

VARIABILITY AND SEXUAL SIZE DIMORPHISM IN CARNIVORES: TESTING THE NICHE VARIATION HYPOTHESIS

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Abstract. The niche variation hypothesis predicts greater morphological variability in populations occupying wide ecological niches than in those occupying narrow ones. Island populations of carnivores are often assumed to have wider niches than mainland populations, because the number of competing species on islands is usually smaller. We compared coefficients of variation and degrees of sexual size dimorphism in skulls and canines of pairs of related insular and mainland populations belonging to 39 carnivore species. Mainland populations were more variable than insular ones. Averaging population values for the different species, we found no significant differences in the variability of insular and mainland taxa. There was no consistent difference in the degree of sexual size dimorphism between insular and mainland carnivores for either skull length or canine diameter. We hypothesize that gene flow is the main source of the greater variability in mainland populations. The niche variation hypothesis is not supported.

Key words: *Carnivora; coefficient of variation; gene flow; island vs. mainland; morphological variability; niche variation hypothesis; sexual size dimorphism.*

INTRODUCTION

Variation is the raw material for evolution. Understanding patterns of variability is thus an important goal of evolutionary biology. Van Valen (1965) formulated the niche variation hypothesis, suggesting that populations of species occupying narrow niches would be less variable in morphological characters related to niche occupation than populations occupying wider niches. This model conceives of variation as adaptive and selected for, because different individuals specialize in different resources. Alternatively, increased variability can result from relaxed stabilizing selection in environments from which competitors are absent. Within-species variability results from both continuous and discontinuous variation (Patterson 1983), the latter usually in the form of sexual dimorphism (Ebenman and Nilsson 1982, Patterson 1983). Because insular populations usually face fewer competing species than do mainland ones, they can be hypothesized to evolve to fill at least part of the vacated niches and so to increase their population variability. On the other hand, the resource base on islands may be restricted, causing morphological variability to be lower (Madsen and Shine 1993). Islands can also be hypothesized to have lower habitat diversity, resulting in reduced variability. Isolation can be yet another factor causing variability of insular populations to be lower than that of mainland ones, by limiting genetic variation owing to gene flow. We therefore compared the opposing predictions sug-

gested by these latter factors and that of the niche variation hypothesis, using insular and mainland carnivore populations.

Although relative niche breadth is hard to define, and Van Valen (1965) himself pointed out that relative breadth of insular niches compared to mainland ones cannot be determined a priori (see also Rothstein 1973), many studies have tried to compare morphological variability in environments perceived as differing in niche breadth, such as islands and mainlands. Empirical tests of the relative continuous variability of insular vs. mainland forms usually do not support the niche variation hypothesis (Grant 1967, 1979, Malmquist 1985, Dennison and Baker 1991, Simberloff et al. 2000; but see Van Valen 1965, Dayan and Simberloff 1994; see also Soulé and Stewart [1970], Patterson [1983], Ebenman [1986], for studies comparing mainland populations). Patterns of sexual dimorphism, however, generally support the model (Ebenman and Nilsson 1982, Nagorsen 1994, Dayan and Simberloff 1994, Simberloff et al. 2000, Pearson et al. 2002, but see Dunham et al. 1978, Blondel et al. 2002), with increased dimorphism on islands, perhaps enabling females and males to reduce intraspecific competition (Rothstein 1973, Shine 1989).

These findings accord well with Rothstein's (1973) suggestion that continuous variation is probably not adaptive, in itself, but reflects relaxed stabilizing selection, especially in large, mobile organisms (Levins 1968, Gould 1975) that perceive the environment in a fine-grained way (i.e., as having smaller patches; Forman 1995) that precludes formation of multiple adaptive peaks. On the other hand, phenotypic variability

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can be easily achieved through accentuation of sexual size dimorphism (SSD) already present owing to sexual selection (Darwin 1871, Ebenman 1986).

Most studies comparing patterns of continuous variability and sexual dimorphism of insular and mainland populations have been conducted on passerine birds, usually one or just a few closely related species (but see Grant 1967). To the best of our knowledge, all such studies of mammals have been carried out either on mustelid or herpestid carnivores (Dayan and Simberloff 1994, Simberloff et al. 2000). Rothstein (1973) criticized the use of such taxonomically restricted data, because outcomes of such studies can result from "sampling error in the choice of the species involved" (Rothstein 1973:599). In the 30 years since Rothstein's (1973) publication, no study of a large number of species has been conducted on the subject of the relative variability of insular and mainland animals (but see Prinzing et al. [2002] for a related multispecies comparison of insular and mainland plants).

Here we analyze patterns of morphological variability and SSD in members of the Carnivora to test whether variability is indeed greater on islands relative to that on nearby mainlands. Carnivores are extremely diverse in size, social structure, diet, and other life history characteristics (Gittleman 1985, Macdonald 1992, Gittleman and Van Valkenburgh 1997, Nowak 1999, Kruuk 2002). Interspecific competition, a major driving force in the niche variation hypothesis, has been widely studied in carnivores (Major and Sherburne 1987, Cypher 1993, Johnson et al. 1996, Palomares and Caro 1999, Arjo et al. 2002, Loveridge and Macdonald 2002), and is believed to promote morphological evolution (Simms 1979, Kiltie 1988, Dayan et al. 1989, 1990, 1992, Thurber et al. 1992, Dayan and Simberloff 1994, Van Valkenburgh and Wayne 1994). Specifically, carnivore SSD is a focus of much research (Erlinge 1979, Gliwicz 1988, Lüps and Roper 1988, Dayan and Simberloff 1994, Gittleman and Van Valkenburgh 1997, Weckerly 1998, Johnson and Macdonald 2001). Furthermore, members of the order are found on many islands worldwide (137 species of wild carnivores inhabited over 500 different islands in historical times; S. Meiri, *unpublished data*). The Carnivora are therefore extremely well suited for a comprehensive study of the niche variation hypothesis.

MATERIALS AND METHODS

In order to analyze size variation in insular and mainland carnivores, we measured carnivore skulls in the following collections: Natural History Museum, London, UK; Zoology Museum of Cambridge University Cambridge, UK; New-Walk Museum Leicester, UK; National Monuments archeozoological collections, London, UK; Harrison Zoological Museum, Sevenoaks, Kent, UK; Royal Museum, Edinburgh, Scotland, UK; Museu de Zoologia, Barcelona, Spain; Museo Nacional de Ciencias Naturales, Madrid, Spain; Muséum

d'Histoire Naturelle de la Ville de Genève, Geneva, Switzerland; Museo Civico di Storia Naturale "Giulio Doria," Genoa, Italy; National Wildlife Institute, Bologna, Italy; Muséum National d'Histoire Naturelle, Paris, France; Laboratoire d'Anatomie Comparée, Paris, France; Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; National Museum of Natural History Leiden "Naturalis", Leiden, The Netherlands; University of Amsterdam Zoological Museum, Amsterdam, The Netherlands; Zoologische Staatssammlung, München, Germany; Museum für Naturkunde, Humboldt Universität zu Berlin, Germany; Staatliche Naturhistorische Sammlungen, Dresden, Germany; Zoological Museum, University of Copenhagen, Denmark; Tel-Aviv University Zoological Museum, Israel; Raffles Museum of Biodiversity Research, Singapore, Malaysia; National Science Museum, Tokyo, Japan; Primate Research Institute, Kyoto University, Japan; University of Alaska Fairbanks, Museum of Natural History, Fairbanks, Alaska, USA; Royal British Columbia Museum, Vancouver, British Columbia, Canada; Royal Ontario Museum, Toronto, Canada; Canadian Museum of Nature, Ottawa, Canada; Field Museum, Chicago, Illinois, USA; Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C. USA; American Museum of Natural History, New York, New York, USA; Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts USA; Natural History Museum of Los Angeles County, Los Angeles, California, USA; The National Museum of Ireland, Dublin, Ireland, UK; the Collections of the Department of Zoology, University College, Cork, Ireland, UK; Ulster Museum, Ulster, Ireland, UK; University of Kansas Museum of Natural History, Lawrence, Kansas, USA; and Museum of Vertebrate Zoology, University of California, Berkeley, California, USA.

Measurements were taken with digital calipers to 0.01 mm precision, or with vernier calipers to 0.02 mm precision (for measurements exceeding 300 mm). We chose two morphological characters: skull length (CBL, Von den Driesch 1976) and maximum diameter of the upper canine. CBL is a commonly used measure of body size in biogeographic research (see, e.g., Rausch 1963, Ralls and Harvey 1985, Dayan et al. 1989, 1990, 1992, Gittleman and Van Valkenburgh 1997, Jones 1997). The upper canine tooth is a main killing apparatus in carnivores (Van Valkenburgh and Ruff 1987, Dayan et al. 1989, 1990, Biknevicius and Van Valkenburgh 2001). Canine size may be strongly correlated with prey size (Dayan et al. 1989, 1990, Dayan and Simberloff 1998) and may thus reflect dietary variation (Holmes and Powell 1994, Johnson and Macdonald 2001). Hence the amount of variation in canine size may be a good measure of feeding niche breadth.

We used only adult specimens (those with complete closure of the dorsal sutures) when analyzing CBL. Only specimens with fully erupted permanent canines were analyzed for canine variation; we did not measure worn teeth. We considered a population (either mainland or insular) to be fit for analysis if we measured at least five individuals of the same sex (see Grant 1967). Interesting patterns of size evolution have been demonstrated for several mammalian taxa introduced to islands (Yom-Tov et al. 1986, 1999), including carnivore species, e.g., *Mustela vison* (Dayan and Simberloff 1994), and *Herpestes javanicus* (Simberloff et al. 2000). However, we chose not to include populations introduced to islands during historical times in our analysis, as the limited time since introduction might not have sufficed for evolution to manifest itself fully (Simberloff et al. 2000). In all analyses, we compared island carnivores with their mainland conspecifics, with one exception, in which an insular endemic was compared to its nearest mainland congener: *Urocyon littoralis*, endemic to the California Channel Islands and the Gulf of California Islands, was compared to its mainland ancestor, *Urocyon cinereoargenteus*. We treated sexes as separate morphospecies for all island-mainland comparisons.

We used mainlands as close as possible to the islands in question. The geographic limits of the mainland populations were chosen to approximate, or at least not greatly exceed, those of the insular populations in both area and latitudinal range. Although what constitutes an island is hard to define and there are varying degrees of insularity (Adersen 1995, Meiri et al. 2004), with respect to the niche variation hypothesis an island can be defined by its greater degree of isolation and usually lower species richness. Variability is represented by the coefficient of variation (CV), a measure independent of size often used in studies of the niche variation hypothesis (Patterson 1983). CV is comparable between different populations when the same measurement is used (Lewontin 1966, Lande 1979), as long as a rank order comparison is made (Patterson 1983). Absolute size of carnivore cranial and dental traits is negatively correlated with CV (Pengilly 1984, Polly 1998, Szuma 2000, Dayan et al. 2002). However, magnitudes of size differences between insular and mainland populations are relatively minor compared with the interspecific size range of the sample (from least weasels to brown bears), and they are random with respect to direction and absolute size (i.e., there is no "island rule"; Meiri et al. 2004); therefore we expect no bias from using CVs in the current study.

