

# Body Size of Insular Carnivores: Little Support for the Island Rule

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**ABSTRACT:** Large mammals are thought to evolve to be smaller on islands, whereas small mammals grow larger. A negative correlation between relative size of island individuals and body mass is termed the “island rule.” Several mechanisms—mainly competitive release, resource limitation, dispersal ability, and lighter predation pressure on islands, as well as a general physiological advantage of modal size—have been advanced to explain this pattern. We measured skulls and teeth of terrestrial members of the order Carnivora in order to analyze patterns of body size evolution between insular populations and their near mainland conspecifics. No correlations were found between the size ratios of insular/mainland carnivore species and body mass. Only little support for the island rule is found when individual populations rather than species are considered. Our data are at odds with those advanced in support of theories of optimal body size. Carnivore size is subjected to a host of selective pressures that do not vary uniformly from place to place. Mass alone cannot account for the patterns in body size of insular carnivores.

**Keywords:** body size, Carnivora, geographic variation, island rule, optimal body size.

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Islands have served as models in the study of evolutionary and ecological phenomena ever since Darwin (1845; Wallace 1868, 1880; MacArthur and Wilson 1967). Their isolation, the relatively low species richness, and, in many cases, their clear faunal history (such as when humans

introduce exotic species) make islands an excellent arena for evolutionary research.

Among the most pronounced microevolutionary changes occurring on islands are changes in body size. These changes are especially apparent in mammals (but by no means only in mammals; Case 1978; Pregil 1986; Alcover and McMinn 1994; McNab 1994; Benton et al. 1997; Brown and Lomolino 1998; Jianu and Weishampel 1999; Clegg and Owens 2002).

Foster (1964) conducted the first systematic analysis of patterns in body size evolution of insular mammals. Surveying the literature, he found that rodents tend toward gigantism on islands, while lagomorphs, carnivores, and artiodactyls are usually characterized by insular dwarfing. Van Valen named these phenomena the “island rule” (Van Valen 1973, p. 32), according to which small mammals grow larger on islands while large mammals are dwarfed. Van Valen (1973, p. 72) concluded, “The regular evolution of mammalian body size on islands is an extraordinary phenomenon which seems to have fewer exceptions than any other ecotypic rule in animals.” Several authors (Case 1978; Heaney 1978; Lawlor 1982; Melton 1982; Davis 1983; Angerbjörn 1985) raised interesting hypotheses about the selective pressures underlying these patterns, highlighting such agents as resource limitation, dispersal ability, competition (or lack thereof), predation, and territoriality.

Lomolino’s (1983, 1985) review expanded Foster’s database to include 375 populations representing more than 74 mammalian species (seven comparisons included individuals of more than one species; Lomolino 1983). Lomolino reinforced Foster’s conclusions as to the frequency of dwarfism and gigantism in various mammalian orders. He then represented the relative size of the insular forms (the ratio between a species insular and mainland sizes, averaged for all populations) as a function of body mass, obtaining a graded trend from gigantism in the smaller species to dwarfism in the larger ones. Lomolino (1985, p. 314) reformulated the island rule in these terms, and this is the accepted modern form of the rule.

The clear, fascinating pattern observed by Lomolino (1985) and the elegant models of Heaney (1978) and Case

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(1978) have been widely discussed in the ecological and evolutionary literature. For example, they were advanced as support for the concept of an optimal mammalian body size (Brown et al. 1993; Damuth 1993). They have fostered controversy over the possibility of different evolutionary patterns and forces for mammals and birds (Clegg and Owen 2002). Furthermore, they have spawned a host of partially contradictory explanations for the perceived rule based on ecology (reviewed by Angerbjörn 1986; Dayan and Simberloff 1998), paleobiology (Gordon 1986), physiology (Lovegrove 2000), and evolution (Demetrius 2000).

We aimed to see whether patterns of size in members of the Carnivora accord with the island rule and, if so, for what reasons. Carnivore evolution on islands has been widely studied ever since Darwin. In his letter to the Linnean society in which he outlined his theory of evolution by natural selection, Darwin (Darwin and Wallace 1858, p. 49) wrote, "To give an imaginary example from changes in progress on an island: Let the organization of a canine animal ... become slightly plastic ... those individuals with the lightest forms ... would be slightly favored ... these causes would ... produce a marked effect, and adapt the form of the fox or dog." The Carnivora are particularly suitable for studies of body size evolution for several reasons: they span a large range of body masses. Members of the order are found on many islands throughout the world (135 species on more than 500 different islands; S. Meiri, unpublished data). They are extremely varied in diet, from almost strict vegetarians through omnivores to piscivores, insectivores, and strict carnivores. Interspecific competition and predation, two selective pressures likely to promote size change, are well documented for many carnivores (Dayan et al. 1989, 1990, 1992; Thurber et al. 1992; Dayan and Simberloff 1994; Palomares and Caro 1999; Arjo et al. 2002). In addition, body size evolution and its underlying mechanisms have been intensively studied in carnivores on both islands and mainland (Rosenzweig 1968; Gittleman 1985; Klein 1986; Kiltie 1988; Dayan et al. 1989, 1990, 1992; Giannico and Nagorsen 1989; Iriarte et al. 1990; Clevenger 1993; Dayan and Simberloff 1994; Nagorsen 1994; Jimenez et al. 1995; Gittleman and Van Valkenburgh 1997; Hilderbrand et al. 1999; Simberloff et al. 2000; Mahoney et al. 2001; McDonald 2002). With respect to the island rule, carnivores were found to have a tendency toward insular dwarfism by Foster (1964) and Lomolino (1985). Lomolino went on to show that a graded trend from gigantism in smaller species to dwarfism in larger ones also prevailed within different orders and families of mammals, including the Carnivora and all (three) carnivore families for which he had data on more than one species.

