

Why are American mink sexually dimorphic? A role for niche separation

Michael D. Thom, Lauren A. Harrington* and David W. Macdonald

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American mink are highly sexually dimorphic, with males being up to twice the size of females. Sexual dimorphism may arise for several reasons, including intra- or inter-sexual selection, inter-sexual competition, or divergent reproductive roles. Whether or not dimorphism arises from competition, a degree of niche separation is expected in dimorphic species. Sexual divergence in feeding niche has been reported for many species, including mink. This is likely to be manifested in a greater degree of dimorphism in those structures, such as teeth, that are used for the acquisition of prey. We tested the hypothesis that teeth and other trophic structures of male mink would be significantly larger than those of females, after controlling for underlying skeletal size differences. Canine and carnassial teeth, and several skull dimensions, were larger than predicted in males. There is good evidence that sexual dimorphism in mink trophic apparatus is greater than predicted from allometry. We examined the development of dimorphism in various features with age and found that it was not consistent. Several trophic features were dimorphic amongst juveniles, and the degree of dimorphism remained relatively constant with age. Dimorphism in canines, and in relative body mass, was less apparent amongst juveniles and increased with increasing age. We discuss our results in the light of contemporary theories on the evolution and maintenance of sexual size dimorphism and argue that niche separation as a result of dimorphism in trophic features, while probably not the driving force behind sexual size dimorphism, may play a role in its maintenance.

M. D. Thom, L. A. Harrington and D. W. Macdonald, Wildlife Conservation Research Unit, Dept of Zoology, Univ. of Oxford, South Parks Road, Oxford, UK, OX1 3PS (a.l.harrington@btinternet.com). Present address for MDT: Animal Behaviour Group, Dept of Veterinary Clinical Science, Univ. of Liverpool, Leahurst, Neston, Cheshire, UK, CH64 7TE.

* Joint first author

Many mammals, including most mustelids, are highly sexually dimorphic (Moors 1980, Shine 1989). There are several possible explanations for sexual size dimorphism (Dayan et al. 1989, Shine 1989, Dayan and Simberloff 1996, 1998), however most of these can be divided into three groups (Hedrick and Temeles 1989). Firstly, Darwin (1871) proposed that sexual selection, expressed either as competition for mates or as mate choice, could lead to sexual dimorphism. Under this hypothesis, larger body size in males may be selected for because of

associated dominance benefits, and hence increased mating opportunities (Cox and LeBoeuf 1977, Erlinge 1979, Moors 1980). This explanation has been supported to some extent, since the degree of size dimorphism across species is highly correlated with the intensity of competition among males for access to females (Selander 1972, Clutton-Brock et al. 1977). Secondly, intrinsic differences in the reproductive roles of males and females could be sufficient to result in dimorphism (Hedrick and Temeles 1989). Female mustelids may be small partly

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because it is more energetically efficient for reproduction, their own reduced energy requirements enabling them to channel more into reproduction (Erlinge 1979, Powell 1979, Moors 1980, Powell and Leonard 1983). Finally, sexual dimorphism could arise through niche separation among the sexes (Darwin 1871). Thus males are expected to be significantly larger than females, particularly in trophic apparatus, as a means of reducing intra-specific competition for food (Brown and Lasiewski 1972, Hedrick and Temeles 1989). Shine (1989) argued that this final explanation has been slow to gain widespread acceptance, largely because of the comparative difficulty of testing the niche separation hypothesis, and the apparent parsimony of the sexual selection hypothesis.

The idea that sexual size dimorphism could evolve as a result of intra-specific competition is very similar to the theory of character displacement among inter-specific guilds (Dayan and Simberloff 1996). Just as species compete for food, so too do members of a sex compete with their conspecific opposite sex (Slatkin 1984, Dayan et al. 1989). The role of ecological factors in driving community-wide character displacement remains in dispute (Dayan and Simberloff 1996) and there are similar disagreements about the degree to which mustelid sexual dimorphism is the result of competition between the sexes. Nevertheless, sexual dimorphism in trophic structures, over and above differences expected from body size allometry, exists in many species (Shine 1989). Furthermore, theoretical treatments have demonstrated that ecological specialisation alone can be sufficient to lead to sexual dimorphism (Slatkin 1984).

The morphological feature being studied has a considerable effect on the interpretation of sexual dimorphism (Dayan and Simberloff 1998). Dayan and Simberloff (1996) have argued that character displacement within carnivore guilds should be studied by examining trophic structures, such as teeth, rather than general measures of size such as mass or skull length. These other, non-trophic traits are more likely to be under different selective pressures, or may be passively responding to selection on trophic structures (Dayan and Simberloff 1996). Indeed, in an examination of sexual dimorphism in mustelines, Holmes and Powell (1994) demonstrated that tooth size varies independently of skull length and that the degree of sexual dimorphism differs between different trophic features. Canine size in particular is thought to be a good measure of trophic status because of the direct involvement of canines in food acquisition (Biknevicius and van Valkenburgh 1996, Dayan and Simberloff 1996, 1998), although there are alternative hypotheses for disproportionately large canines in males (Venge 1973, Whitehead and Walde 1993). Dayan et al. (1990) found equal size ratios for canines among morphospecies of Sind desert felines, but no such size-ratio equality in non-trophic measures such as skull

length. They interpreted this as support for an ecological role in sexual size dimorphism in canine teeth.