We compared CVs of insular and nearest mainland pairs of populations of the same morphospecies with the nonparametric Wilcoxon matched-pairs test for paired samples. The insular populations that we used all diverged from mainland populations belonging to the same species (except for *Urocyon*). Therefore all of our data are independent of variability evolution

above the species level. Felsenstein (1985:13) outlined the rationale for such a paired test, writing "we could use contrasts between pairs that we were fairly sure had a common ancestor not shared with any member of another pair, and these contrasts could then be safely assumed to be independent."

Below the species level, populations are not independent data points, because several mainland populations, at least, may share a phylogenetic history, and also because males and females from the same population were treated as independent, which they surely are not. However, the lack of phylogenetic hypotheses for populations within virtually all species in our database, as well as gene flow between mainland populations, prevents us from using phylogenetic correction methods with data for all populations (Garland et al. 1999).

In order to avoid inflating the number of the degrees of freedom, we computed the mean variability of all insular populations within each species, and of all mainland populations within each species (note that when the same mainland population was used as the source population for more than one insular population, its variability was used only once when we computed the mean), and we ran the paired test using species averages only. Such a paired design is recommended by Garland et al. (1999) for comparing populations within species. In addition, we ran independent-contrasts analysis on the species-averaged data. We constructed a phylogeny of all species using the supertree of Bininda-Emonds et al. (1999), with island-mainland pairs as sister OTUs (operational taxonomic units) with branch lengths of 10 000 years (roughly the time since separation of almost all the islands that we are dealing with from their near mainland). Canine or CBL CV in this analysis is one variable, island or mainland is the other. Performing contrasts using the generalized least squares approach allows for a *t* test-like model, in which the null hypothesis is that island-mainland contrasts are zero. Independent contrasts were computed using the CAIC (Comparative Analysis by Independent Contrasts) software (version 2.6; Purvis and Rambaut 1995). However, because of the problems associated with averaging population data and the inherent lack of power resulting from the more than fourfold reduction in the number of degrees of freedom, results of this analysis should be viewed as conservative.

We therefore also retain the original, population-level analysis because of the extremely labile nature of population variability (Berry 1998). High lability of the dependent variable probably makes the correction for variation between populations of the same species overly conservative, as is often the case when "controlling for phylogeny" of highly labile traits (Felsenstein 1985, Gittleman et al. 1996, Bjorklund 1997, Cunningham et al. 1998, Losos and Glor 2003).

Although populations within species are independent from evolution at higher levels, different phylogenetic

trajectories can cause the degree of variability between islands and mainlands to differ between different clades within the Carnivora. To test for such an interaction between phylogeny and variability, we compared patterns in different carnivore families to those of the entire order. We also ran a nested ANOVA, with the difference in cv between insular and mainland population as the dependent variable, and examined the percentage of variance in the ranks of family, genus, and species. This procedure can control for most of the phylogenetic signal within the data (Bell 1989, Smith 1994).

We also examined whether body size affects the magnitude and direction of the difference in insular vs. mainland variability, using a Spearman rank correlation test. Body mass was calculated as the midpoint of mass of specimens of a morphospecies measured in this study. When such data were unavailable, we used masses (for the sexes separately) obtained from the literature. We used the same mass for insular and mainland populations because data for each population are almost always lacking and because, in a previous study (Meiri et al. 2004), we found no consistent differences between body sizes of insular and mainland populations. In a separate analysis, we compared only instances in which the geographic area inhabited by insular populations exceeds that of the mainland population we chose. We did this to examine the degree to which the total area from which specimens originated influences the amount of variation.

We computed SSD as the size ratio of the male mean to the female mean, for cases in which we had data for both sexes on both islands and mainlands. We used ratios to avoid statistical problems associated with the use of residuals (Smith 1999). The use of ratios is justified both because ratios dominate the ecological literature (Dayan and Simberloff 1998) and because most objections to their use are unjustified: our paired testing procedure should encounter none of the difficulties associated with dealing with such ratios (discussed in Smith [1999]).

We compared the degree of SSD between islands and their nearest mainlands with the Wilcoxon matched-pairs test. All statistical tests were run with STATISTICA 6 software (StatSoft Israel 2004).

RESULTS

The cvs for the different island-mainland pairs are shown in Appendices A and B. Canine cvs of 155 population pairs belonging to 37 species and CBL cvs of 152 population pairs belonging to 36 species were compared. In total, 39 carnivore species in seven of the eight fissioned families are represented. A Wilcoxon matched-pairs test revealed that, for both morphological variables, cvs of insular populations were lower than those of mainland ones (for canines, $n = 155$, $T = 4171.5$, $P = 0.0008$; for CBL, $n = 152$, $T = 3334.5$, $P < 0.00001$). cvs were also lower on islands for each

sex, for both canines (for females, $n = 66$, $T = 743$, $P = 0.021$; for males, $n = 89$, $T = 1405.5$, $P = 0.015$) and CBL (for females, $n = 65$, $T = 636$, $P = 0.007$; for males, $n = 87$, $T = 1080$, $P = 0.0004$). The differences in cv of mainland and insular populations were not correlated with body mass for either variable (Spearman rank correlation: for canines, $r = 0.021$, $P = 0.791$; for CBL, $r = 0.038$, $P = 0.645$).

There were no differences in the canine cvs of insular and mainland values when species averages were compared ($n = 37$ species, $T = 237$, $P = 0.202$), but data on CBL suggested that insular cv may be higher ($n = 36$ species, $T = 226$, $P = 0.093$). Independent-contrasts analysis did not reveal significant differences between insular and mainland cvs (t test for single means: canines, $n = 37$, $t = 1.30$, $P = 0.20$; for CBL, $n = 36$, $t = 1.36$, $P = 0.18$).

When we selected only cases in which the geographical area of the insular populations exceeded that of the mainland ones, variability was not significantly greater on the mainlands for canines (Wilcoxon matched-pairs test, $n = 29$, $T = 149$, $P = 0.139$), but it was for CBL ($n = 28$, $T = 99$, $P = 0.018$), as it is in the whole sample. Furthermore, the differences between insular and mainland cvs did not differ significantly between pairs in which the islands are larger and those where they are smaller than the corresponding mainland, for either trait (Mann-Whitney U test: for canines, $U = 1834$, $P = 0.973$; for CBL, $U = 1525$, $P = 0.288$).

We compared the frequency of higher vs. lower cv on mainlands in each family to the observed frequency in the entire order. We excluded Herpestidae from this analysis because of small sample size ($n = 3$ for canines, $n = 2$ for CBL). Only one family (Felidae), and only for CBL, showed a different pattern than that for carnivores as a whole (13 instances of higher variation on the islands vs. eight on the mainlands, $P < 0.019$). This result is not significant if we apply a correction for multiple testing (Rice 1989, Cabin and Mitchell 2000).

A nested ANOVA revealed that only at the species level, and only for CBL, did the taxonomic category affect the difference between insular and mainland populations (canine diameter: family, $F = 0.7$, $P = 0.65$; genus, $F = 1.44$, $P = 0.14$; species, $F = 1.12$, $P = 0.35$. CBL: family, $F = 1.26$, $P = 0.28$; genus, $F = 0.92$, $P = 0.55$; species, $F = 1.76$, $P = 0.049$).

The degree of sexual size dimorphism in canine diameter was similar on islands and mainlands (Fig. 1; Wilcoxon matched-pairs test, $n = 55$, $T = 684$, $P = 0.614$). The same was true for CBL (Fig. 2; Wilcoxon matched-pairs test, $n = 52$, $T = 658$, $P = 0.778$). Results were virtually identical when we analyzed logs of ratios rather than raw ratios (cf. Smith 1999).

DISCUSSION

Islands usually have fewer species than the nearby mainland (MacArthur and Wilson 1967, Whittaker

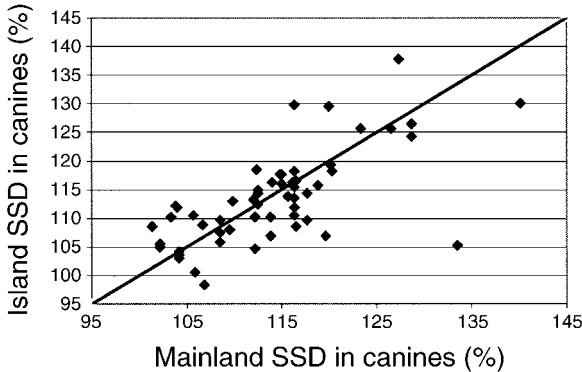


FIG. 1. Sexual size dimorphism (SSD) in canine diameter of island carnivore populations as a function of the SSD of the corresponding mainland populations. SSD is calculated as mean male size divided by mean female size. The line of equality is shown (not a regression line).

1998). The islands in our sample are no exception: the only island with a carnivore community as diverse as that of the mainland is Sumatra (30 species, the same as in the Malay Peninsula south of the Isthmus of Kra). The situation is much the same at the family level: the only case in which an island has more species of a carnivore family is the mustelids on Sumatra (nine species vs. seven on the mainland).

However, continuous variability is usually higher on the mainland, exactly opposite to the prediction of the niche variation hypothesis. When we use average values and phylogenetic comparative methods, the pattern disappears, but the hypothesis remains unsupported. Sexual size dimorphism does not differ consistently between islands and mainlands. It is not that there are no cases in which variation or SSD is greater on the islands. In Appendix A, for instance, insular variation in canines is higher in 58 of 155 cases (and for CBL in 47 out of 152), sometimes markedly so (e.g., Honshu vs. East Asian female *Mustela sibirica*). These cases may indeed stem from exactly the mechanism posited by the niche variation model (Van Valen 1965), but this minority result obviously cannot be considered as an ecological generalization.

These figures do, however, point to the danger of selecting only one species as a model for animals as a whole: choosing one species at random would have a high probability of arriving at a wrong conclusion in this case. We agree with Rothstein (1973) that such an analysis requires a large, diverse database.

What causes the greater variability of mainland populations in most cases? The fact that the area from which mainland populations were sampled was often somewhat larger than that of the area from which insular populations were sampled cannot explain the entire pattern. When we limit the geographic range of the mainland areas from which populations were sampled, cv for CBL is still smaller on the islands. Areal size is not perceived as influencing variability per se, but

rather as acting through greater habitat diversity (Grant 1967, 1979). It is unlikely that the large islands in Appendix A and B are consistently less diverse in habitats than the corresponding mainlands (e.g., Britain has greater elevational and latitudinal ranges than Belgium and The Netherlands). Thus, we suspect that habitat diversity is not responsible for the greater variation on the mainland. Genetic bottlenecks affecting insular populations (Berry 1998) are also not a very likely cause, as some introduced mammals show extremely rapid morphological changes in their new settings (Yom Tov et al. 1986, 1999, Dayan and Simberloff 1994, Berry 1998, Simberloff et al. 2000). All insular carnivores in our database (except *Urocyon littoralis*, isolated since the late Pleistocene; Nowak 1999) inhabit land-bridge islands isolated as early as the early Holocene. If variability is adaptive, significant evolutionary change would have had enough time to occur. We are left with gene flow as the major mechanism generating diversity in mainland populations. Especially in large, mobile animals such as carnivores, gene flow between populations might continually replenish variation lost to selection or drift.