## Material and Methods

In order to analyze body size variation in insular and mainland carnivores, we measured skulls of carnivores in the following collections: Natural History Museum, London; Zoology Museum of Cambridge University; New Walk Museum; National Monuments Archeozoological collections, London; Harrison Zoological Museum; the Royal Museum, Edinburgh; Muséum National d'Histoire Naturelle, Paris; Laboratoire d'Anatomie Comparée, Paris; Institut Royal des Sciences Naturelles de Belgique; National Museum of Natural History Leiden "Naturalis"; University of Amsterdam, Zoological Museum; Zoologische Staatssammlung, München; Zoological Museum University of Copenhagen; Tel Aviv University, Zoological Museum; Raffles Museum of Biodiversity Research; National Science Museum, Tokyo; Primate Research Institute, Kyoto University; University of Alaska Fairbanks, Museum of Natural History; Royal British Columbia Museum; Royal Ontario Museum; Canadian Museum of Nature; Field Museum; Carnegie Museum of Natural History; National Museum of Natural History–Smithsonian Institution; American Museum of Natural History; Museum of Comparative Zoology, Harvard University; National Museum of Ireland; Collections of the Department of Zoology, University College, Cork, and the Ulster Museum.

Measurements were taken using digital calipers to 0.01-mm precision or vernier calipers to 0.02-mm precision (for measurements exceeding 300 mm). We chose three measurements as measures of body size: skull length (condylobasal length [CBL]; Von den Driesch 1976), the maximum diameter of the upper canine, and the length of the lower first molar ( $M_1$ , the lower carnassial tooth). The CBL is a common measure of body size in biogeographic research (e.g., Rausch 1963; Ralls and Harvey 1985; Ellison et al. 1993; Quin et al. 1996; Jones 1997). The upper canine tooth is considered to be a main killing apparatus in carnivores (Dayan et al. 1989, 1990; Biknevicius and Van Valkenburgh 2001). Its size may be more strongly correlated to prey size than to the carnivore body size (Dayan et al. 1989, 1990; Dayan and Simberloff 1998). Canines are therefore used not merely as an index of size: if prey species undergo size changes on islands in accordance with the island rule, then canine size may evolve to track those changes, therefore displaying the same overall pattern. The  $M_1$  length is a common measure for size in much paleontological research (Gingerich et al. 1982; Klein 1986; Koch 1986; Alroy 1998). This tooth is believed to have relatively low intraspecific variability (Gingerich 1974; Gingerich and Schoeninger 1979; Gingerich and Winkler 1979; Pengilly 1984; Szuma 2000; Dayan et al. 2002) and is thus considered to be a suitable size index (Gingerich 1974; Damuth 1990; Janis 1990; MacFadden and Hulbert

1990; Alroy 1998). We used only adult specimens (those in which there is complete suture closure) when measuring CBL. We considered specimens with fully erupt permanent dentition adults for the canine and lower carnassial measurements, even if they were not identified as adults by the criterion for skulls outlined above. We did not measure worn teeth. We recorded sex and location data for each specimen (as well as body mass where available). We considered a population (either mainland or insular) fit for analysis if we measured a minimum of five individuals of the same sex. Interesting patterns of size evolution have been demonstrated for several mammalian taxa that were introduced to islands (Yom-Tov et al. 1986, 1999), including carnivore species (e.g., *Mustela vison*: Dayan and Simberloff 1994; *Herpestes javanicus*: Simberloff et al. 2000). However, we chose not to include populations introduced to islands during historical times in our analysis, since the limited time since the introductions might not have sufficed for body size evolution to manifest itself fully.

We used specimens belonging to 37 different species from 137 pairs of populations for comparisons of insular and mainland CBL. Specimens belonging to 38 different species from 140 population pairs were used for comparisons of upper canine diameters. Specimens belonging to 38 different species from 144 population pairs were used for comparisons of  $M_1$  length. In all analyses, we compared island carnivores with their mainland conspecifics with one exception, in which an insular endemic was compared with its nearest mainland congener: *Urocyon littoralis*, endemic to the California Channel Islands and the Gulf of California Islands, was compared with its sole congener, mainland *Urocyon cinereoargenteus*. Since sexual size dimorphism is often pronounced in carnivores, sexes were treated as separate morphospecies for all island/mainland comparisons.

