Total			90.8

the computer program, five males and seven females were wrongly classified, corresponding to 90.8% correct classification (Table 2). The canonical vector contrasts mandible height, M_1 length and condyl breadth versus palatal length.

4. DISCUSSION

Discriminant analysis is a very robust method with respect to lack of multinormality and equality of group dispersions (Pimentel, 1981). The high agreement between calculated and observed degree of correct classifications shows that possible lack of fulfilment of the assumption behind the method has not influenced the results.

The bivariate and multivariate analyses demonstrate a clear-cut sexual size dimorphism in the skull of Norwegian lynx, males being on average 5–10% larger than the females. This is contrary to the results obtained by Werdelin (1981), who found no significant size differences between the sexes and stated that the Scandinavian lynx seems to be the least sexually differentiated of the lynxes. This discrepancy might be rooted in the fact that Werdelin (1981) did not take age dependent variation into account. Adult lynx, particularly males, show significant increase in several skull dimensions after the age of sexual maturity (Andersen & Wiig, 1984), and in the present paper we have corrected for this growth.

According to Ewer (1973) the brain size and jaw and neck musculature are among the most important factors affecting the shape of the carnivore skull. Yurgenson (1947) showed that the skull dimorphism of several species of mustelids was associated with the feeding apparatus, while Petrov (1956) demonstrated that the sexual dimorphism in the skull of stoats was particularly associated with the masticatory apparatus. Wiig (1986) found the sexual dimorphism in skulls of minks, badgers and otters to be related to jaw and neck muscles. In lynx, the skull dimensions showing the most pronounced sexual size dimorphism, *i.e.* those having the highest D^2 -values, are those of the mandible, the profile and the condylobasal lengths, the dental and palatal lengths as well as the rostrum and mastoid breadths. Based on the discriminant analysis, the males have higher mandible, longer lower carnassial, and broader occipital condyl in relation to palatal length than females.

Naturally, larger male skulls will have larger jaw muscles and larger absolute gape than the smaller female skulls (Greaves, 1983), which is also reflected in larger dental and palatal lengths. The mandible height was the most dimorphic dimensions, being 10% larger in the males, while the postorbital constriction showed very little size dimorphism, being, however, 2% smaller in the males. Both these latter dimensions

are connected with the masticatory work. In most carnivores, the anterior fibres of the temporalis, together with the zygomatico — mandibularis muscle, are responsible for exerting the main force when the jaws are fully open (Ewer, 1973). The temporalis muscle is attached to the lower jaw in the proximal part of the mandible, and to the skull in the post-orbital area. A decrease of the postorbital constriction will consequently give way for an increase of the anterior part of the temporalis muscle, and thus an increase of the the force of the fully opened jaw (Wiig, 1982)

According to Radinsky (1981) a broad mastoid reflects either a relatively large brain or more powerfull neck muscles. Usually there exists a negative allometric relation between brain size and skull size (e.g. Ewer, 1973; Radinsky, 1981). If the mastoid breadth reflects brain size, the smaller female skulls should have relatively broader mastoid breadth (Wiig, 1986) and, thus, leading to a less prominent sexual dimorphism. The dimorphism in mastoid breadth is, however, nearly as high as in e.g. the condylobasal length. Thus, male lynxes seem to have more powerfull neckmuscles than females, which is also indicated from the relatively larger occipital condyl. Powerfull neckmuscles are functionally related to the killing technique in felids, where one of the canine teeth enter inbetween two neck vertebrae of the prey, forcing them appart and thus breaking the spinal cord (Leyhausen, 1965). The shock produced when the canines encounter sudden resistance must be transmitted back through the skull to the body by the neck musculature (Ewer, 1973).

In conclusion, the sexual dimorphism in the skull of lynx is found to be functionally related with the feeding apparatus as has also been demonstrated in several mustelid species (Yurgenson, 1947; Petrov, 1956; Wiig, 1986).

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DYMORFIZM PŁCIOWY W ROZMIARACH CZASZKI RYSIA Z NORWEGII

Streszczenie

Zbadano dymorfizm płciowy 16 wymiarów czaszki rysia *Lynx lynx* (Linnaeus, 1758) na podstawie 130 zwierząt w wieku od 17 do 60 miesięcy. W celu uniknięcia związanej z wiekiem zmienności osobniczej, wszystkie wymiary sprowadzono do wartości odpowiadających średniemu wiekowi całej próby, wynoszącemu 33.9 miesięcy (Tabela 1). Było to możliwe dzięki skorelowaniu wymiarów czaszki z wiekiem zwierząt przy użyciu analizy kowariancji (ANCOVA).

W 15 spośród 16 wymiarów czaszki samców były większe od czaszek samic ($p < 0.01$), a tylko jeden wymiar (szerokość zaoczodołowa) był większy u samic ($p < 0.025$). Wieloczynnikowy rozdział pomiędzy płciami był wysoce istotny statystycznie ($p < 0.001$). Stopień dymorfizmu płciowego wynosił 6—7% w większości mierzonych cech, wahając się od 4% (szerokość rozstawu kłykci potylicznych) do 10% (wysokość gałęzi żuchwy). Szerokość zaoczodołowa była o 2% węższa u samców.

Stwierdzono, że dymorfizm płciowy w rozmiarach czaski funkcjonalnie związany jest z różnicami w aparacie żuwacym.