In theory (Soulé and Stewart 1970, Rothstein 1973), SSD, rather than continuous variability, is more likely to be elevated on islands, enabling the sexes to specialize on different foods. Empirical evidence (Ebenman and Nilsson 1982, Dayan and Simberloff 1994, Nagorsen 1994; but see Simberloff et al. 2000, Blondel et al. 2002) often supports this prediction. Carnivores, however, do not show a consistent direction in differences in the degree of SSD between islands and nearby mainlands.

Sexual size dimorphism often results from selective pressures related to sexual selection. For example, selective pressures related to competition between males, such as agonistic behavior and threat displays, probably play an important role in the evolution of carnivore SSD (Erlinge 1979, Lüps and Roper 1988, Holmes and

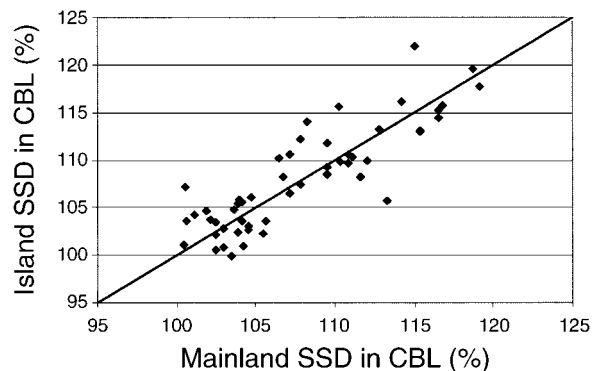


FIG. 2. Sexual size dimorphism in skull length (CBL) of island carnivore populations as a function of the SSD of the corresponding mainland populations. SSD is calculated as mean male size divided by mean female size. The line of equality is shown (not a regression line).

Powell 1994, Gittleman and Van Valkenburgh 1997). In some species, increased SSD may have been selected to facilitate resource partitioning between sexes (Brown and Lasiewski 1972, Simms 1979, Shine 1989, Dayan et al. 1989, Dayan and Simberloff 1998, Johnson and Macdonald 2001).

We do not suggest, however, that our data point to the existence of any phylogenetic constraints, because there can be fairly large differences between insular and mainland populations in the degree of variability and SSD. The highest degree of difference between insular and mainland degrees of SSD is shown in the most dimorphic species (*Mustela* spp.): the highest differences in canine SSD, in both directions (either insular or mainland populations more dimorphic) are found in *Mustela erminea* (SSD in Ireland is 129.9% vs. 116.4% in Britain, on Vancouver Island it is 105.2% vs. 133.4% on the mainland). Large differences in the degree of SSD in both directions are also found in other species (e.g., *Meles meles*). Sexually dimorphic species probably will be dimorphic throughout their ranges, because selective forces related to mating behavior (Lüps and Roper 1988, Gittleman and Van Valkenburgh 1997, Weckerly 1998; see also Johnson and Macdonald 2001) will probably be present throughout a species' range. However, the exact degree of SSD for different populations of these species often differs geographically (e.g., Ralls and Harvey 1985, Dayan and Simberloff 1994, Nagorsen 1994, Lynch et al. 1996, 1997). That SSD does not always differ in the same direction between islands and mainlands cannot be taken as evidence that this trait is in any way constrained to be invariant.

Be that as it may, the niche variation hypothesis predicts that SSD in canines will increase on the more species-depauperate islands. The fact that there are no such consistent differences in the degree of SSD between islands and mainlands implies that interspecific competition is not generally weaker on islands despite lower carnivore species richness, or that the insular resource base is also restricted, therefore restricting the range of adaptive variation. Alternatively, the hypothesis that greater SSD will evolve to enable a species to "fill" an empty niche may simply be incorrect. Individual cases in which SSD is smaller on islands may indeed result from a more restricted food niche, whereas cases in which the situation is reversed may attest to insular character release. In any event, the null hypothesis, that insular populations are no more likely than mainland ones to have greater SSD, is not falsified. It is interesting to note, in this respect, that there is a relationship between a higher degree of insular SSD and higher CVs on the same island (and vice versa) for CBL; in 33 of 52 cases, the difference of insular vs. mainland SSD and the difference of insular vs. mainland CV (calculated as the average of male and female CVs) have the same sign ($\chi^2 = 5.42$, $P = 0.020$). No such pattern is apparent for canines; the

sign is the same in 30 of 55 cases, not significantly more than expected (expected values are based on the frequency of the signs actually observed; $\chi^2 = 0.10$, $P = 0.753$).

Niches and morphospace do not "exist" without the organisms that occupy them (Gould 2002). The width of a niche is usually thought to be inversely proportional to the number of sympatric species within a guild (Rothstein 1973), but is this really so? Are the niches of peninsular Malaysian cats really narrower than those of Borneo cats because Malaya has eight species of cats and Borneo merely five? The largest felid on Borneo is the clouded leopard (*Neofelis nebulosa*), whereas peninsular Malaysia also harbors two larger felid species: the leopard (*Panthera pardus*) and tiger (*P. tigris*), and both locations have the same species of small cats (*Felis planiceps*, *F. marmorata*, and *F. bengalensis*). Hence the realized morphospace in Borneo is smaller, whereas realized species niches might actually resemble those of the mainland. Also in Southeast Asia, Sumatra has seven cat species, and the nearby island of Java has only four, but the largest of the Java cats (tiger) is larger than its Sumatran conspecific (Meiri 2004), whereas the smallest guild member (*F. bengalensis*) is smaller on Java (Meiri et al. 2004). The often-smaller variability and similar degree of SSD of insular carnivores may result from shrinkage of the whole Eltonian food pyramid. Insular faunas differ from mainland ones not only in faunal composition, but also in the sizes even of the same species. Population densities also often differ between mainland and insular conspecifics. Treating carnivore insular niches as wider owing to the existence of fewer competitors ignores the fact that the number, and perhaps size distribution, of potential prey may also be smaller on islands.

In sum, it appears that mainland populations are as variable as insular ones, or even more variable, possibly reflecting gene flow. There are no consistent differences in the degree of SSD between islands and mainlands, further undermining the notion of wider insular niches. As for realized niche width, the situation is obscure. Even in relation to simple variables such as diet, it is very difficult to give an account of an organism's niche, because the resource base is largely unknown. We concur with Van Valen (1965) that no a priori prediction that islands will have narrower niches than mainlands can be given with assurance.

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LITERATURE CITED

- Adersen, H. 1995. Research on Islands: classic, recent and prospective approaches. Pages 7–21 in P. M. Vitousek, L. L. Loope, and H. Adersen, editors. *Islands. Biological diversity and ecosystem function*. Springer-Verlag, Berlin, Germany.
- Arjo, W. M., D. H. Pletscher, and R. R. Ream. 2002. Dietary overlap between wolves and coyotes in northwestern Montana. *Journal of Mammalogy* **83**:754–766.
- Bell, G. 1989. A comparative method. *American Naturalist* **133**:553–571.
- Berry, R. J. 1998. Evolution of small mammals. Pages 35–50 in P. R. Grant, editor. *Evolution on islands*. Oxford University Press, Oxford, UK.
- Biknevicius, A. R., and B. Van Valkenburgh. 2001. Design for killing: craniodental adaptations of predators. Pages 393–428 in J. L. Gittleman, editor. *Carnivore behavior, ecology, and evolution*. Volume 2. Cornell University Press, Ithaca, New York, USA.
- Bininda-Emonds, O. R. P., J. L. Gittleman, and A. Purvis. 1999. Building large trees by combining phylogenetic information: a complete phylogeny of the extant Carnivora (Mammalia). *Biological Reviews* **74**:143–175.
- Bjorklund, M. 1997. Are “comparative methods” always necessary? *Oikos* **80**:607–612.
- Blondel, J., P. Perret, M.-C. Ansett, and C. Thebaud. 2002. Evolution of sexual size dimorphism in birds: test of hypotheses using blue tits in contrasted Mediterranean habitats. *Journal of Evolutionary Biology* **15**:440–450.
- Brown, J. H., and R. C. Lasiewski. 1972. Metabolism of weasels: the cost of being long and thin. *Ecology* **53**:939–943.
- Cabin, R. J., and R. J. Mitchell. 2000. To Bonferroni or not to Bonferroni: when and how are the questions? *Bulletin of the Ecological Society of America* **81**:246–248.
- Cunningham, C. W., K. E. Omland, and T. H. Oakley. 1998. Reconstructing ancestral character states: a critical reappraisal. *Trends in Ecology and Evolution* **13**:361–366.
- Cypher, B. L. 1993. Food item use by three sympatric canids in southern Illinois. *Transactions of the Illinois State Academy of Science* **86**:139–144.
- Darwin, C. R. 1871. *The descent of man and selection in relation to sex*. John Murray, London, UK.
- Dayan, T., and D. Simberloff. 1994. Character displacement, sexual size dimorphism, and morphological variation among British and Irish mustelids. *Ecology* **75**:1063–1073.
- Dayan, T., and D. Simberloff. 1998. Size patterns among competitors: ecological character displacement and character release in mammals, with special reference to island populations. *Mammal Review* **28**:99–124.
- Dayan, T., D. Simberloff, E. Tchernov, and Y. Yom-Tov. 1989. Inter- and intraspecific character displacement in mustelids. *Ecology* **70**:1526–1539.
- Dayan, T., D. Simberloff, E. Tchernov, and Y. Yom-Tov. 1990. Feline canines: community-wide character displacement in the small cats of Israel. *American Naturalist* **136**:39–60.
- Dayan, T., D. Simberloff, E. Tchernov, and Y. Yom-Tov. 1992. Canine carnassials: character displacement in the wolves, jackals and foxes of Israel. *Biological Journal of the Linnean Society* **45**:315–331.
- Dayan, T., D. Wool, and D. Simberloff. 2002. Variation and covariation of skulls and teeth: modern carnivores and the interpretation of fossil mammals. *Paleobiology* **28**:508–526.
- Dennison, M. D., and A. J. Baker. 1991. Morphometric variability in continental and Atlantic island populations of chaffinches (*Fringilla coelebs*). *Evolution* **45**:29–39.
- Dunham, A. E., D. W. Tinkle, and J. W. Gibbons. 1978. Body size in island lizards: a cautionary tale. *Ecology* **59**:1230–1238.
- Ebenman, B. 1986. Sexual size dimorphism in the great tit *Parus major* in relation to the number of coexisting congeners. *Oikos* **47**:355–359.
- Ebenman, B., and S. G. Nilsson. 1982. Components of niche width in a territorial bird species: habitat utilization in males and females of the chaffinch (*Fringilla coelebs*) on islands and mainland. *American Naturalist* **119**:331–344.
- Erlinge, S. 1979. Adaptive significance of sexual dimorphism in weasels. *Oikos* **33**:233–245.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist* **70**:1–15.
- Forman, R. T. T. 1995. *Land mosaics. The ecology of landscapes and regions*. Cambridge University Press, Cambridge, UK.
- Garland, T., Jr., P. E. Midford, and A. R. Ives. 1999. An introduction to phylogenetically based statistical methods, with a new method for confidence intervals on ancestral values. *American Zoologist* **39**:374–388.
- Gittleman, J. L. 1985. Carnivore body size: ecological and taxonomic correlates. *Oecologia* **67**:540–554.
- Gittleman, J. L., C. G. Anderson, M. Kot, and H. K. Luh. 1996. Phylogenetic lability and rates of evolution: a comparison of behavioral, morphological and life history traits. Pages 166–205 in E. P. Martins, editor. *Phylogenies and the comparative method in animal behavior*. Oxford University Press, Oxford, UK.
- Gittleman, J. L., and B. Van Valkenburgh. 1997. Sexual dimorphism in the canines and skulls of carnivores: effects of size, phylogeny and behavioural ecology. *Journal of Zoology* **242**:97–117.
- Gliwicz, J. 1988. Sexual dimorphism in small mustelids: body diameter limitation. *Oikos* **53**:411–414.
- Gould, S. J. 1975. On the scaling of tooth size in mammals. *American Zoologist* **15**:351–362.
- Gould, S. J. 2002. *The structure of evolutionary theory*. Harvard University Press, Cambridge, Massachusetts, USA.
- Grant, P. R. 1967. Bill length variability in birds of the Tres Marias Islands, Mexico. *Journal of Zoology* **45**:805–815.
- Grant, P. R. 1979. Ecological and morphological variation of Canary Island blue tits, *Parus caeruleus* (Aves: Paridae). *Biological Journal of the Linnean Society* **11**:103–129.
- Holmes, T. and R. A. Powell. 1994. Morphology, ecology and the evolution of sexual dimorphism in North American *Martes*. Pages 72–84 in S. W. Buskirk, A. S. Harestad, M. G. Raphael, and R. A. Powell, editors. *Martens, sables, and fishers: biology and conservation*. Comstock Publishing Associates, Ithaca, New York, USA.
- Johnson, D. D. P., and D. W. Macdonald. 2001. Why are group-living badgers (*Meles meles*) sexually dimorphic? *Journal of Zoology* **255**:199–204.