Average CBL, canine diameter, or  $M_1$  length of each insular population was divided by average value of the corresponding nearest mainland population, yielding the relative insular body size (Lomolino's size [relative;  $S_R$ ]). We used mainlands as close as possible to the island in question. The geographical limits of the mainland populations were chosen so that they approximated, or at least did not greatly exceed, those of the insular populations in both size and latitudinal range. The  $S_R$  were cubed following Lomolino's (1985) analysis to determine the number of populations that show insular dwarfism versus gigantism. Relative size of the insular forms was then regressed against the logarithm of the morphospecies body mass. Mass data were taken from nearest mainland specimen labels (mass for each morphospecies was calculated as the midpoint of the mass range). When such data were not available, mass was taken from the literature. We conducted these analyses for both the individual populations

and for average  $S_R$  and mass values for each species or morphospecies. We used mass since it is the most common surrogate for size in the literature (Peters 1983; Calder 1984; Schmidt-Nielsen 1984). Mass was also the variable chosen to represent absolute size in the formulation of the island rule (Lomolino 1985; note that in that study, linear measurements were cubed because the allometric exponent for scaling length and mass is three). It can be argued that other measures, such as head plus body length, are better surrogates for size than is mass, since mass may be influenced by seasonal and daily fluctuations and by reproductive condition (Ralls and Harvey 1985; Dunning 1993). However, the correlation of head plus body length and body mass in the terrestrial mammals and in the Carnivora among them is very tight (Silva 1998), so using either size index is likely to produce the same result. One might also argue that it is better to regress the relative size of the insular forms against measurements obtained in this study rather than from the literature. However, using the same measurements both for the relative size index and as an index for total body size would have resulted in regressing a ratio against its denominator, and we therefore refrained from doing so. In order to see whether the same pattern observed for mammals as a whole and for carnivores in particular (Lomolino 1985) holds at lower taxonomic levels, we conducted the same analyses for the different families in our database. We also reanalyzed Lomolino's (1983) raw data for mammals and for carnivores for comparison with our results.

We computed averages for each population using Microsoft Excel. Since homoscedasticity cannot be assumed or even expected (owing to differences in variance between islands and mainlands; Van Valen 1965; Dayan and Simberloff 1994; Meiri 2002), we used nonparametric correlation (Spearman's rank correlation). It can be argued that, since we have a strong prior hypothesis of a negative correlation between  $S_R$  and mass (Lomolino 1985), one-tailed probabilities should be computed. However, since we are looking for patterns in nature, two-tailed probabilities were computed as well. We also ran Pearson's product moment correlation in order to obtain the equations needed to predict the body mass for which size of the insular forms is the same as that of mainland ones ( $SR = 100\%$ ). Analyses of frequencies and correlations were calculated using STATISTICA 6 software.

## Results

The results of the island/mainland comparisons for each population are available in tables 1–3 in the online edition of the *American Naturalist*.

*General Tendency*

We compared the number of populations that show insular dwarfism with the number that show insular gigantism, in both instances following Lomolino's definition of a minimum difference of 5% in cubed linear measurements. The results are listed in table 4. For CBL, there are more cases of insular dwarfism than of gigantism ( $P = .003$ ). Such a pattern may also be true for the canines ( $P = .069$ ) but not for the lower carnassials ( $P = .225$ ). However, because dwarves do not comprise more than 50% of the populations for any variable, it cannot be said that carnivores as a whole tend to show insular dwarfism. Likewise, in none of the carnivore families for either of the morphological traits did the proportion of either dwarves or giants significantly exceed 50%. Likewise, in no single island does the number of either giants or dwarves significantly exceed 50%, except for Borneo, where the number of dwarves is significantly higher than that of giants (for both CBL and canine diameter but not  $M_1$ ), and Newfoundland, where for canine diameter (only) the number giants (four) was significantly greater than that of dwarves (0).

*The Island Rule*

The results for the correlations between  $S_R$  and body mass are given in table 5. Using two-tailed tests, we found no significant correlations between  $S_R$  and mass, although some values are marginal ( $M_1$  for both sexes and for males, using separate populations, lower molars of members of the Ursidae, and CBL of populations where our sample size is at least 10). With one-tailed tests, these correlations are significant, as is the correlation between average species  $S_R$  for canines, in the direction opposite of that predicted by the rule (Lomolino 1985). Thus, support for the island rule in our data is at best weak. This is true whether we average  $S_R$  values of all populations for each species or morphospecies, treat all populations individually, or look for patterns within more restricted taxonomic groups. When we correct for multiple testing of a common prior hypothesis (Cabin and Mitchell 2000), none of the results are significant.

Our results differ substantially from those of Lomolino (1983, 1985), who has shown significant negative correlations between insular and mainland size for separate mammalian orders (Carnivora included) as well as for the class as a whole. This discrepancy does not result from different analytic procedures. Lomolino (1983, 1985) used only male measurements "when available" (Lomolino 1985, p. 125), otherwise he used mixed sex samples. Using the same methods (species means, averaging the  $S_R$  and mass values for all populations of each species), we obtain

**Table 4:** Frequency of dwarfism and gigantism

	Dwarves	= <sup>a</sup>	Giants
CBL	57	46	34
Canines	64	31	45
$M_1$	64	29	51

<sup>a</sup> Cubed  $S_R$  of populations in this category is 95%–105%.

no significant correlation between these variables for either size index regardless of whether we use the whole sample of populations or males only (table 5). When we analyze the carnivore data of Lomolino (1983), a significant negative correlation between mass and  $S_R$  arises ( $n = 17$ , Spearman's  $r = -0.5607$ , one-tailed  $P = .0096$ ). When we computed a product-moment correlation for Lomolino's data, the regression equation obtained,  $y = -0.118x + 1.40$ , predicts that the body size for which  $SR = 100\%$  is 3.39, corresponding to a mass of 2,477 g. Our data predict  $SR = 100\%$  at masses ranging from near 0 (females, species average, CBL) to 18,156,433 g (Canidae, populations,  $M_1$ ). Our results also differ from the results obtained from an analysis of Lomolino's (1983) data for the Mammalia as a whole. The correlation according to these data is significant ( $n = 74$ , Spearman's  $r = -0.56$ ,  $P < .001$ ), and the intercept is 2.85, corresponding to a mass of 701 g. Thus, we cannot support Lomolino's (1983) claim that the particular mammalian order does not matter and only size is important.