Sexual dimorphism in size results from inter-sexual differences in growth rates, and sex-specific selection should lead to sex-biased development (Badyaev 2002). Differential growth rates in trophic structures, over and above differences in underlying growth rate, would provide strong evidence for differential sexual selection. Previous authors have tended to either ignore possible age effects or to consider sexual size dimorphism in adults alone, yet it is essential to determine the details of growth in order to be able to understand the ultimate mechanisms underlying the evolution of sexual size dimorphism (Badyaev 2002).

American mink, *Mustela vison* Schreber, exhibit pronounced sexual size dimorphism, with males typically up to twice the size of females (Eagle and Whitman 1987, Kondo et al. 1988, Dunstone 1993, Macdonald and Strachan 1999). Males generally consume larger prey than do females (Sealander 1943, Birks and Dunstone 1985), with the degree of dietary overlap estimated at between 40 and 68% (Birks and Dunstone 1985). Indeed, Yamaguchi and Macdonald (2003) suggest that intra-specific resource competition is a significant factor determining range size in American mink, with males in particular being forced to maintain large ranges to compensate for resource depression due to cohabiting females (Powell 1994). We used carcasses from three feral island populations of mink to assess the degree of sexual dimorphism, and hypothesized that sex differences in the trophic apparatus, over and above underlying differences in overall body size, should exist as a result of feeding niche divergence. We used known-age individuals to look at the development of sexual dimorphism with growth, and the degree of sexual dimorphism in the trophic structures of adults.

Methods

Study populations

Mink carcasses were collected from three islands: (1) North Uist, (2) South Harris (both in the UK), and (3) Hiiumaa, Estonia. The Isles of North Uist and South Harris are part of the Hebridean archipelago, off the west coast of Scotland. South Harris forms a single land mass with the islands of North Harris and Lewis, separated from North Uist by the Sound of Harris. Mink were introduced to Lewis and North Harris for fur farming, and have been present as a feral population since at least the 1960s, although they did not reach South Harris until the 1980s. The last fur farm on Lewis and North Harris closed down in 1961, although the first feral animal was not detected until 1969. Although there have been sporadic sightings of mink on North Uist since the mid-1970s, there was no confirmation of

this until 1999 (Harrington 2003). Mink were never introduced deliberately to North Uist, and it is assumed that the animals now occurring there are a founder population arriving naturally from South Harris. By using the islets in the Sound of Harris, a mink could potentially reach North Uist (hereafter Uist) from South Harris (hereafter Harris) without having to swim more than 1 km at a time. Hiiumaa island is part of the western Estonian archipelago in the Baltic sea, about 22 km from the Estonian mainland. Mink were introduced to fur farms on Hiiumaa in 1973; captive breeding ceased in 1996, with the last captive animal being killed in 1998 (T. Maran, pers. comm.). The first confirmed report of feral American mink on this island was 1983, although they are believed to have been present in the wild much earlier than this (Maran 1991).

Carcass preparation and measurements

Mink carcasses were stored frozen. Before measurement they were thawed for 24 h, and weighed to the nearest 1 g. Head-body length (HBL) was measured – with the mink stretched out on its back – to the nearest 1 cm. Heads were removed, and skulls prepared by cutting away the skin, then cleaned either by boiling for 4 to 6 hours, or incubating in sodium perborate tetrahydrate (McDonald and Vaughan 1999). Eight measurements were taken from each skull (in accordance with Macdonald and Strachan 1999 and Harrington and Macdonald 2002), as follows:

condylobasal length (CBL) – from prosthian to occipital condyles
mastoid breadth (MSB) – measured at greatest width
zygomatic breadth (ZGB) – from zygion to zygion
palatal length (PTL) – from prosthian to aboral medial edge of palate
post-orbital breadth (POB) – least breadth aboral of the postorbital processes
inter-orbital breadth (IOB) – measured at least width
muzzle breadth (MZB) – measured between the outer lateral canine surfaces
braincase volume (BCV)

We used the antero-posterior diameter of the canine alveolus (tooth socket) as an indirect measure of antero-posterior canine width. We did not measure canine length as many canines were broken and we were unable to accurately correct for missing canine tips. Upper left incisor length was measured from the tooth tip to the bone, and antero-posterior upper and lower carnassial lengths were measured at the longest point.

All skull and teeth measurements except BCV were measured using digital callipers to the nearest 0.01 cm. BCV was measured by filling the braincase with number

9 lead shot, until level with the foramen magnum. The shot was emptied into a 50 ml cylinder and the volume measured to the nearest 0.5 ml.

The upper left canine tooth (upper right in the few cases where the left tooth was severely damaged) was removed for ageing by assessment of annular rings in the dentine; this technique has been calibrated for American mink (Kondo et al. 1988). Ages were estimated by Matson's laboratory (Box 308, Milltown, MT 59581, USA).

As many skulls were damaged or were missing teeth, not all data were available for each skull. Sample sizes thus varied considerably between analyses.

Analysis

To test the repeatability of skull measurements, a further nine repeated measures were taken non-sequentially on a sub-set of nine skulls. The seven skull dimension variables excluding BCV were tested for repeatability, as were upper and lower carnassial length, and canine alveolus diameter. The variation among individuals was compared with the variation within individuals (repeated measurements) using nested ANOVA. Measurement error was calculated as the percentage of overall variance attributable to within-individual (repeat) measurements (Bailey and Byrnes 1990).