- Johnson, W. E., T. K. Fuller, and W. L. Franklin. 1996. Sympatry in Canids: a review and assessment. Pages 189–218 in J. L. Gittleman, editor. Carnivore behaviour, ecology, and evolution. Volume 2. Cornell University Press, Ithaca, New York, USA.
- Jones, M. 1997. Character displacement in Australian dasyurid carnivores: size relationships and prey size patterns. *Ecology* **78**:2569–2587.
- Kiltie, R. A. 1988. Interspecific size regularities in tropical felid assemblages. *Oecologia* **76**:97–105.
- Kruuk, H. 2002. Hunter and hunted. Relationships between carnivores and people. Cambridge University Press, Cambridge, UK.
- Lande, R. 1979. On comparing coefficients of variation. *Systematic Zoology* **26**:214–217.
- Levins, R. 1968. Evolution in changing environments. Princeton University Press, Princeton, New Jersey, USA.
- Lewontin, R. C. 1966. On the measurement of relative variability. *Systematic Zoology* **15**:141–142.
- Losos, J. B. and R. E. Glor. 2003. Phylogenetic comparative methods and the geography of speciation. *Trends in Ecology and Evolution* **18**:220–227.
- Loveridge, A. J., and D. W. Macdonald. 2002. Habitat ecology of two sympatric species of jackals in Zimbabwe. *Journal of Mammalogy* **83**:599–607.
- Lüps, P., and T. J. Roper. 1988. Tooth size in the European badger (*Meles meles*) with special reference to sexual dimorphism, diet and intraspecific aggression. *Acta Theriologica* **33**:21–33.
- Lynch, J. M., J. H. H. Conroy, A. C. Kitchener, D. J. Jefferies, and T. J. Hayden. 1996. Variation in cranial form and sexual dimorphism among five European populations of the otter *Lutra lutra*. *Journal of Zoology* **238**:81–96.
- Lynch, J. M., R. Whelan, A. I. IlFituri, and T. J. Hayden. 1997. Craniometric variation in the Eurasian badger, *Meles meles*. *Journal of Zoology* **242**:31–44.
- MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.
- Macdonald, D. W. 1992. The velvet claw. a natural history of the carnivores. BBC Books, London, UK.
- Madsen, T., and R. Shine. 1993. Phenotypic plasticity in body sizes and sexual dimorphism in European grass snakes. *Evolution* **47**:321–325.
- Major, J. T., and J. A. Sherburne. 1987. Interspecific relationships of coyotes, bobcats, and red foxes in western Maine. *Journal of Wildlife Management* **51**:606–616.
- Malmquist, M. G. 1985. Character displacement and biogeography of the pygmy shrew in northern Europe. *Ecology* **66**:372–377.
- Meiri, S. 2004. Carnivore body size: aspects of geographic variation. Dissertation. Tel Aviv University, Tel Aviv, Israel.
- Meiri, S., T. Dayan, and D. Simberloff. 2004. Body size of insular carnivores: little support for the island rule. *American Naturalist* **163**:469–479.
- Nagorsen, D. W. 1994. Body weight variation among insular and mainland American martens. Pages 85–97 in S. W. Buskirk, A. S. Harestad, M. G. Raphael, and R. A. Powell, editors. Martens, sables, and fishers: biology and conservation. Comstock Publishing Associates, Ithaca, New York, USA.
- Nowak, R. M. 1999. Walker's Mammals of the world. Sixth edition. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Palomares, F., and T. M. Caro. 1999. Interspecific killing among mammalian carnivores. *American Naturalist* **153**:492–508.
- Patterson, B. D. 1983. Grasshopper mandibles and the niche variation hypothesis. *Evolution* **37**:375–388.
- Pearson, D., R. Shine, and A. Williams. 2002. Geographic variation in sexual size dimorphism within a single snake species (*Morelia spilota*, Pythonidae). *Oecologia* **131**:418–426.
- Pengilly, D. 1984. Developmental versus functional explanation for patterns of variability and correlation in the dentition of foxes. *Journal of Mammalogy* **63**:34–43.
- Polly, P. D. 1998. Variability in mammalian dentitions: size-related bias in the coefficient of variation. *Biological Journal of the Linnean Society* **64**:83–99.
- Prinzing, A., W. Durka, S. Klotz, and R. Brandl. 2002. Geographic variability of ecological niches of plant species: are competition and stress relevant? *Ecography* **25**:721–729.
- Purvis, A., and A. Rambaut. 1995. Comparative analysis by independent contrasts (CAIC): an Apple Maintosh application for analysing comparative data. *Computer Applications in the Biosciences [CABIOS, now Bioinformatics]* **11**:247–251.
- Ralls, K., and P. H. Harvey. 1985. Geographic variation in size and sexual dimorphism of North American weasels. *Biological Journal of the Linnean Society* **25**:119–167.
- Rausch, R. L. 1963. Geographic variation in size in North American brown bears, *Ursus arctos* L., as indicated by condylobasal length. *Canadian Journal of Zoology* **41**:33–45.
- Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution* **43**:223–225.
- Roberts, T. J. 1977. The mammals of Pakistan. Ernest Benn, London.
- Rothstein, S. I. 1973. Niche-variation model—Is it valid? *American Naturalist* **107**:598–620.
- Shine, R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Quarterly Review of Biology* **64**:419–461.
- Simberloff, D., T. Dayan, C. Jones, and G. Ogura. 2000. Character displacement and release in the small Indian mongoose, *Herpestes javanicus*. *Ecology* **81**:2086–2099.
- Simms, D. A. 1979. North American weasels: resource utilization and distribution. *Canadian Journal of Zoology* **57**:504–520.
- Smith, R. J. 1994. Degrees of freedom in interspecific allometry: an adjustment for the effects of phylogenetic constraint. *American Journal of Physical Anthropology* **93**:95–107.
- Smith, R. J. 1999. Statistics of sexual size dimorphism. *Journal of Human Evolution* **36**:423–459.
- Soulé, M., and B. R. Stewart. 1970. The “niche variation” hypothesis: a test and alternatives. *American Naturalist* **104**:85–97.
- StatSoft Israel. 2004. STATISTICA 6. StatSoft Israel, Kefar Saba, Israel.
- Szuma, E. 2000. Variation and correlation patterns in the dentition of the red fox from Poland. *Annales Zoologici Fennici* **37**:113–127.
- Thurber, J. M., R. O. Peterson, J. D. Woolington, and J. A. Vucetich. 1992. Coyote coexistence with wolves on the Kenai Peninsula, Alaska. *Canadian Journal of Zoology* **70**:2494–2498.
- Van Valen, L. M. 1965. Morphological variation and the width of the ecological niche. *American Naturalist* **99**:377–390.
- Van Valkenburgh, B., and C. B. Ruff. 1987. Canine tooth strength and killing behaviour in large carnivores. *Journal of Zoology* **212**:379–397.
- Van Valkenburgh, B., and R. K. Wayne. 1994. Shape divergence associated with size convergence in sympatric East African jackals. *Ecology* **75**:1567–1581.
- Von den Driesch, A. 1976. A guide to the measurement of animal bones from archaeological sites. Peabody Museum

- Bulletin I, Harvard University, Cambridge, Massachusetts, USA.
- Weckerly, F. W. 1998. Sexual-size dimorphism: influence of mass and mating systems in the most dimorphic mammals. *Journal of Mammalogy* **79**:33–52.
- Whittaker, R. 1998. *Island biogeography—ecology, evolution and conservation*. Oxford University Press, Oxford, UK.
- Yom-Tov, Y., W. O. Green, and J. D. Coleman. 1986. Morphological trends in the common brushtail possum, *Trichosurus vulpecula* in New Zealand. *Journal of Zoology* **208**:583–593.
- Yom-Tov, Y., S. Yom-Tov, and H. Møller. 1999. Competition, coexistence and adaptation amongst rodent invaders to Pacific and New Zealand islands. *Journal of Biogeography* **26**:947–958.

APPENDIX A

A table showing sample sizes, coefficients of variation of canine diameters, and body masses in island and nearest mainland population pairs is available in ESA's Electronic Data Archive: *Ecological Archives* EO86-078-A1.

APPENDIX B

A table showing sample sizes, coefficients of variation of skull length (CBL), and body masses in island and nearest mainland population pairs is available in ESA's Electronic Data Archive: *Ecological Archives* EO86-078-A2.

Ecological Archives E086-078-A2

Shai Meiri, Tamar Dayan, and Daniel Simberloff. 2005. Variability and sexual size dimorphism in carnivores: testing the niche variation hypothesis. *Ecology* 86:1432–1440.

Appendix B (Table B1). Sample sizes, coefficients of variation of skull length (CBL) and body masses in island and nearest-mainland population pairs. See [Notes](#) at end of table for details.