**Discussion**

Carnivores do not tend toward dwarfism on islands, and neither do members of the different carnivore families. Nor do we see any particular islands for which this is the case, except for Newfoundland and Borneo. When we regressed  $S_R$  on mass, we found no significant correlations for species within the order or within the different families. Using one-tailed tests, we did find a few cases for which the degree of dwarfism increases with mass. The amount of variation explained is in any case minimal. Ancestral size might be one of the factors affecting the direction and intensity of deviation in descendant's size, but it would probably rank as one of many such factors, not a decisive one. One might argue that obtaining a significant correlation between body mass and carnassial size, but not between mass and CBL, suggests that different selective forces are acting on carnivore body size (as manifested by CBL) and tooth size (Dayan et al. 1989, 1990, 1992; Dayan and Simberloff 1994). This argument may sound plausible, since insular rodents usually exhibit gigantism, and artiodactyls show insular dwarfism, so teeth of insular carni-

**Table 5:** Summary statistics for correlations between  $S_R$  and body mass

Trait and test	Sex	$n$	Spearman's $r$	$P$ (two-tailed)	$P$ (one-tailed)
CBL:					
Species averages	Both	36	.0569	.7415	.3707 <sup>a</sup>
Morphospecies averages	Females	25	.0023	.9913	.4956 <sup>a</sup>
Morphospecies averages	Males	32	-.0710	.7010	.3505
Canines:					
Species averages	Both	37	.2582	.1229	.0614 <sup>a</sup>
Morphospecies averages	Females	26	.1186	.5638	.2819 <sup>a</sup>
Morphospecies averages	Males	33	.1976	.2704	.1352 <sup>a</sup>
$M_i$ :					
Species averages	Both	37	-.1202	.4786	.2393
Morphospecies averages	Females	26	.1378	.5021	.2510 <sup>a</sup>
Morphospecies averages	Males	34	-.2295	.1916	.0958
CBL:					
Populations	Both	137	-.1152	.1798	.0899
Populations	Females	56	-.1128	.4079	.2040
Populations	Males	67	-.0970	.3888	.1944
Populations ( $n \geq 7$ )	Both	84	-.0990	.3703	.1851
Populations ( $n \geq 10$ )	Both	52	-.2351	.0934	.0467
Canines:					
Populations	Both	140	-.0146	.8644	.4322
Populations	Females	58	-.0087	.9486	.4743
Populations	Males	82	-.0043	.9696	.4848
Populations ( $n \geq 7$ )	Both	88	-.0191	.8596	.4298
Populations ( $n \geq 10$ ) <sup>b</sup>	Both	52	-.0720	.6118	.3059
$M_i$ :					
Populations	Both	144	-.1590	.0570	.0285
Populations	Females	59	-.0559	.6559	.3280
Populations	Males	85	-.2086	.0554	.0277
Populations ( $n \geq 7$ )	Both	87	-.1189	.2727	.1363
Populations ( $n \geq 10$ )	Both	56	-.1250	.3570	.1785
CBL:					
Canidae	Both	21	-.0010	.9960	.4980
Felidae	Both	13	.3470	.2450	.1225 <sup>a</sup>
Lutrinae	Both	9	.4830	.1880	.0940 <sup>a</sup>
Mustelidae	Both	67	-.0168	.8929	.4465
Mustelidae <sup>c</sup>	Both	58	-.0832	.5347	.2674
Ursidae	Both	9	-.1580	.6850	.3425
Viverridae	Both	22	.1770	.4306	.2153 <sup>a</sup>
Canines:					
Canidae	Both	20	-.0256	.9145	.4573
Felidae	Both	17	.4034	.1083	.0542 <sup>a</sup>
Lutrinae	Both	10	.0000	1.0000	
Mustelidae	Both	72	.0353	.7687	.3844 <sup>a</sup>
Mustelidae <sup>c</sup>	Both	62	-.0020	.9874	.4937
Ursidae	Both	7	-.2315	.6175	.3088
Viverridae	Both	18	.2541	.3089	.1545 <sup>a</sup>
$M_i$ :					
Canidae	Both	23	.0510	.8170	.4085 <sup>a</sup>
Felidae	Both	15	.4010	.1380	.0690 <sup>a</sup>
Herpestidae	Both	4	-.4000	.6000	.3000
Lutrinae	Both	11	-.0330	.9230	.4615
Mustelidae	Both	71	.0521	.6662	.3331 <sup>a</sup>
Mustelidae <sup>c</sup>	Both	60	-.0157	.9053	.4527
Ursidae	Both	10	-.6100	.0610	.0305
Viverridae	Both	18	-.1743	.4890	.2445

Note: Species and morphospecies averages are average  $S_R$  values for all population pairs. Other comparisons are for individual population pairs. Tests where  $n \geq 7$  and  $n \geq 10$  were conducted only when the minimal number of individuals for either island or mainland reached 7 or 10. Correlation for the Herpestidae was computed using  $M_i$ , only because of small sample size for CBL and canines.