Animals were classified into three age classes on the basis of dental annuli and the time of capture, assuming a birth date of 1st May (Dunstone 1993). Individuals with no dental annuli (age 0) captured between May and October were classed as juveniles, and assumed to be less than 6 months old. The remaining age 0 animals were classified as sub-adults, and considered to be between 6 and 12 months of age. All animals with visible annular dentine rings were classified as adults. When considering adults alone, we used chronological age as a covariate in parametric analyses to control for age-related variation in size.

General linear models with sequential sums of squares were used for the analysis of individual variables. All continuous variables were log-transformed, and residuals were tested for normality. Some sex difference in trophic structure size is expected due to allometry; this underlying (absolute) size difference was removed by including a standardizing measure of skeletal size in the model. Ralls and Harvey (1985) considered CBL to be a better standardizing measure than HBL, because the latter is subject to greater measurement error. We used CBL to control for skeletal size in analyses of individual skull measures, but used body mass when testing differences in overall skull dimensions that included CBL. Residuals were plotted to demonstrate relative size differences in variables between the sexes (Ranta et al. 1994). Because BCV represents a volume, we standardized this measure

by means of the index $iBCV = (BCV/CBL^3) \times 10,000$. We used principal components analysis (PCA) to reduce the highly correlated skull variables to a set of components. The first such component produced typically describes the size variation in the data, while the second, and any subsequent, components are said to represent size-independent shape variation (Lynch and Hayden 1995). The PCAs were performed on untransformed skull variables (and BCV rather than $iBCV$); no rotation was used. All analyses were conducted using MINITAB software (MINITAB Inc. 2000).

Results

Repeatability

The percent measurement error (ME) for all seven skull measures was low, the highest being ZBG with a ME of 0.91%. For all skull measures, between-individual variance was significantly greater than within-individual variance (all $F_{8,80} > 983$, $p < 0.001$). Measurement error was much higher for the three tooth measures. Upper carnassial ME was 7.25%, lower carnassial ME 4.29%, and canine alveolus ME 7.07%. The between-individual variance was nevertheless always significantly greater than that within individuals (all $F_{8,80} > 116$, $p < 0.001$). All measures were thus considered to be repeatable (Bailey and Byrnes 1990).

Age

The Harris sample had by far the greatest proportion of young animals, with 76% estimated to be less than one year of age. This was probably the result of greater summer trapping effort in this population (Table 1). The Hiiumaa population had the fewest non-adult animals, since this population was not trapped until December when only sub-adults could, by definition, remain in the population. Uist was intermediate between these two (Table 1; Kruskal-Wallis: $H_2 = 16.94$, $p < 0.001$). No age 0 animals were captured before July. Therefore, where we refer to juveniles in the analysis, these individuals were approximately 3 to 6 months of age.

The median adult age was higher on Hiiumaa (median 2.0) than on Uist or Harris (both 1.0; Kruskal-Wallis: $H_2 = 8.67$, $p = 0.013$). Adult age did not differ between

Table 1. Age structure of the three populations, broken down into juveniles (age 0–6 months), sub-adults (7–12) and adults (1 year +). Cells show N and (% of total sample).

Population	Trap dates	Juvenile	Sub-adult	Adult
Hiiumaa	Dec 1998–Apr 1999	0 (0)	18 (44)	23 (56)
Harris	Oct 1992–May 1995	77 (50)	40 (26)	37 (24)
Uist	Jul 1999–Apr 2000	5 (13)	17 (45)	16 (42)

the sexes in any of the populations (Hiiumaa: $H_2 = 1.53$, $p = 0.216$; Uist: $H_2 = 0$, $p = 1$; Harris: $H_2 = 1.91$, $p = 0.167$).

Age effects on sexual dimorphism

The relationship between age and sexual size dimorphism was examined for the Harris data alone, since this population contained the greatest number of individuals in each age class.

Month of capture was a significant predictor of mass (controlling for sex and age; $F_{11,128} = 3.34$, $p < 0.001$) due to seasonal fluctuations in body mass, so month was included in the analyses of the mass variable. After controlling for CBL, the interaction sex \times age was significant ($F_{1,115} = 8.56$, $p = 0.004$), the result of male ($F_{1,61} = 12.47$, $p = 0.001$) but not female ($F_{1,44} = 3.61$, $p = 0.064$) mass increasing relative to CBL with age (Fig. 1; mean adult body mass given in Table 3).

The relationship between age and HBL, however, did not differ significantly between the sexes (interaction term $F_{1,115} = 0.07$, $p = 0.797$; month included in the model), and there was no significant sex difference in HBL after controlling for CBL and age ($F_{1,115} = 2.32$, $p = 0.131$). Furthermore, there was no significant relationship between HBL and age, after controlling for CBL ($F_{1,115} = 0.81$, $p = 0.369$).

A principal components analysis (PCA) of all eight skull variables produced two factors explaining 92.5% of the variance in the skull size data (Table 2). The first of these was negatively associated with most variables, and explains the size variance in the data. The second component was positively associated with POB.