Species	Sex	Island	Sample size	Mainland	Sample size	Island CV	Mainland CV	log body mass (g)
<i>Alopex lagopus</i>	M	Flaherty	5	Quebec N. of 55N	21	2.95	3.51	3.53
<i>Alopex lagopus</i>	F	St. Lawrence	52	Alaska W. of 159W	18	2.48	2.90	3.42
<i>Alopex lagopus</i>	M	St. Lawrence	57	Alaska W. of 159W	21	2.68	2.35	3.53
<i>Alopex lagopus</i>	F	St. Matthew	7	Alaska W. of 159W	18	3.50	2.90	3.42
<i>Alopex lagopus</i>	M	St. Matthew	9	Alaska W. of 159W	21	1.58	2.35	3.53
<i>Aonyx cinerea</i>	F	Java	17	Sumatra	6	3.66	2.47	3.48 ³
<i>Arctogalidia trivirgata</i>	F	Borneo	24	Indochina S. of 16N	7	2.86	3.27	3.19 ⁵
<i>Arctogalidia trivirgata</i>	M	Borneo*	24	Malay Peninsula S. Of 7N	8	3.84	3.67	3.38 ⁶
<i>Arctogalidia trivirgata</i>	F	Sumatra	8	Indochina S. of 16N	7	2.10	3.27	3.19 ⁵
<i>Bassariscus astutus</i>	F	Espiritu Santo	8	Baja California S. of 27N	11	1.43	1.58	2.95 ¹
<i>Bassariscus astutus</i>	M	Espiritu Santo	6	Baja California S. of 27N	7	1.71	1.75	3.00 ¹
<i>Bassariscus astutus</i>	F	San Jose	6	Baja California S. of 27N	11	1.44	1.58	2.95 ¹
<i>Bassariscus astutus</i>	M	San Jose	6	Baja California S. of 27N	7	1.31	1.75	3.00 ¹
<i>Canis aureus</i>	M	Sri Lanka	5	India S. of 20N	14	4.98	3.03	4.05 ⁶
<i>Canis lupus</i>	F	Prince of Wales	15	Alaska and BC, 54-60N, 127-135W	15	2.77	3.79	4.52 ⁶
<i>Canis lupus</i>	M	Prince of Wales	11	Alaska and BC, 54-60N, 127-133W	10	3.11	3.67	4.54 ⁶
<i>Canis lupus</i>	F	Vancouver Island	27	BC S. of 55N, W of 120W	7	3.22	1.79	4.52 ⁶
<i>Canis lupus</i>	M	Vancouver Island	35	BC S. of 55N, W of 120W	11	3.31	5.00	4.54 ⁶
<i>Felis benegalensis</i>	M	Bali	5	Java	18	4.16	4.33	3.52 ⁶
<i>Felis benegalensis</i>	F	Borneo*	6	Malay Peninsula S. Of 7N	6	3.32	2.64	3.35 ⁶
<i>Felis benegalensis</i>	M	Borneo*	12	Malay Peninsula S. Of 12N	5	3.64	2.81	3.52 ⁶
<i>Felis benegalensis</i>	F	Java	24	Sumatra	9	3.24	4.54	3.35 ⁶
<i>Felis benegalensis</i>	M	Java	19	Sumatra	7	5.78	4.22	3.52 ⁶
<i>Felis benegalensis</i>	F	Sumatra*	9	Malay Peninsula S. Of 7N	6	4.54	2.64	3.35 ⁶
<i>Felis benegalensis</i>	M	Sumatra*	7	Malay Peninsula S. Of 12N	5	4.22	2.81	3.52 ⁶
<i>Felis concolor</i>	F	Vancouver Island	13	BC and Washington 47-55N, W of 120W	5	4.16	4.00	4.63 ⁶
<i>Felis lynx</i>	M	Newfoundland	26	SE Canada and Maine S. of 55N, E of 67W	5	4.13	3.42	3.94
<i>Felis planiceps</i>	M	Borneo*	9	Malay Peninsula S. of 6N	9	4.15	5.73	3.20 ⁶
<i>Felis silvestris</i>	M	Britain	21	Belgium and France N. of 47N	6	5.16	6.00	3.70 ¹
<i>Herpestes smithii</i>	M	Sri Lanka	9	India S. of 19N	5	5.20	2.99	3.32 ¹
<i>Herpestes urva</i>	F	Taiwan	10	China S. of 27N, E. of 118E	5	3.32	1.68	3.30 ¹
<i>Lontra canadensis</i>	M	Baranof	7	Alaska and BC, 56-60N, 126-140W	7	2.76	2.86	3.93
<i>Lontra canadensis</i>	M	Chichagof	6	Alaska and BC, 56-60N, 126-140W	7	2.20	2.86	3.93
<i>Lontra canadensis</i>	M	Prince of Wales	5	Alaska and BC, 56-60N, 126-140W	7	0.43	2.86	3.93
<i>Lontra canadensis</i>	F	Vancouver Island	8	BC and Washington 47-55N, W. of 122W	14	3.55	2.36	3.91
<i>Lutra lutra</i>	F	Britain	9	Belgium and France N. of 47N	6	3.73	4.40	3.83 ⁶
<i>Lutra lutra</i>	F	Ireland	15	Britain	9	2.10	3.73	3.83 ⁶
<i>Lutra lutra</i>	M	Ireland	18	Britain	10	2.58	3.36	4.00 ⁶
<i>Lutra lutra</i>	F	Sri Lanka	8	India S. of 26N	6	5.07	3.57	3.83 ⁶
<i>Martes americana</i>	F	Chichagof	34	Alaska & BC 54-60N, 129-135W	19	2.92	3.75	2.80

Species	Sex	Island	Sample size	Mainland	Sample size	Island CV	Mainland CV	log body mass (g)
<i>Martes americana</i>	M	Chichagof	53	Alaska and BC 54-60N, 129-136W	20	2.38	2.71	3.14
<i>Martes americana</i>	F	Louise	9	Moresby	15	1.32	1.98	2.80
<i>Martes americana</i>	M	Louise	7	Moresby	33	1.98	1.41	3.14
<i>Martes americana</i>	F	Mitkof	16	Alaska and BC 54-60N, 129-135W	19	3.40	3.75	2.80
<i>Martes americana</i>	M	Mitkof	26	Alaska and BC 54-60N, 129-136W	20	2.80	2.71	3.14
<i>Martes americana</i>	F	Moresby	15	BC 51-55N, W. of 126W	13	1.98	2.00	2.80
<i>Martes americana</i>	M	Moresby	33	BC 51-55N, W. of 126W	16	1.41	2.96	3.14
<i>Martes americana</i>	F	Prince of Wales	8	Alaska and BC 54-60N, 129-135W	19	1.81	3.75	2.80
<i>Martes americana</i>	M	Prince of Wales	12	Alaska and BC 54-60N, 129-136W	20	1.27	2.71	3.14
<i>Martes americana</i>	F	Vancouver Island	83	BC and Washington 45-54N, W. of 121W	25	2.12	4.36	2.80
<i>Martes americana</i>	M	Vancouver Island	119	BC and Washington 45-54N, W. of 121W	44	1.99	3.32	3.14
<i>Martes flavigula</i>	F	Borneo*	18	Malay Peninsula S. of 9N	11	2.31	2.61	3.40 ⁷
<i>Martes foina</i>	M	Sjaelland	10	Denmark (Jutland)	5	2.57	2.49	3.13
<i>Martes martes</i>	M	Sjaelland	8	Denmark (Jutland)	6	1.20	1.42	3.22 ⁷
<i>Meles meles</i>	F	Britain*	13	Belgium and the Netherlands	9	4.64	2.82	4.00 ⁷
<i>Meles meles</i>	M	Britain*	26	Belgium	11	3.77	3.64	4.06 ⁷
<i>Meles meles</i>	F	Ireland	31	Britain	13	2.94	4.64	4.00 ⁷
<i>Meles meles</i>	M	Ireland	21	Britain	26	2.05	3.77	4.06 ⁷
<i>Meles meles</i>	F	Sjaelland	14	Denmark (Jutland)	52	2.47	2.76	4.00 ⁷
<i>Meles meles</i>	M	Sjaelland	17	Denmark (Jutland)	55	2.32	2.60	4.06 ⁷
<i>Melogale moschata</i>	F	Hainan	8	Vietnam and China, 21-26N, E of 102E	8	2.12	5.42	2.91
<i>Melogale moschata</i>	F	Taiwan	28	China S. of 30N, E. of 113E	6	2.85	5.51	2.91
<i>Mustela erminea</i>	F	Admiralty	8	Alaska and BC 54-60N, 127-140W	16	2.05	3.30	1.91
<i>Mustela erminea</i>	M	Admiralty	18	Alaska and BC 54-60N, 127-140W	39	3.83	3.92	2.35
<i>Mustela erminea</i>	F	Britain*	58	Belgium	47	4.01	3.60	2.32
<i>Mustela erminea</i>	M	Britain*	66	Belgium	44	3.94	6.22	2.56
<i>Mustela erminea</i>	M	Chichagof	5	Alaska and BC 54-60N, 127-140W	39	4.86	3.92	2.35
<i>Mustela erminea</i>	F	Ireland	46	Britain	58	5.17	4.01	2.32
<i>Mustela erminea</i>	M	Ireland	73	Britain	66	3.81	3.94	2.56
<i>Mustela erminea</i>	M	Kodiak	11	Alaska S. of 61N, W. of 149	18	3.68	4.46	2.35
<i>Mustela erminea</i>	F	Mitkof	9	Alaska and BC 54-60N, 127-140W	16	2.03	3.30	1.91
<i>Mustela erminea</i>	M	Mitkof	18	Alaska and BC 54-60N, 127-140W	39	3.01	3.92	2.35
<i>Mustela erminea</i>	F	Newfoundland*	8	Labrador S. of 54N, E of 58W	9	1.63	3.24	1.91
<i>Mustela erminea</i>	M	Newfoundland*	45	Labrador S. of 54N, E of 58W	35	3.64	4.64	2.35
<i>Mustela erminea</i>	M	Prince of wales	17	Alaska and BC 54-60N, 127-140W	39	4.48	3.92	2.35
<i>Mustela erminea</i>	F	Sjaelland	20	Denmark, Germany and Sweden, 53-60N	6	3.07	4.02	2.32
<i>Mustela erminea</i>	M	Sjaelland	19	Denmark, Germany and Sweden, 53-60N	13	3.86	4.33	2.56
<i>Mustela erminea</i>	F	Tukarak	12	Ontario, 50-60N, 75-90W	5	2.32	2.58	1.91
<i>Mustela erminea</i>	M	Tukarak	12	Ontario and Quebec, 50-60N, 75-90W	18	4.93	4.08	2.35
<i>Mustela erminea</i>	F	Vancouver Island	7	BC and Washington 49-54N, W. of 122W	15	3.09	6.89	1.91
<i>Mustela erminea</i>	M	Vancouver Island	17	BC and Washington 48-54N, W. of 122W	40	2.90	5.64	2.35
<i>Mustela nivalis</i>	F	Britain*	40	Belgium	82	3.93	5.30	1.77 ⁷
<i>Mustela nivalis</i>	M	Britain*	122	Belgium	155	3.73	5.09	2.06 ⁷
<i>Mustela nivalis</i>	F	Sardinia	8	Italy	10	7.86	6.60	1.77 ⁷
<i>Mustela nivalis</i>	M	Sardinia	23	Italy	57	3.50	4.62	2.06 ⁷
<i>Mustela nivalis</i>	M	Sjaelland	9	Denmark, Germany and Sweden, 53-60N	5	3.85	0.44	2.06 ⁷
<i>Mustela putorius</i>	F	Britain*	13	Belgium	45	2.42	6.95	2.84 ⁷
<i>Mustela putorius</i>	M	Britain*	38	Belgium	79	5.70	5.86	3.05 ⁷
<i>Mustela putorius</i>	F	Sjaelland	8	Denmark (Jutland)	8	3.81	2.53	2.84 ⁷