<sup>a</sup> One-tailed probabilities in the direction opposite of the prior hypothesis (positive correlations).

<sup>b</sup> In this comparison, the largest carnivore is *Canis lupus*. All other comparisons span the entire mass range in the order (*Mustela nivalis* to *Ursus arctos*).

<sup>c</sup> Mustelidae without Lutrinae.

vores might be evolving to accommodate prey size. However, no such pattern is found for the canines, and the fact that  $P$  levels of the correlation between  $M_1$  and body mass rise when sample size is enlarged, while the reverse is true for CBL, makes us suspect that the weak pattern observed is merely a statistical artifact.

Our findings bear importantly on the island rule as an ecological phenomenon and on our understanding of the evolution of body size in general. Our data suggest that the correct definition of the island rule may be closer in spirit to the one given by Foster (1964), who considered the rule separately for each mammalian order, than to the definition of Van Valen (1973), who formulated the rule in terms of body size irrespective of order (see also Lomolino 1983, p. 69). Large carnivores do not tend to be dwarfed on islands, nor do small ones tend toward gigantism. However, an examination of other mammalian orders may give a different picture. The almost uniformly small rodents are famous for their tendency toward gigantism on islands (Foster 1964; Berry 1970, 1996; Lomolino 1985). However, striking examples of dwarfism are known from the artiodactyls (cervids and hippopotamids: Sondaar 1977, 1991; Simmons 1988; Lister 1996; Burney et al. 1997), an order of almost uniformly large mammals (Gardezi and da Silva 1999), and from the largest of recent land mammals, the proboscidea (Diamond 1987; Roth 1990; Vartanyan et al. 1993). Carnivores, with their large variation of body sizes, diets, and lifestyles, show no clear trend.

A question that begs an explanation is, why is there a clear correlation between mass and  $S_R$  in Lomolino's data but not in ours? This question is particularly interesting, because we included in our analysis 13 (CBL) and 14 (canines,  $M_1$ ) of the 17 species of carnivores analyzed in his work (Lomolino 1983). Although our sample is considerably larger in numbers of both species and populations, both data sets span virtually the entire range of body masses within the Carnivora (from *Mustela nivalis* to *Ursus arctos*). We have no clear answer to this question. It might be argued that his reliance on various data sources might obscure the consistency of his results (cf. Lawlor's 1982 critique of Foster's data), whereas we measured skulls directly and refrained from using published data of  $S_R$  values. However, this hypothesis can be verified only by a direct analysis of the populations mentioned in his work. Certainly, our results differ from his even for the same species: Lomolino (1983) reports  $S_R$  values of 177% for *Mustela vison* and 51% for *Canis lupus*, the largest deviations in size (in each direction) recorded among all mammals in his database. Corresponding values in this study (average cubed  $S_R$  of all populations, CBL) are 99% for mink (largest cubed  $S_R$  of a population: 114%) and 84% for wolves (smallest cubed  $S_R$  of a population: 80%).

Explaining our results may seem unnecessary, since basically our analyses failed to reject the null hypothesis; that is, we found no consistent trend in the relative sizes of insular forms. With regard to selective pressures that were thought to generate the pattern observed by Lomolino (1985), a close inspection of the data reveals that, in some cases, size patterns conform to expectations, whereas other times they do not. Regarding competitive release on islands, for example, we find that tigers on Sumatra (*Panthera tigris sumatrae*) are smaller than on Java (*P. t. corbetti*). A possible explanation is the presence of leopards (*Panthera pardus*) on Java. This species is absent from Sumatra, and therefore one can argue that Java tigers cannot grow smaller, since the "small panther" niche is already occupied by the (admittedly small) Java leopard. But the situation becomes confusing when we consider another species of big cat: the puma (*Felis concolor*). On Vancouver Island, it is the only felid. The lynx (*Felis lynx*) common on the mainland (albeit not reaching the coastal regions of southern British Columbia; Wilson and Ruff 1999) is absent. Furthermore, the puma's common prey on Vancouver Island, the black-tailed deer *Odocoileus hemionus columbianus*, is smaller than the subspecies found in the puma's habitat on the southern part of the British Columbia mainland (*O. h. hemionus*; Shackleton 1999). One might then predict the large *F. concolor* (or at least its females) will become dwarfed on Vancouver Island. In fact, it is slightly larger there than on the mainland. Some predation theory suggests that the absence of predators can lead small mammals to become larger and large ones to become smaller (Heaney 1978; Michaux et al. 2002). This prediction fits well the fact that British least weasels (*Mustela nivalis*) are indeed larger than mainland ones but fails to explain why Kodiak Island ermines are smaller, and Kodiak bears larger, than their conspecifics on the mainland. Data for these bears and Java tigers also rule out resource limitation on islands as a uniform explanation for trends in the upper size range. It should also be borne in mind that the structure of Eltonian pyramids may imply that carnivores are at a higher risk of running out of resources than herbivores are and that dwarfism should therefore take place at lower body masses (Lomolino 1985) or on larger islands, but this does not appear to be the case: for example, we would expect tigers and pumas to be dwarfed on islands, but we did not find this result, as noted above.