A plot of both PCA axes revealed separation by sex on component 1, and by age on component 2 (Fig. 2). Month was a significant predictor of PC1 score (controlling for mass, age and sex: $F_{10,104} = 3.07$, $p = 0.002$), and so was included as a factor in subsequent models. After controlling for mass, males had significantly lower PC1 scores than did females ($F_{1,103} = 38.62$, $p < 0.001$),

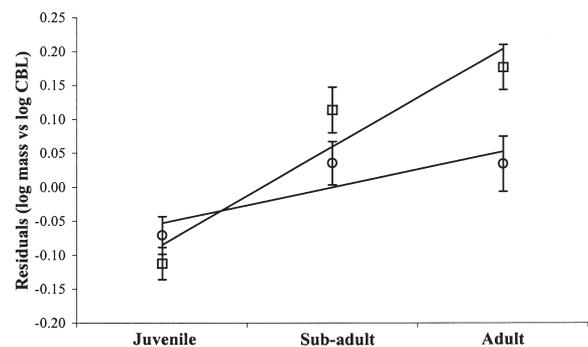


Fig. 1. Mean (\pm SE) of the residuals of the regression of log mass on log CBL for males (squares) and females (circles) of three different age classes on Harris.

Table 2. Factor loadings for a principal components analysis of 8 skull variables. All adult and juvenile animals from Harris were included (154 individuals).

Variable	Factor 1	Factor 2
Eigenvalue	6.16	1.24
Cumulative variance	0.770	0.925
CBL	-0.970	-0.119
MSB	-0.952	-0.154
ZGB	-0.942	-0.241
PTL	-0.955	-0.097
POB	-0.381	0.903
IOB	-0.905	-0.104
MZB	-0.963	-0.102
BCV	-0.785	0.548

indicating larger overall skull size. Age was a significant covariate in this model ($F_{1,121} = 29.75$, $p < 0.001$), as the skulls of both sexes continued to increase in relative size with age (Fig. 3; mean adult measures in Table 3). However, the interaction term sex \times age was not significant ($F_{1,103} = 0.77$, $p = 0.383$) suggesting that there was no difference in the rate of relative skull growth between the sexes and that the inter-sexual difference in skull size was relatively constant over all age groups.

Male PC2 scores were significantly lower than those of females after controlling for mass ($F_{1,121} = 5.73$, $p = 0.018$), and the interaction term sex \times age was not significant ($F_{1,121} = 0.08$, $p = 0.779$), indicating relatively smaller POB in males at all ages. Age was, however, a significantly negative covariate in the model ($F_{1,121} = 86.79$, $p < 0.001$), indicating that in both sexes relative PC2 values declined with increasing age.

Post-hoc tests showed that the sex \times age interaction was significant for CBL (controlling for mass), ZGB and MZB (controlling for CBL; all $p < 0.032$). In the latter two cases, there was an increasing disparity between relative male and female skull dimension with age (Fig. 4). The interaction term was not statistically significant for the remaining variables (all $p > 0.06$). In both sexes, relative POB and iBCV significantly declined with age

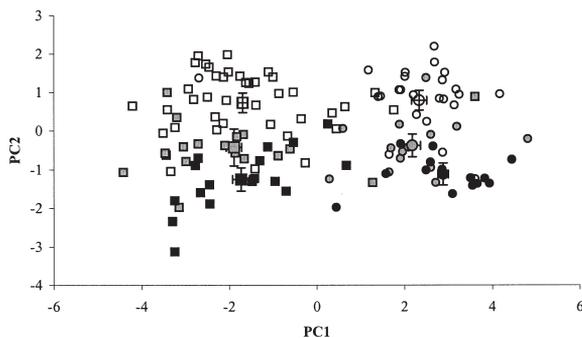


Fig. 2. The first two PCA axes, explaining 92.5% of the variance in the skull dimension data. Males (squares) and females (circles) shown as juveniles (open symbols), sub-adults (grey symbols) and adults (filled symbols). Group centroids (\pm SE) are shown.

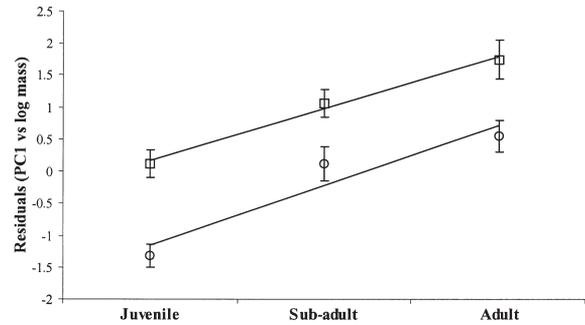


Fig. 3. Mean (\pm SE) of the residuals of the regression of PC1 on log mass for three different age classes on Harris. Males (squares) had significantly larger skulls than females (circles) at all ages ($p < 0.001$).

(both $p < 0.001$), while relative PTL, IOB and MSB were uncorrelated with age (all $p > 0.109$).

Age-related changes in canine alveolus diameter were significantly different among the sexes (controlling for CBL; interaction age \times sex; $F_{1,131} = 5.39$, $p = 0.022$), the result of male but not female canine alveoli enlarging with age relative to overall body size (Fig. 5). There was no such relationship with upper ($F_{1,131} = 0.23$, $p = 0.630$) or lower ($F_{1,125} = 0.06$, $p = 0.806$) carnassial length, and no age effect in either case (upper: $F_{1,131} = 0.07$, $p = 0.785$; lower: $F_{1,125} = 0.34$, $p = 0.560$), although there was a significant sex effect for both upper and lower carnassials (upper: $F_{1,131} = 17.03$, $p < 0.001$; lower: $F_{1,125} = 29.12$, $p < 0.001$; controlling for CBL in all cases) indicating that male carnassials were relatively larger at all ages (Fig. 6). There was no significant age \times sex interaction in incisor length ($F_{1,133} = 0.17$, $p = 0.678$), neither was there any difference between the sexes across ages (controlling for CBL; $F_{1,133} < 0.01$, $p = 0.963$). However, after controlling for size (CBL) differences, relative incisor length decreased with age ($F_{1,133} = 6.54$, $p = 0.012$) suggesting that while relative skull length increases with age in both sexes, relative incisor length does not.