Species	Sex	Island	Sample size	Mainland	Sample size	Island CV	Mainland CV	log body mass (g)
<i>Mustela putorius</i>	M	Sjaelland	16	Denmark (Jutland)	17	4.07	3.39	3.05 ⁷
<i>Mustela sibirica</i>	F	Honshu	13	E Asia, 30-45N, E of 115E	6	6.50	3.06	2.60 ²
<i>Mustela sibirica</i>	M	Honshu	90	E Asia, 30-45N, E of 115E	7	6.28	7.12	2.89
<i>Mustela sibirica</i>	M	Kyushu	5	Honshu	90	10.17	6.28	2.89
<i>Mustela sibirica</i>	M	Sado	9	Honshu	90	3.88	6.28	2.89
<i>Mustela sibirica</i>	M	Shikoku	5	Honshu	90	4.80	6.28	2.89
<i>Mustela vison</i>	M	Admiralty	5	Alaska and BC 55-59N, 127-135W	12	1.59	3.82	3.12
<i>Mustela vison</i>	F	Baranof	13	Alaska and BC 55-59N, 130-135W	9	2.45	3.52	2.89
<i>Mustela vison</i>	M	Baranof	29	Alaska and BC 55-59N, 127-135W	12	3.34	3.82	3.12
<i>Mustela vison</i>	F	Chichagof	7	Alaska and BC 55-59N, 130-135W	9	1.50	3.52	2.89
<i>Mustela vison</i>	M	Chichagof	8	Alaska and BC 55-59N, 127-135W	12	2.18	3.82	3.12
<i>Mustela vison</i>	F	Nunivak	10	Alaska 60-62N, W. of 157W	7	2.75	5.02	2.89
<i>Mustela vison</i>	M	Nunivak	11	Alaska 58-62N, W. of 157W	28	3.04	5.84	3.12
<i>Mustela vison</i>	F	Vancouver Island	19	BC and Washington 48-54N, W. of 121W	13	4.34	4.34	2.89
<i>Mustela vison</i>	M	Vancouver Island	25	BC and Washington 48-54N, W. of 122W	9	3.46	4.76	3.12
<i>Nyctereutes procyonoides</i>	M	Kyushu*	5	GifuPrefecture, Honshu	41	1.63	3.40	3.69
<i>Paguma larvata</i>	F	Borneo*	9	Malay Peninsula S. of 9N	6	3.59	5.47	3.47
<i>Paguma larvata</i>	M	Borneo*	6	Malay Peninsula S. of 9N	6	3.83	4.09	3.78 ⁴
<i>Paguma larvata</i>	F	Sumatra*	9	Malay Peninsula S. of 9N	6	3.24	5.47	3.47
<i>Paguma larvata</i>	M	Sumatra*	5	Malay Peninsula S. of 9N	6	1.41	4.09	3.78 ⁴
<i>Panthera tigris</i>	M	Java	6	Sumatra	6	3.15	4.21	5.08 ³
<i>Panthera tigris</i>	M	Sumatra	6	Malaya, Vietnam and Thailand S. of 17S	7	4.21	4.06	5.34 ³
<i>Paradoxurus hermaphroditus</i>	M	Bali	6	Java	14	6.32	3.90	3.52 ¹
<i>Paradoxurus hermaphroditus</i>	F	Borneo*	11	Malay Peninsula S. of 9N	18	4.36	6.64	3.51 ⁶
<i>Paradoxurus hermaphroditus</i>	M	Borneo*	23	Malay Peninsula S. of 9N	24	3.64	5.63	3.52 ¹
<i>Paradoxurus hermaphroditus</i>	F	Java	31	Sumatra	14	3.51	3.70	3.51 ⁶
<i>Paradoxurus hermaphroditus</i>	M	Java	15	Sumatra	17	3.86	3.26	3.52 ¹
<i>Paradoxurus hermaphroditus</i>	M	Palawan	5	Borneo	23	2.87	3.64	3.52 ¹
<i>Paradoxurus hermaphroditus</i>	F	Sumatra*	14	Malay Peninsula S. of 9N	18	3.70	6.64	3.51 ⁶
<i>Paradoxurus hermaphroditus</i>	M	Sumatra*	17	Malay Peninsula S. of 9N	24	3.26	5.63	3.52 ¹
<i>Paradoxurus hermaphroditus</i>	M	Terutau	7	Malay Peninsula S. of 9N	24	3.53	5.63	3.52 ¹
<i>Procyon lotor</i>	M	Key Largo	9	Florida	20	1.53	4.80	3.93 ⁶
<i>Procyon lotor</i>	M	No name key	5	Florida	20	3.01	4.80	3.93 ⁶
<i>Procyon lotor</i>	F	Vancouver Island	18	Washington N. of 46N, W. of 120W	7	2.42	1.84	3.81 ⁶
<i>Procyon lotor</i>	M	Vancouver Island	17	Washington N. of 46N, W. of 120W	8	2.53	2.55	3.93 ⁶
<i>Urocyon (cinereoargenteus) littoralis</i>	F	San Clemente	5	California, 32-34N, W. of 116W	8	2.77	3.31	3.50 ⁶
<i>Urocyon (cinereoargenteus) littoralis</i>	F	San Miguel	6	California, 33-35N, W. of 117W	10	2.16	2.19	3.50 ⁶
<i>Urocyon (cinereoargenteus) littoralis</i>	F	Santa Catalina	5	California, 32-34N, W. of 116W	8	2.34	3.31	3.59 ⁶
<i>Urocyon (cinereoargenteus)</i>	M	Santa Catalina	6	California, 32-34N, W. of 116W	9	4.18	2.41	3.59 ⁶

Species	Sex	Island	Sample size	Mainland	Sample size	Island CV	Mainland CV	log body mass (g)
<i>Urocyon littoralis</i>								
<i>Urocyon (cinereoargenteus) littoralis</i>	M	Santa Cruz	5	California, 33-35N, W. of 117W	23	2.78	3.35	3.59 ⁶
<i>Urocyon (cinereoargenteus) littoralis</i>	M	Santa Rosa	6	California, 33-35N, W. of 117W	23	3.37	3.35	3.59 ⁶
<i>Ursus americanus</i>	M	Kuiu	6	Kupreanof	5	8.17	3.06	5.19 ⁶
<i>Ursus americanus</i>	M	kupreanof	5	Alaska 55-60N, E. of 132W	10	3.06	4.06	5.19 ⁶
<i>Ursus americanus</i>	M	Vancouver Island	6	BC S. of 55N, W of 122W	7	4.76	3.86	5.19 ⁶
<i>Ursus arctos</i>	F	Admiralty	20	Alaska and BC, 55-60N, 127-140W	11	4.78	5.63	5.48 ¹
<i>Ursus arctos</i>	M	Admiralty	37	Alaska and BC, 54-61N, 127-143W	7	5.98	10.69	5.65 ¹
<i>Ursus arctos</i>	F	Baranof	5	Alaska and BC, 55-60N, 127-140W	11	5.04	5.63	5.48 ¹
<i>Ursus arctos</i>	F	Chichagof	9	Alaska and BC, 55-60N, 127-140W	11	4.12	5.63	5.48 ¹
<i>Ursus arctos</i>	M	Chichagof	11	Alaska and BC, 54-61N, 127-143W	7	8.05	10.69	5.65 ¹
<i>Ursus arctos</i>	F	Kodiak	12	Alaska S. of 60N, W. of 150W	28	2.58	3.70	5.48 ¹
<i>Ursus arctos</i>	M	Kodiak	8	Alaska S. of 60N, W. of 150W	21	2.69	4.61	5.65 ¹
<i>Viverricula indica</i>	F	Hainan	8	China, 15-26N, E of 102E	14	1.46	2.83	3.41
<i>Viverricula indica</i>	M	Hainan	5	China, 15-26N, E of 102E	15	2.29	3.68	3.47 ⁶
<i>Viverricula indica</i>	M	Sri Lanka	10	India S. of 23N	6	3.35	4.63	3.47 ⁶
<i>Viverricula indica</i>	F	Taiwan	6	China 23-26N, E. of 113E	13	5.05	2.63	3.41
<i>Viverricula indica</i>	M	Taiwan	7	China 23-26N, E. of 113E	13	4.46	3.54	3.47 ⁶
<i>Vulpes vulpes</i>	F	Britain*	24	Belgium	18	3.71	2.28	3.74
<i>Vulpes vulpes</i>	M	Britain*	29	Belgium	21	4.00	3.31	3.85
<i>Vulpes vulpes</i>	F	Ireland	45	Britain	24	2.95	3.71	3.74
<i>Vulpes vulpes</i>	M	Ireland	51	Britain	29	2.91	4.00	3.85
<i>Vulpes vulpes</i>	F	Newfoundland	9	SE Canada and Maine S. of 55N, E of 70W	9	5.12	5.06	3.63 ³
<i>Vulpes vulpes</i>	M	Newfoundland	6	SE Canada and Maine S. of 55N, E of 70W	18	2.55	4.73	3.70
<i>Vulpes vulpes</i>	M	Tukarak	7	Ontario and Quebec, 50-60N, 76-85W	10	3.95	4.86	3.70

Notes: Islands marked with an asterisk are larger than the area on the corresponding mainland over which specimens were measured. Sources for mass data are: Creel and Macdonald 1995 (1), Johnson et al. 2000 (2), Nowak 1999 (3), Roberts 1977 (4), Shukor 1996 (5), Silva and Downing 1995 (6) and Weckerly 1998 (7). Where no source is given, body mass data are from tag data of specimens measured in this study (these data are available upon request, from the corresponding author). BC is British Columbia. Malaya is the Malay Peninsula.

LITERATURE CITED

Creel, S., and D. Macdonald. 1995. Sociality, group size, and reproductive suppression among carnivores. *Advances in the Study of Behaviour* **24**:203–257.

Johnson, D. D. P., D. W. Macdonald, and A. J. Dickman. 2000. An analysis and review of the sociobiology of the Mustelidae. *Mammal Review* **30**:171–196.

Nowak, R. M. 1999. Walker's Mammals of the world. Sixth Edition. Johns Hopkins University Press, Baltimore, Maryland, USA.

Roberts, T. J. 1977. The mammals of Pakistan. Ernest Benn. London, UK.

Shukor, N. M. 1996. The mammalian fauna on the islands at the northern tip of Sabah, Borneo. *Fieldiana-Zoology* **0 (83)** I–IV, 1–51.

Silva, M., and J. A. Downing. 1995. CRC Handbook of mammalian body masses. CRC Press, New York, New York, USA.

Weckerly, F. W. 1998. Sexual-size dimorphism: influence of mass and mating systems in the most dimorphic mammals. *Journal of Mammalogy* **79**:33–52.

Ecological Archives E086-078-A2

Shai Meiri, Tamar Dayan, and Daniel Simberloff. 2005. Variability and sexual size dimorphism in carnivores: testing the niche variation hypothesis. *Ecology* 86:1432–1440.

Appendix B (Table B1). Sample sizes, coefficients of variation of skull length (CBL) and body masses in island and nearest-mainland population pairs. See [Notes](#) at end of table for details.