Dispersal ability, thought to generate insular gigantism through founder effects (Lomolino 1983), seems to be of little relevance for carnivores. Except for a few introduced species (not analyzed here), almost all island carnivores inhabit continental shelf islands and thus were probably part of the mainland population as late as the early Holocene. They are therefore almost all probably insular rel-

icts rather than colonizers. The only recent native oceanic island carnivores (Alcover and McMinn 1994) are the eight native Madagascar species, the Sulawesi palm civet (*Macrogalidia musschenbroekii*), the extinct Falkland Island wolf (*Duscicyon australis*), and the island fox (*Urocyon littoralis*), an insular dwarf. The latter species is the only oceanic island carnivore for which one can assign a near mainland relative and is therefore the only oceanic island carnivore in our database.

Climatic factors (cf. Bergmann's rule) apparently do not exert uniform selective pressures on insular populations (Yom-Tov et al. 1999), but in some instances, a pattern in accordance with Bergmann's rule is apparent. For example, red foxes (*Vulpes vulpes*) are bigger on more northerly Britain than they are in Belgium, and Eurasian otters (*Lutra lutra*) are smaller on more equatorial Sri Lanka than they are in southern India. However, similar size clines are not seen in other cases: for example, the latter species is smaller in Britain than in northwest Europe, and leopard cats (*Felis bengalensis*) are smaller on Java than on more equatorial Sumatra, despite the fact that all the above species follow Bergmann's rule on the mainland (foxes: Cavallini 1995; otters and cats: Meiri et al. 2004).

We do not claim that no patterns of geographic variation in size exist in insular carnivores. The question of why all carnivore species on Borneo tend to be smaller than their mainland counterparts, for example, begs further study, although with 27 species of carnivores (more than in the whole of Europe), Borneo is hardly a typical island. The influence of island size on body size (Heaney 1978; Marquet and Taper 1998) is another interesting area for research, but this is beyond the scope of this work. This said, none of the proposed mechanisms seem to be driving a vast majority of carnivoran mainland-island size differences.

#### What Constitutes an Island?

A quick glance at a map confirms that Britain is indeed an island. However, it was construed as the species source and therefore functions as a "mainland" according to several of the main protagonists dealing with size variation in insular mammals (Berry 1970, 1996; Angerbjörn 1986; Dayan and Simberloff 1994; Lister 1996). Is Britain an island? A mainland? Or both? And is it the same for all animals? British red deer (*Cervus elaphus*) are smaller than conspecifics on the European mainland (Matthews 1952), as are wildcats (*Felis silvestris*) and badgers (*Meles meles*; this study), while weasels (*Mustela nivalis*) and stoats (*Mustela erminea*) are larger. Why then are murids smaller on Britain than on adjacent islands but stoats are larger (compared with Irish populations)? For still smaller islands near it, Britain is believed to be the source for some mammals. The question to ask is, is Britain, at nearly 230,000

km<sup>2</sup>, really an island for a 20-g (Silva and Downing 1995) house mouse (*Mus musculus*)? Probably the most logical approach is to tailor the definition in any particular case to the taxon (Haila 1990).

#### Optimal Body Size

Optimal body size is an elegant explanation for the pattern observed by Lomolino (1983, 1985), but little support can be found in our data for theories of body size optimality. Brown et al. (1993) suggested on physiological grounds that 100 g is approximately the optimal body mass for a terrestrial mammal and that patterns of variation in body size of insular mammals support this hypothesis. Marquet and Taper (1998) similarly felt that critical body mass in island mammals is "about 100 g." They have shown that very small islands do not support species that are either much larger or much smaller than about 100 g and that increasingly larger and smaller species persist only on land-masses of progressively larger area. This observation led them to predict that the smaller the island and the farther the mass of a species is from 100 g, the larger the expected change in body mass necessary for species survival. Maurer et al. (1992) suggested that 250 g is approximately the body mass at which island forms tend not to diverge from their mainland relatives. They interpreted this as the size at which no ecological advantage is gained by evolving toward either larger or smaller size. Damuth (1993) likewise claimed there is an optimal body size, but he argued from population density scaling that it is approximately 1 kg. He argued further that the relatively sparse competition and predation pressures on islands enable mammals to evolve toward this optimal size.

Thus, optimal mammal body sizes suggested in the literature span a full order of magnitude (or slightly more, if alternative values of  $b_0$  and  $b_1$  mentioned by Brown et al. [1993, p. 577] are used). Insular mammal data that are claimed to support these hypotheses themselves span an order of magnitude. The insular mammal mass ranges of Marquet and Taper (1998) predict a logarithmic no-change value of 1.71 (table 1 in Marquet and Taper 1998), corresponding to a mass of 51 g, whereas data of Lomolino (1983) point to a no-change mass of 701 g for all mammals. Lomolino's data for carnivores point to a no-change mass of 2,477 g, and so, taken together, values advanced as supporting the island rule span two orders of magnitude. Our carnivore data do not show the correlation between mass and  $S_R$  claimed to support these theories. From our admittedly nonsignificant regressions, the extrapolated predicted sizes for which no size change is expected span 23 orders of magnitude and include masses never attained by any carnivore. The large discrepancy between the results of different analyses suggests that data from insular car-

nivores cannot be advanced as supporting an optimal body size and that simple theoretical optimal body sizes do not explain size patterns for insular carnivores.