Sexual dimorphism among adults

Male mink were significantly heavier than females after controlling for CBL (Table 3). However, the effect was weak, and post-hoc analyses showed the sex difference in mass to be non-significant in each population after controlling for CBL (Hiiumaa: $F_{1,16} = 1.23$, $p = 0.284$; Uist: $F_{1,4} = 3.31$, $p = 0.129$; Harris: $F_{1,20} = 3.62$, $p = 0.072$), although this may have been due to small sample size. HBL was not significantly different among the sexes after controlling for CBL (Table 3).

A PCA of all adult skull dimensions produced a single component with an eigenvalue of greater than 1, which explained 86% of the variance in the data (Table 4). This component was significantly affected by sex (Table 3):

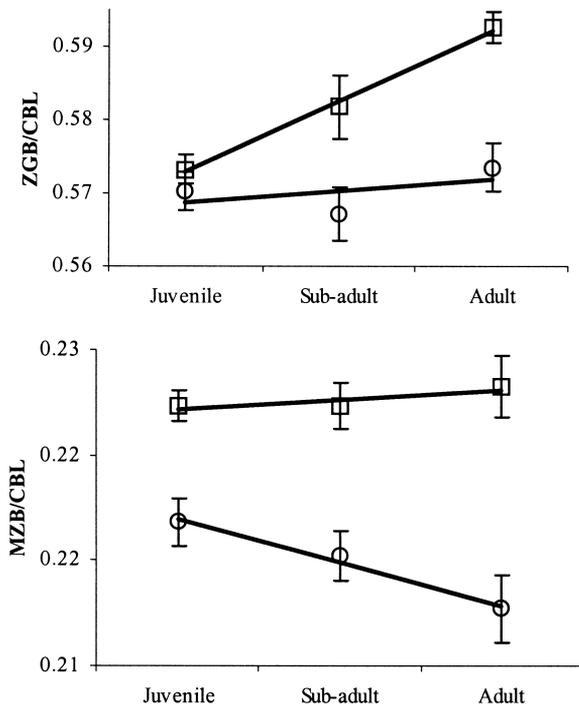


Fig. 4. The sex difference in both ZGB (top) and MZB (bottom) relative to CBL increased with age. In separate GLMs controlling for CBL, the interaction term of both models was significant (ZGB $p = 0.004$; MZB $p = 0.032$).

males had smaller PC1 scores than females, indicating that male skulls were larger across populations, after controlling for sex differences in mass. Post-hoc tests showed male skulls to be significantly larger than those of females, after controlling for CBL, in MSB, ZGB, IOB and MZB ($p < 0.008$) and significantly smaller in CBL (controlling for mass), POB and iBCV (both controlling for CBL; all $p < 0.040$). There was no significant sex difference in PTL.

Of the teeth measurements used, canine alveolus width and both upper and lower carnassials were larger in adult males than in adult females, relative to skull length, while incisors were not (Table 3). Of all the teeth measures, only upper carnassial length was significantly influenced by adult age (Table 3).

The observation that CBL is relatively smaller in males than in females after controlling for mass indicates that CBL routinely underestimates absolute size dimorphism, a result consistent with Holmes and Powell's (1994) findings for a range of mustelids. As a result, when using CBL to control for allometry, estimates of dimorphism in the dependent variables could be exaggerated. To test this, we repeated the analyses of each size variable using HBL as the covariate measure of body size. In each case our conclusions remained qualitatively unchanged by this substitution.

Discussion

Our results demonstrate that significant sexual dimorphism exists in the trophic apparatus of mink, over and above differences in skull and body dimensions. Specifically, and in addition to the other allometries in the sizes of the two sexes, canines were disproportionately wider in males than in females, both upper and lower carnassials were disproportionately longer in males, and there were several inter-sexual differences in skull size and shape. Unlike less dimorphic mustelids such as the badger, *Meles meles* L. (Johnson and Macdonald 2001), we found some evidence for greater body weight in male mink than in female mink, after controlling for skeletal size. This difference, however, was not apparent in juvenile mink but appeared to develop with age, suggesting that males gain relatively more mass than do females as they grow.