Species	Sex	Island	Sample size	Mainland	Sample size	Island CV	Mainland CV	log body mass (g)
<i>Alopex lagopus</i>	M	Flaherty	5	Quebec N. of 55N	21	2.95	3.51	3.53
<i>Alopex lagopus</i>	F	St. Lawrence	52	Alaska W. of 159W	18	2.48	2.90	3.42
<i>Alopex lagopus</i>	M	St. Lawrence	57	Alaska W. of 159W	21	2.68	2.35	3.53
<i>Alopex lagopus</i>	F	St. Matthew	7	Alaska W. of 159W	18	3.50	2.90	3.42
<i>Alopex lagopus</i>	M	St. Matthew	9	Alaska W. of 159W	21	1.58	2.35	3.53
<i>Aonyx cinerea</i>	F	Java	17	Sumatra	6	3.66	2.47	3.48 ³
<i>Arctogalidia trivirgata</i>	F	Borneo	24	Indochina S. of 16N	7	2.86	3.27	3.19 ⁵
<i>Arctogalidia trivirgata</i>	M	Borneo*	24	Malay Peninsula S. Of 7N	8	3.84	3.67	3.38 ⁶
<i>Arctogalidia trivirgata</i>	F	Sumatra	8	Indochina S. of 16N	7	2.10	3.27	3.19 ⁵
<i>Bassariscus astutus</i>	F	Espiritu Santo	8	Baja California S. of 27N	11	1.43	1.58	2.95 ¹
<i>Bassariscus astutus</i>	M	Espiritu Santo	6	Baja California S. of 27N	7	1.71	1.75	3.00 ¹
<i>Bassariscus astutus</i>	F	San Jose	6	Baja California S. of 27N	11	1.44	1.58	2.95 ¹
<i>Bassariscus astutus</i>	M	San Jose	6	Baja California S. of 27N	7	1.31	1.75	3.00 ¹
<i>Canis aureus</i>	M	Sri Lanka	5	India S. of 20N	14	4.98	3.03	4.05 ⁶
<i>Canis lupus</i>	F	Prince of Wales	15	Alaska and BC, 54-60N, 127-135W	15	2.77	3.79	4.52 ⁶
<i>Canis lupus</i>	M	Prince of Wales	11	Alaska and BC, 54-60N, 127-133W	10	3.11	3.67	4.54 ⁶
<i>Canis lupus</i>	F	Vancouver Island	27	BC S. of 55N, W of 120W	7	3.22	1.79	4.52 ⁶
<i>Canis lupus</i>	M	Vancouver Island	35	BC S. of 55N, W of 120W	11	3.31	5.00	4.54 ⁶
<i>Felis benegalensis</i>	M	Bali	5	Java	18	4.16	4.33	3.52 ⁶
<i>Felis benegalensis</i>	F	Borneo*	6	Malay Peninsula S. Of 7N	6	3.32	2.64	3.35 ⁶
<i>Felis benegalensis</i>	M	Borneo*	12	Malay Peninsula S. Of 12N	5	3.64	2.81	3.52 ⁶
<i>Felis benegalensis</i>	F	Java	24	Sumatra	9	3.24	4.54	3.35 ⁶
<i>Felis benegalensis</i>	M	Java	19	Sumatra	7	5.78	4.22	3.52 ⁶
<i>Felis benegalensis</i>	F	Sumatra*	9	Malay Peninsula S. Of 7N	6	4.54	2.64	3.35 ⁶
<i>Felis benegalensis</i>	M	Sumatra*	7	Malay Peninsula S. Of 12N	5	4.22	2.81	3.52 ⁶
<i>Felis concolor</i>	F	Vancouver Island	13	BC and Washington 47-55N, W of 120W	5	4.16	4.00	4.63 ⁶
<i>Felis lynx</i>	M	Newfoundland	26	SE Canada and Maine S. of 55N, E of 67W	5	4.13	3.42	3.94
<i>Felis planiceps</i>	M	Borneo*	9	Malay Peninsula S. of 6N	9	4.15	5.73	3.20 ⁶
<i>Felis silvestris</i>	M	Britain	21	Belgium and France N. of 47N	6	5.16	6.00	3.70 ¹
<i>Herpestes smithii</i>	M	Sri Lanka	9	India S. of 19N	5	5.20	2.99	3.32 ¹
<i>Herpestes urva</i>	F	Taiwan	10	China S. of 27N, E. of 118E	5	3.32	1.68	3.30 ¹
<i>Lontra canadensis</i>	M	Baranof	7	Alaska and BC, 56-60N, 126-140W	7	2.76	2.86	3.93
<i>Lontra canadensis</i>	M	Chichagof	6	Alaska and BC, 56-60N, 126-140W	7	2.20	2.86	3.93
<i>Lontra canadensis</i>	M	Prince of Wales	5	Alaska and BC, 56-60N, 126-140W	7	0.43	2.86	3.93
<i>Lontra canadensis</i>	F	Vancouver Island	8	BC and Washington 47-55N, W. of 122W	14	3.55	2.36	3.91
<i>Lutra lutra</i>	F	Britain	9	Belgium and France N. of 47N	6	3.73	4.40	3.83 ⁶
<i>Lutra lutra</i>	F	Ireland	15	Britain	9	2.10	3.73	3.83 ⁶
<i>Lutra lutra</i>	M	Ireland	18	Britain	10	2.58	3.36	4.00 ⁶
<i>Lutra lutra</i>	F	Sri Lanka	8	India S. of 26N	6	5.07	3.57	3.83 ⁶
<i>Martes americana</i>	F	Chichagof	34	Alaska & BC 54-60N, 129-135W	19	2.92	3.75	2.80

Species	Sex	Island	Sample size	Mainland	Sample size	Island CV	Mainland CV	log body mass (g)
<i>Martes americana</i>	M	Chichagof	53	Alaska and BC 54-60N, 129-136W	20	2.38	2.71	3.14
<i>Martes americana</i>	F	Louise	9	Moresby	15	1.32	1.98	2.80
<i>Martes americana</i>	M	Louise	7	Moresby	33	1.98	1.41	3.14
<i>Martes americana</i>	F	Mitkof	16	Alaska and BC 54-60N, 129-135W	19	3.40	3.75	2.80
<i>Martes americana</i>	M	Mitkof	26	Alaska and BC 54-60N, 129-136W	20	2.80	2.71	3.14
<i>Martes americana</i>	F	Moresby	15	BC 51-55N, W. of 126W	13	1.98	2.00	2.80
<i>Martes americana</i>	M	Moresby	33	BC 51-55N, W. of 126W	16	1.41	2.96	3.14
<i>Martes americana</i>	F	Prince of Wales	8	Alaska and BC 54-60N, 129-135W	19	1.81	3.75	2.80
<i>Martes americana</i>	M	Prince of Wales	12	Alaska and BC 54-60N, 129-136W	20	1.27	2.71	3.14
<i>Martes americana</i>	F	Vancouver Island	83	BC and Washington 45-54N, W. of 121W	25	2.12	4.36	2.80
<i>Martes americana</i>	M	Vancouver Island	119	BC and Washington 45-54N, W. of 121W	44	1.99	3.32	3.14
<i>Martes flavigula</i>	F	Borneo*	18	Malay Peninsula S. of 9N	11	2.31	2.61	3.40 ³
<i>Martes foina</i>	M	Sjaelland	10	Denmark (Jutland)	5	2.57	2.49	3.13
<i>Martes martes</i>	M	Sjaelland	8	Denmark (Jutland)	6	1.20	1.42	3.22 ⁷
<i>Meles meles</i>	F	Britain*	13	Belgium and the Netherlands	9	4.64	2.82	4.00 ⁷
<i>Meles meles</i>	M	Britain*	26	Belgium	11	3.77	3.64	4.06 ⁷
<i>Meles meles</i>	F	Ireland	31	Britain	13	2.94	4.64	4.00 ⁷
<i>Meles meles</i>	M	Ireland	21	Britain	26	2.05	3.77	4.06 ⁷
<i>Meles meles</i>	F	Sjaelland	14	Denmark (Jutland)	52	2.47	2.76	4.00 ⁷
<i>Meles meles</i>	M	Sjaelland	17	Denmark (Jutland)	55	2.32	2.60	4.06 ⁷
<i>Melogale moschata</i>	F	Hainan	8	Vietnam and China, 21-26N, E of 102E	8	2.12	5.42	2.91
<i>Melogale moschata</i>	F	Taiwan	28	China S. of 30N, E. of 113E	6	2.85	5.51	2.91
<i>Mustela erminea</i>	F	Admiralty	8	Alaska and BC 54-60N, 127-140W	16	2.05	3.30	1.91
<i>Mustela erminea</i>	M	Admiralty	18	Alaska and BC 54-60N, 127-140W	39	3.83	3.92	2.35
<i>Mustela erminea</i>	F	Britain*	58	Belgium	47	4.01	3.60	2.32
<i>Mustela erminea</i>	M	Britain*	66	Belgium	44	3.94	6.22	2.56
<i>Mustela erminea</i>	M	Chichagof	5	Alaska and BC 54-60N, 127-140W	39	4.86	3.92	2.35
<i>Mustela erminea</i>	F	Ireland	46	Britain	58	5.17	4.01	2.32
<i>Mustela erminea</i>	M	Ireland	73	Britain	66	3.81	3.94	2.56
<i>Mustela erminea</i>	M	Kodiak	11	Alaska S. of 61N, W. of 149	18	3.68	4.46	2.35
<i>Mustela erminea</i>	F	Mitkof	9	Alaska and BC 54-60N, 127-140W	16	2.03	3.30	1.91
<i>Mustela erminea</i>	M	Mitkof	18	Alaska and BC 54-60N, 127-140W	39	3.01	3.92	2.35
<i>Mustela erminea</i>	F	Newfoundland*	8	Labrador S. of 54N, E of 58W	9	1.63	3.24	1.91
<i>Mustela erminea</i>	M	Newfoundland*	45	Labrador S. of 54N, E of 58W	35	3.64	4.64	2.35
<i>Mustela erminea</i>	M	Prince of wales	17	Alaska and BC 54-60N, 127-140W	39	4.48	3.92	2.35
<i>Mustela erminea</i>	F	Sjaelland	20	Denmark, Germany and Sweden, 53-60N	6	3.07	4.02	2.32
<i>Mustela erminea</i>	M	Sjaelland	19	Denmark, Germany and Sweden, 53-60N	13	3.86	4.33	2.56
<i>Mustela erminea</i>	F	Tukarak	12	Ontario, 50-60N, 75-90W	5	2.32	2.58	1.91
<i>Mustela erminea</i>	M	Tukarak	12	Ontario and Quebec, 50-60N, 75-90W	18	4.93	4.08	2.35
<i>Mustela erminea</i>	F	Vancouver Island	7	BC and Washington 49-54N, W. of 122W	15	3.09	6.89	1.91
<i>Mustela erminea</i>	M	Vancouver Island	17	BC and Washington 48-54N, W. of 122W	40	2.90	5.64	2.35
<i>Mustela nivalis</i>	F	Britain*	40	Belgium	82	3.93	5.30	1.77 ⁷
<i>Mustela nivalis</i>	M	Britain*	122	Belgium	155	3.73	5.09	2.06 ⁷
<i>Mustela nivalis</i>	F	Sardinia	8	Italy	10	7.86	6.60	1.77 ⁷
<i>Mustela nivalis</i>	M	Sardinia	23	Italy	57	3.50	4.62	2.06 ⁷
<i>Mustela nivalis</i>	M	Sjaelland	9	Denmark, Germany and Sweden, 53-60N	5	3.85	0.44	2.06 ⁷
<i>Mustela putorius</i>	F	Britain*	13	Belgium	45	2.42	6.95	2.84 ⁷
<i>Mustela putorius</i>	M	Britain*	38	Belgium	79	5.70	5.86	3.05 ⁷
<i>Mustela putorius</i>	F	Sjaelland	8	Denmark (Jutland)	8	3.81	2.53	2.84 ⁷