### Conclusions

Patterns of variation in body size of insular carnivores are more complicated than the island rule (Lomolino 1985) predicts. Island carnivores do often differ from mainland ones in very striking ways. However, they do not do so in a very predictable and apparent pattern. The size of an insular carnivore is influenced by several selective forces (Mayr 1963; Angerbjörn 1986; Lawton 1996), from abiotic ones through life-history variables to the composition of the sympatric fauna. With so many factors influencing size (cf. Case 1978; Dayan and Simberloff 1998; Yom-Tov et al. 1999) and with a large number of species that differ from one another not only in size but in a host of other ways, not to mention a large number of islands of various sizes and different biotic and abiotic settings, it is perhaps not surprising that no clear pattern emerges. A detailed ecological study is needed to decipher the nature of these factors for every insular population.

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Table 1

Island-mainland comparisons (CBL)

Species	Log mass (g)	Size (relative)	Island	<i>n</i>	Mainland	<i>n</i>	Sex
<i>Alopex lagopus</i>	3.42	100.58%	St. Lawrence	51	Alaska W of 156°W	34	F
<i>A. lagopus</i>	3.42	98.04%	St. Matthew	7	Alaska W of 156°W	34	F
<i>A. lagopus</i>	3.53	99.47%	Flaherty	5	Quebec N of 55°N	21	M
<i>A. lagopus</i>	3.53	100.19%	St. Lawrence	56	Alaska W of 156°W	36	M
<i>A. lagopus</i>	3.53	99.56%	St. Matthew	9	Alaska W of 156°W	36	M
<i>Aonyx cinerea</i>	3.48 (3)	100.04%	Java	15	Sumatra	6	F
<i>Arctogalidia trivirgata</i>	3.19 (5)	97.89%	Borneo	19	Indochina S of 16°N	7	F
<i>A. trivirgata</i>	3.19 (5)	98.49%	Sumatra	8	Indochina S of 16°N	7	F
<i>A. trivirgata</i>	3.38 (6)	99.62%	Borneo	22	Indochina S of 16°N	10	M
<i>Canis aureus</i>	4.05 (6)	101.38%	Sri Lanka	5	India S of 20°N	14	M
<i>Canis lupus</i>	4.52 (6)	94.93%	Prince of Wales	15	Alaska and BC, 54°62°N, 127°150°W	22	F
<i>C. lupus</i>	4.52 (6)	93.70%	Vancouver Island	27	BC S of 55°N, W of 120°W	7	F
<i>C. lupus</i>	4.54 (6)	92.64%	Prince of Wales	10	Alaska and BC, 54°62°N, 127°150°W	12	M
<i>C. lupus</i>	4.54 (6)	96.22%	Vancouver Island	35	BC S of 55°N, W of 120°W	11	M
<i>Felis bengalensis</i>	3.35 (6)	93.61%	Borneo	6	Malaya S Of 7°N	6	F
<i>F. bengalensis</i>	3.35 (6)	95.24%	Java	19	Sumatra	8	F
<i>F. bengalensis</i>	3.35 (6)	96.70%	Sumatra	8	Malaya S Of 7°N	6	F
<i>F. bengalensis</i>	3.52 (6)	94.96%	Bali	5	Java	18	M
<i>F. bengalensis</i>	3.52 (6)	93.30%	Borneo	12	Malaya S Of 12°N	5	M
<i>F. bengalensis</i>	3.52 (6)	99.74%	Java	18	Sumatra	7	M
<i>F. bengalensis</i>	3.52 (6)	95.63%	Sumatra	7	Malaya S Of 12°N	5	M
<i>Felis concolor</i>	4.63 (6)	102.21%	Vancouver Island	12	BC S of 55°N, W of 120°W	6	F
<i>Felis lynx</i>	3.94	96.58%	Newfoundland	26	Main, Labrador, and Quebec E of 67°N	5	M
<i>Felis planiceps</i>	3.20 (6)	99.57%	Borneo	9	Malaya	9	M
<i>Felis silvestris</i>	3.70 (1)	97.50%	Britain	21	France N of 47°N and Belgium	6	M
<i>Herpestes smithii</i>	3.32 (1)	100.29%	Sri Lanka	5	India S of 19°N	9	M
<i>Herpestes urva</i>	3.30 (1)	91.65%	Taiwan	8	China S of 27°N, E of 118°E	5	F
<i>Lontra canadensis</i>	3.91	104.22%	Vancouver Island	7	BC and Washington, 45°55°N, W of 121°W	16	F
<i>L. canadensis</i>	3.93	102.97%	Baranof	6	Alaska and BC, 55° 59°N, 126°150°W	6	M
<i>L. canadensis</i>	3.93	102.20%	Chichagof	6	Alaska and BC, 52° 59°N, 126°150°W	6	M
<i>L. canadensis</i>	3.93	101.18%	Prince of Wales	5	Alaska and BC, 52° 59°N, 126°150°W	6	M
<i>Lutra lutra</i>	3.83 (6)	97.16%	Britain	8	France N of 46°N and Belgium	6	F
<i>L. lutra</i>	3.83 (6)	101.81%	Ireland	15	Britain	8	F
<i>L. lutra</i>	3.83 (6)	97.15%	Sri Lanka	8	India S of 26°N	6	F
<i>L. lutra</i>	4.00 (6)	101.30%	Ireland	18	Britain	10	M
<i>Martes americana</i>	2.8	101.82%	Chichagof	34	Alaska and BC, 54°62°N, 127°150°W	20	F
<i>M. americana</i>	2.8	99.66%	Mitkof	16	Alaska and BC, 54°62°N, 127°150°W	20	F
<i>M. americana</i>	2.8	102.88%	Moresby	15	BC between 50° and 55°N, W of 126°W	16	F
<i>M. americana</i>	2.8	99.63%	Prince of Wales	8	Alaska and BC, 54°62°N, 127°150°W	20	F
<i>M. americana</i>	2.8	100.15%	Vancouver Island	81	BC and Washington, 45°54°N, W of 121°W	25	F
<i>M. americana</i>	3.14	102.28%	Chichagof	53	Alaska and BC, 54°62°N, 127°150°W	25	M
<i>M. americana</i>	3.14	99.35%	Mitkof	26	Alaska and BC, 54°62°N, 127°150°W	25	M
<i>M. americana</i>	3.14	106.79%	Moresby	33	BC between 50° and 55°N, W of 126°W	22	M
<i>M. americana</i>	3.14	102.40%	Prince of Wales	12	Alaska and BC, 54°62°N, 127°150°W	25	M
<i>M. americana</i>	3.14	103.55%	Vancouver Island	115	BC and Washington, 45°54°N, W of 121°W	44	M
<i>Martes flavigula</i>	3.40 (3)	92.68%	Borneo	18	Malaya and Thailand S of 10°N	12	F
<i>Martes foina</i>	3.13	97.61%	Sjaelland	10	Denmark (Jutland)	5	M