Since canines function primarily in seizing and killing prey it is reasonable to suppose that canine size should relate directly to prey size (Dayan et al. 1989). The larger canines of male mink demonstrated in this study is consistent with their specializing on larger prey (Birks and Dunstone 1985), most likely to be lagomorphs in Europe (and muskrats, *Ondatra zibethicus* L., for much of their evolution). Similarly, the dimorphism in skull shape can be functionally related to killing and feeding behaviour. Specifically, after accounting for differences in skull length, mastoid breadth, zygomatic arch breadth, inter-orbital breadth and muzzle breadth were all greater in adult male than in adult female mink. In contrast, condylobasal length, post-orbital breadth and braincase volume were all smaller. Both narrow post-orbital breadth and large zygomatic breadth suggest larger temporalis muscles in males (Radinsky 1981a,b) and thus greater bite strength (Biknevicus and van Valkenburgh 1996). Greater mastoid breadth in males is also indicative of more powerful neck musculature (Radinsky 1981a,b). A relatively small braincase in males is consistent with the negative allometry noted for this feature among all carnivores (Radinsky 1981a,b). Overall skull size in males was also larger than predicted from allometric scaling. This seems compatible with the hypothesis that male morphology is adapted to handling different, and larger, prey than do females (although Shine 1989, 1991 suggests that this is only likely to be the case in gape-limited predators, such as snakes). Similar inter-sexual differences in skull shape and size have previously been reported in American mink (Wiig 1982a, 1985, 1986, Zagrebely 2000), as well as in other mustelids including ferrets, *Mustela putorius furo* L. (Lawes and Andrews 1987), weasels, *M. nivalis* L. (Schmidt 1992), black-footed ferrets *M. nivalis* Audubon and Bachman (Anderson et al. 1986), badgers *Meles meles* (Wiig 1986) and otters *Lutra lutra* L. (Wiig 1986, Lynch et al. 1996).

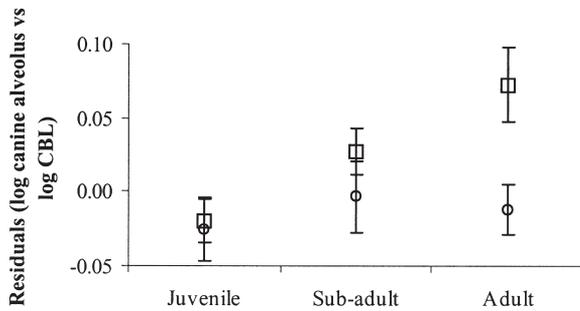


Fig. 5. Mean (\pm SE) of the residuals of the regression of log canine alveolus on log CBL for males (squares) and females (circles) of three different age classes on Harris.

Interestingly, we found that in contrast to the increase in relative body mass of males with age, dimorphism in relative skull size was apparent in juveniles. Badyaev (2002) suggests that there is an association between the timing of selection favouring sexual size dimorphism and the development of sexual size dimorphism, which would suggest that dimorphism in trophic features is important at the juvenile stage. We did, however, find that the sex difference in relative zygomatic and muzzle breadth increases with age in mink, indicating that there may be further sexual selection acting on these structures

and continued refinement of skull shape with age. For example, the decrease detected in relative POB with age (in both sexes) is consistent with the findings of Wiig (1982b) who also found a decrease in POB in mink from Norway. Wiig suggested that the decrease occurs by bone resorption in this area to make way for a larger temporalis muscle.

Carnassial teeth were disproportionately larger in male mink than in females. Gittleman and van Valkenburgh (1997) found that across carnivores there was a tendency for carnassials to be less dimorphic than canines, and this trend was confirmed here – while canines were 20 to 30% larger in males, carnassials were only around 10% larger. This suggests a greater degree of selection for size on canines, which Dayan and Simberloff (1998) suggested is due to their role in killing, rather than consuming, prey. An alternative argument is that canines are used in threat displays, which may lead to selection on canine size (Whitehead and Walde 1993). Another important role for canines among male mink is during mating, when they are used to cling to the neck of the female during often violent mating bouts (Venge 1973). Males with larger canines could be more successful at extending copulation, thereby increasing reproductive success. Thom et al. (2004), however, found no correlation between canine size and copulation duration

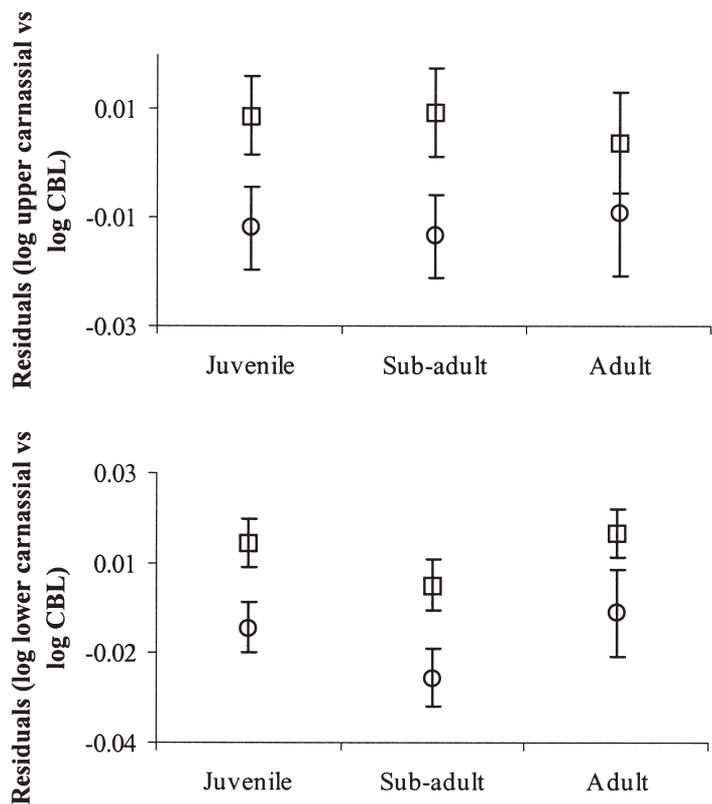


Fig. 6. Mean (\pm SE) of the residuals of the regression of log carnassial width on log CBL for three different age classes on Harris. Both upper and lower carnassials were significantly larger in males (squares) than in females (circles) at all ages (both $p < 0.001$).