Species	Sex	Island	Sample size	Mainland	Sample size	Island CV	Mainland CV	log body mass (g)
<i>Mustela putorius</i>	M	Sjaelland	16	Denmark (Jutland)	17	4.07	3.39	3.05 ⁷
<i>Mustela sibirica</i>	F	Honshu	13	E Asia, 30-45N, E of 115E	6	6.50	3.06	2.60 ²
<i>Mustela sibirica</i>	M	Honshu	90	E Asia, 30-45N, E of 115E	7	6.28	7.12	2.89
<i>Mustela sibirica</i>	M	Kyushu	5	Honshu	90	10.17	6.28	2.89
<i>Mustela sibirica</i>	M	Sado	9	Honshu	90	3.88	6.28	2.89
<i>Mustela sibirica</i>	M	Shikoku	5	Honshu	90	4.80	6.28	2.89
<i>Mustela vison</i>	M	Admiralty	5	Alaska and BC 55-59N, 127-135W	12	1.59	3.82	3.12
<i>Mustela vison</i>	F	Baranof	13	Alaska and BC 55-59N, 130-135W	9	2.45	3.52	2.89
<i>Mustela vison</i>	M	Baranof	29	Alaska and BC 55-59N, 127-135W	12	3.34	3.82	3.12
<i>Mustela vison</i>	F	Chichagof	7	Alaska and BC 55-59N, 130-135W	9	1.50	3.52	2.89
<i>Mustela vison</i>	M	Chichagof	8	Alaska and BC 55-59N, 127-135W	12	2.18	3.82	3.12
<i>Mustela vison</i>	F	Nunivak	10	Alaska 60-62N, W. of 157W	7	2.75	5.02	2.89
<i>Mustela vison</i>	M	Nunivak	11	Alaska 58-62N, W. of 157W	28	3.04	5.84	3.12
<i>Mustela vison</i>	F	Vancouver Island	19	BC and Washington 48-54N, W. of 121W	13	4.34	4.34	2.89
<i>Mustela vison</i>	M	Vancouver Island	25	BC and Washington 48-54N, W. of 122W	9	3.46	4.76	3.12
<i>Nyctereutes procyonoides</i>	M	Kyushu*	5	GifuPrefecture, Honshu	41	1.63	3.40	3.69
<i>Paguma larvata</i>	F	Borneo*	9	Malay Peninsula S. of 9N	6	3.59	5.47	3.47
<i>Paguma larvata</i>	M	Borneo*	6	Malay Peninsula S. of 9N	6	3.83	4.09	3.78 ⁴
<i>Paguma larvata</i>	F	Sumatra*	9	Malay Peninsula S. of 9N	6	3.24	5.47	3.47
<i>Paguma larvata</i>	M	Sumatra*	5	Malay Peninsula S. of 9N	6	1.41	4.09	3.78 ⁴
<i>Panthera tigris</i>	M	Java	6	Sumatra	6	3.15	4.21	5.08 ³
<i>Panthera tigris</i>	M	Sumatra	6	Malaya, Vietnam and Thailand S. of 17S	7	4.21	4.06	5.34 ³
<i>Paradoxurus hermaphroditus</i>	M	Bali	6	Java	14	6.32	3.90	3.52 ¹
<i>Paradoxurus hermaphroditus</i>	F	Borneo*	11	Malay Peninsula S. of 9N	18	4.36	6.64	3.51 ⁶
<i>Paradoxurus hermaphroditus</i>	M	Borneo*	23	Malay Peninsula S. of 9N	24	3.64	5.63	3.52 ¹
<i>Paradoxurus hermaphroditus</i>	F	Java	31	Sumatra	14	3.51	3.70	3.51 ⁶
<i>Paradoxurus hermaphroditus</i>	M	Java	15	Sumatra	17	3.86	3.26	3.52 ¹
<i>Paradoxurus hermaphroditus</i>	M	Palawan	5	Borneo	23	2.87	3.64	3.52 ¹
<i>Paradoxurus hermaphroditus</i>	F	Sumatra*	14	Malay Peninsula S. of 9N	18	3.70	6.64	3.51 ⁶
<i>Paradoxurus hermaphroditus</i>	M	Sumatra*	17	Malay Peninsula S. of 9N	24	3.26	5.63	3.52 ¹
<i>Paradoxurus hermaphroditus</i>	M	Terutau	7	Malay Peninsula S. of 9N	24	3.53	5.63	3.52 ¹
<i>Procyon lotor</i>	M	Key Largo	9	Florida	20	1.53	4.80	3.93 ⁶
<i>Procyon lotor</i>	M	No name key	5	Florida	20	3.01	4.80	3.93 ⁶
<i>Procyon lotor</i>	F	Vancouver Island	18	Washington N. of 46N, W. of 120W	7	2.42	1.84	3.81 ⁶
<i>Procyon lotor</i>	M	Vancouver Island	17	Washington N. of 46N, W. of 120W	8	2.53	2.55	3.93 ⁶
<i>Urocyon (cinereoargenteus) littoralis</i>	F	San Clemente	5	California, 32-34N, W. of 116W	8	2.77	3.31	3.50 ⁶
<i>Urocyon (cinereoargenteus) littoralis</i>	F	San Miguel	6	California, 33-35N, W. of 117W	10	2.16	2.19	3.50 ⁶
<i>Urocyon (cinereoargenteus) littoralis</i>	F	Santa Catalina	5	California, 32-34N, W. of 116W	8	2.34	3.31	3.59 ⁶
<i>Urocyon (cinereoargenteus) littoralis</i>	M	Santa Catalina	6	California, 32-34N, W. of 116W	9	4.18	2.41	3.59 ⁶
<i>Urocyon (cinereoargenteus) littoralis</i>	M	Santa Cruz	5	California, 33-35N, W. of 117W	23	2.78	3.35	3.59 ⁶
<i>Urocyon (cinereoargenteus) littoralis</i>	M	Santa Rosa	6	California, 33-35N, W. of 117W	23	3.37	3.35	3.59 ⁶
<i>Ursus americanus</i>	M	Kuiu	6	Kupreanof	5	8.17	3.06	5.19 ⁶
<i>Ursus americanus</i>	M	kupreanof	5	Alaska 55-60N, E. of 132W	10	3.06	4.06	5.19 ⁶
<i>Ursus americanus</i>	M	Vancouver Island	6	BC S. of 55N, W of 122W	7	4.76	3.86	5.19 ⁶
<i>Ursus arctos</i>	F	Admiralty	20	Alaska and BC, 55-60N, 127-140W	11	4.78	5.63	5.48 ¹
<i>Ursus arctos</i>	M	Admiralty	37	Alaska and BC, 54-61N, 127-143W	7	5.98	10.69	5.65 ¹
<i>Ursus arctos</i>	F	Baranof	5	Alaska and BC, 55-60N, 127-140W	11	5.04	5.63	5.48 ¹
<i>Ursus arctos</i>	F	Chichagof	9	Alaska and BC, 55-60N, 127-140W	11	4.12	5.63	5.48 ¹
<i>Ursus arctos</i>	M	Chichagof	11	Alaska and BC, 54-61N, 127-143W	7	8.05	10.69	5.65 ¹

Species	Sex	Island	Sample size	Mainland	Sample size	Island CV	Mainland CV	log body mass (g)
<i>Ursus arctos</i>	F	Kodiak	12	Alaska S. of 60N, W. of 150W	28	2.58	3.70	5.48 ¹
<i>Ursus arctos</i>	M	Kodiak	8	Alaska S. of 60N, W. of 150W	21	2.69	4.61	5.65 ¹
<i>Viverricula indica</i>	F	Hainan	8	China, 15-26N, E of 102E	14	1.46	2.83	3.41
<i>Viverricula indica</i>	M	Hainan	5	China, 15-26N, E of 102E	15	2.29	3.68	3.47 ⁶
<i>Viverricula indica</i>	M	Sri Lanka	10	India S. of 23N	6	3.35	4.63	3.47 ⁶
<i>Viverricula indica</i>	F	Taiwan	6	China 23-26N, E. of 113E	13	5.05	2.63	3.41
<i>Viverricula indica</i>	M	Taiwan	7	China 23-26N, E. of 113E	13	4.46	3.54	3.47 ⁶
<i>Vulpes vulpes</i>	F	Britain*	24	Belgium	18	3.71	2.28	3.74
<i>Vulpes vulpes</i>	M	Britain*	29	Belgium	21	4.00	3.31	3.85
<i>Vulpes vulpes</i>	F	Ireland	45	Britain	24	2.95	3.71	3.74
<i>Vulpes vulpes</i>	M	Ireland	51	Britain	29	2.91	4.00	3.85
<i>Vulpes vulpes</i>	F	Newfoundland	9	SE Canada and Maine S. of 55N, E of 70W	9	5.12	5.06	3.63 ³
<i>Vulpes vulpes</i>	M	Newfoundland	6	SE Canada and Maine S. of 55N, E of 70W	18	2.55	4.73	3.70
<i>Vulpes vulpes</i>	M	Tukarak	7	Ontario and Quebec, 50-60N, 76-85W	10	3.95	4.86	3.70

Notes: Islands marked with an asterisk are larger than the area on the corresponding mainland over which specimens were measured. Sources for mass data are: Creel and Macdonald 1995 (1), Johnson et al. 2000 (2), Nowak 1999 (3), Roberts 1977 (4), Shukor 1996 (5), Silva and Downing 1995 (6) and Weckerly 1998 (7). Where no source is given, body mass data are from tag data of specimens measured in this study (these data are available upon request, from the corresponding author). BC is British Columbia. Malaya is the Malay Peninsula.

LITERATURE CITED

Creel, S., and D. Macdonald. 1995. Sociality, group size, and reproductive suppression among carnivores. *Advances in the Study of Behaviour* **24**:203–257.

Johnson, D. D. P., D. W. Macdonald, and A. J. Dickman. 2000. An analysis and review of the sociobiology of the Mustelidae. *Mammal Review* **30**:171–196.

Nowak, R. M. 1999. *Walker's Mammals of the world*. Sixth Edition. Johns Hopkins University Press, Baltimore, Maryland, USA.

Roberts, T. J. 1977. *The mammals of Pakistan*. Ernest Benn. London, UK.

Shukor, N. M. 1996. The mammalian fauna on the islands at the northern tip of Sabah, Borneo. *Fieldiana-Zoology* **0 (83)** I–IV, 1–51.

Silva, M., and J. A. Downing. 1995. *CRC Handbook of mammalian body masses*. CRC Press, New York, New York, USA.

Weckerly, F. W. 1998. Sexual-size dimorphism: influence of mass and mating systems in the most dimorphic mammals. *Journal of Mammalogy* **79**:33–52.