Table 3. Sex differences in size variables among adult mink (1 year +) from three populations. Month was included as a factor, and age as a covariate in the model. For all variables except the first principal component (PC1), underlying size differences were removed statistically by including CBL as a covariate in the model. In the case of PC1, mass was used. The site \times sex interaction term was non-significant in all models ($p > 0.093$ in all cases), the effect of site is shown. Raw variable means (\pm SE) are shown for males and females. In all cases where the site effect was significant, post-hoc analyses demonstrated Hiiumaa animals to be larger than those from either of the remaining populations.

Variable	Site effect	Female mean	Male mean	Sex effect	Age effect
Mass	$F_{2,44} = 0.49$ $p = 0.615$	633.4 (± 20.9)	1191.3 (± 51.6)	$F_{1,44} = 5.48$ $p = \mathbf{0.024}$	$F_{1,44} = 3.39$ $p = 0.072$
HBL*	$F_{1,40} = 8.44$ $p = \mathbf{0.006}$	354.7 (± 4.78)	410.3 (± 6.28)	$F_{1,40} < 0.01$ $p = 0.947$	$F_{1,40} = 1.52$ $p = 0.224$
Skull – PC1	$F_{2,31} = 22.1$ $p < \mathbf{0.001}$	1.87 (± 0.26)	- 2.09 (± 0.39)	$F_{1,31} = 13.17$ $p = \mathbf{0.001}$	$F_{1,31} = 0.06$ $p = 0.813$
Canine width	$F_{2,42} = 4.96$ $p = \mathbf{0.012}$	3.16 (± 0.05)	3.94 (± 0.07)	$F_{1,42} = 17.35$ $p < \mathbf{0.001}$	$F_{1,42} = 2.17$ $p = 0.148$
Upper carnassial	$F_{2,42} = 2.10$ $p = 0.135$	6.68 (± 0.07)	7.38 (± 0.05)	$F_{1,42} = 8.31$ $p = \mathbf{0.006}$	$F_{1,42} = 4.28$ $p = \mathbf{0.045}$
Lower carnassial	$F_{2,41} = 23.88$ $p < \mathbf{0.001}$	7.36 (± 0.09)	8.03 (± 0.09)	$F_{1,41} = 13.57$ $p = \mathbf{0.001}$	$F_{1,41} = 6.69$ $p = 0.412$
Incisor	$F_{2,43} = 2.28$ $p = 0.114$	2.82 (± 0.06)	3.23 (± 0.07)	$F_{1,43} = 0.04$ $p = 0.838$	$F_{1,43} = 1.63$ $p = 0.208$

* Uist population excluded from this analysis.

in males. Furthermore, although we are unable to eliminate intra-sexual competition as a source of selection on canine diameter, we found sex differences in trophic structures other than canines, so even if canine dimorphism can be attributed to their use in threat displays, this is insufficient to account for other forms of dimorphism in mink. The fact that dimorphism in separate features appears to develop at different rates and at different stages in a mink's life suggests that these features are not developmentally linked. The increase in male but not female canine diameter with age relative to body size supports the hypothesis of contemporary selection on canines. The relative canine-width increase in males with age, which does not occur in carnassials, suggests different roles for these types of teeth in mink, with carnassials (as for skull size overall) being of greater importance in juveniles than are canines. This would be consistent with the fact that weaned animals must use carnassials to consume flesh, and suggests that canines

Table 4. Factor loadings for a principle components analysis of 8 skull variables in adults only. Data from all three populations were included (55 individuals: 23 from Hiiumaa, 17 from Uist and 42 from South Harris). Only one factor had an eigenvalue > 1 .

Variable	Factor 1
Eigenvalue	6.88
Cumulative variance	0.860
CBL	- 0.968
MSB	- 0.972
ZGB	- 0.971
PTL	- 0.963
POB	- 0.658
IOB	- 0.940
MZB	- 0.975
BCV	- 0.926

may play an altogether different role (in addition to their vital role in killing), perhaps being used in aggressive contexts, which would become more important later in life.

The sex differences in trophic apparatus suggest some degree of niche separation between males and females. However, data demonstrating an ecological basis for niche separation are typically lacking (Dayan and Simberloff 1996). Limited resource availability in at least one niche dimension is a prerequisite for exploitation competition, but demonstrating resource limitation is particularly difficult (Moors 1980). There is no convincing evidence that prey are limiting for American mink in Europe. Furthermore, Moors (1980) found no correlation between the extent of dietary overlap and the degree of sexual size dimorphism among mustelids, concluding that there was insufficient evidence for competition driving sexual dimorphism in this group.

Nevertheless, for mustelids in general (Moors 1980, McDonald 2002), and mink in particular (Sealander 1943, Birks and Dunstone 1985), there is some evidence of sexual differences in the size of prey consumed. Male mink in coastal Scotland prey significantly more on lagomorphs than do females, which tend to specialize on fish and crustaceans (Birks and Dunstone 1985). Similarly, indigenous male mink in Michigan consumed more muskrats, while females ate more small rodents and frogs (Sealander 1943). Ireland (1990) demonstrated a significant positive correlation between body size and the proportion of lagomorphs in the diet, and a negative association for fish. Furthermore, Yamaguchi et al. (2003) demonstrate sex differences in habitat use that may reflect differences in diet.

Studying contemporary species may identify factors maintaining sexual dimorphism, but provides little

information on its origin (Hedrick and Temeles 1989). Furthermore, more than one mechanism may be important in the maintenance of dimorphism (and different mechanisms may be responsible for absolute dimorphism in body size versus relative dimorphism in trophic features). So although there is some evidence to suggest a role for character displacement in canine dimorphism among mink and other mustelids, other factors are likely to be important. In fact, inter-sexual competition is almost certainly not the primary cause of sexual dimorphism, whether in body size or trophic apparatus. This is because in carnivores males are almost always (and in the case of mustelids, always) larger than females (Moors 1980). If sexual dimorphism arose via inter-sexual competition, males should be smaller in approximately 50% of cases (Gittleman and van Valkenburgh 1997). Thus sexual dimorphism – not necessarily in trophic structures – is most likely to have arisen for other reasons, with niche separation perhaps being a beneficial side-effect (Moors 1980).

What alternative mechanisms could have lead to sexual dimorphism in mink? Although sexual selection on mink canines is considered to be unlikely for the reasons discussed above, there may be intra-sexual selection on body size (Andersson 1994). Male polecats and ferrets are reported to fight during the breeding season (Lavers 1973), and captive mink are more aggressive at this time (MacLennan and Bailey 1969). If larger males have higher reproductive success, this could be reinforced by female choice (Andersson 1994). Alternatively, the reproductive roles of males and females may be sufficiently different to result in body size dimorphism (Hedrick and Temeles 1989). This could be due either to greater energetic (Erlinge 1979, Sandell 1989) or hunting (King 1989) efficiency of small body size.

An alternative hypothesis to explain the degree of sexual dimorphism in mustelids was proposed by Powell and King (1997). They suggested that, since female mustelids may be size limited as a result either of energy limitations or the necessity to enter small burrows when hunting, they should not increase their growth rate during periods of high food availability. Males, on the other hand, should benefit significantly from larger size and should be larger if they are born during periods of abundant food. However Powell and King (1997) were unable to find any evidence for greater size dimorphism during periods of food abundance in any of the three New Zealand stoat populations they examined for this effect, and other supporting evidence is limited. While it is possible that fluctuations in food availability may influence the degree of dimorphism in mink and other species, our observations were consistent across three quite disparate populations, suggesting that underlying devel-

opmental differences are a more likely explanation for the patterns we describe.

Whatever factors originally led to size dimorphism in mink, there is some evidence for contemporary selection maintaining it. Lynch and Hayden (1995) demonstrated that relative dimorphism in cranial features was reduced in ranch mink, indicating contemporary selection which is absent in the captive environment. Although both sexual selection and divergent niches meet this description, our data suggest that there is greater selection on the relative size of trophic than on non-trophic structures in mink. While there was evidence for only minimal body mass dimorphism (in relation to overall skeletal body size), there was greater dimorphism in several skull features related to feeding mechanics. Even more strikingly incisors, which are unlikely to have a role in either food acquisition or consumption, did not differ allometrically between males and females, whereas carnassials and canines did. Furthermore, the fact that dimorphism in trophic features exists in younger animals suggests that males may have a competitive advantage in feeding and/or hunting from an early age. This would be consistent with the fact that small males also prefer larger prey species (Ireland 1990). However, this need not necessarily be related to inter-sexual competition but may have an energetic basis. Males, at least during the breeding season, generally travel further than females (Yamaguchi and Macdonald 2003), they sustain a greater growth rate post-weaning (Dunstone 1993), and (as we have shown) they may continue to gain relatively more body weight during the later stages of growth. All would require relatively greater energy consumption in males. Indeed, Balharry (1994) has shown that male pine martens (*Martes martes* L.; a similar sized mustelid) have a higher mass-specific energy consumption than females. Furthermore, despite their greater overall absolute body size, which has been estimated to require 1.5 times the energy intake of females, there is apparently little sex difference in the amount of time spent foraging (Dunstone 1993). This would imply either that males are hunting more successfully or that they are taking larger prey, or both. Thus, dimorphism in trophic features may confer greater strength on males (in terms of killing and feeding ability) and thus provide males with the ability to increase their energy intake without a concomitant increase in the time spent doing so. It is possible that such an advantage in males provides a mechanism whereby sexual size dimorphism in absolute body size (for whatever reason) is achieved. An energetic explanation for niche separation would be consistent with the fact that males are always the larger of the sexes, it does not require there to be competition between the sexes, nor does it require that resources are limited.

Conclusions

For small mustelids, including American mink, it seems likely that either energetic selection for small female body size, or sexual selection for large males, initially drove dimorphism in overall body size. The attendant ability to consume alternative prey (or for males to hunt more efficiently) may then have put selective pressure on the trophic apparatus of either or both sexes, adjusting them to optimal sizes for the most abundant prey. The benefits of niche separation (whether this is related to inter-sexual competition or to an energetic advantage in males) may be sufficient to maintain, or increase the extent of, sexual dimorphism, particularly in trophic structures. Either these different mechanisms continue to operate simultaneously to maintain sexual size dimorphism (Hedrick and Temeles 1989), or one mechanism which was initially responsible for sexual dimorphism, is replaced by another which maintains it (Lande 1980). In the case of mink, it seems likely that there is contemporary disruptive selection on trophic structures.

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