<i>Martes martes</i>	3.22 (7)	100.66%	Sjaelland	8	Denmark (Jutland)	6	M
<i>Meles meles</i>	4.00 (7)	93.14%	Ireland	31	Britain	12	F
<i>M. meles</i>	4.00 (7)	92.94%	Britain	12	France N of 48°N, Netherlands and Belgium	10	F
<i>M. meles</i>	4.00 (7)	100.10%	Sjaelland	14	Denmark (Jutland)	52	F
<i>M. meles</i>	4.06 (7)	97.80%	Ireland	21	Britain	25	M
<i>M. meles</i>	4.06 (7)	105.17%	Britain	25	France N of 48°N, Netherlands and Belgium	15	M
<i>M. meles</i>	4.06 (7)	101.71%	Sjaelland	17	Denmark (Jutland)	55	M
<i>Melogale moschata</i>	2.91	100.03%	Hainan	8	Vietnam and China, 21°26°N, E of 102°E	6	F
<i>M. moschata</i>	2.9	95.70%	Taiwan	21	China S of 30°N, E of 113°E	5	M
<i>Mustela erminea</i>	2.32	105.10%	Britain	52	Belgium	47	F
<i>M. erminea</i>	2.32	91.46%	Ireland	43	Britain	52	F
<i>M. erminea</i>	1.91	99.94%	Mitkof	8	Alaska and BC, 54°61°N, 127°150°W	14	F
<i>M. erminea</i>	1.91	103.10%	Newfoundland	8	Labrador, NB, NS	26	F
<i>M. erminea</i>	2.32	99.77%	Sjaelland	20	Denmark (Jutland)	6	F
<i>M. erminea</i>	1.91	97.05%	Tukarak	12	Ontario, 50°60°N, 75°90°W	5	F
<i>M. erminea</i>	1.91	98.94%	Vancouver Island	7	BC and Washington, 46°54°N, W of 121°W	24	F
<i>M. erminea</i>	2.69	106.95%	Britain	59	Belgium, Netherlands	45	M
<i>M. erminea</i>	2.69	95.89%	Ireland	67	Britain	59	M
<i>M. erminea</i>	2.35	97.43%	Kodiak	10	Alaska S of 61°N, 149°159°W	8	M
<i>M. erminea</i>	2.35	98.61%	Mitkof	18	Alaska and BC, 54°61°N, 127°150°W	38	M
<i>M. erminea</i>	2.35	103.01%	Newfoundland	45	Labrador, NB, NS	60	M
<i>M. erminea</i>	2.35	97.48%	Prince of Wales	8	Alaska and BC, 54°61°N, 127°150°W	38	M
<i>M. erminea</i>	2.69	103.02%	Sjaelland	19	Denmark, Germany, and Sweden, 53°60°N	13	M
<i>M. erminea</i>	2.35	95.91%	Tukarak	12	Ontario and Quebec, 50°60°N, 75°90°W	18	M
<i>M. erminea</i>	2.35	95.48%	Vancouver Island	15	BC and Washington, 46°54°N, W of 121°W	69	M
<i>Mustela nivalis</i>	1.77 (7)	104.69%	Britain	36	Belgium	82	F
<i>M. nivalis</i>	2.06 (7)	109.74%	Britain	111	Belgium	155	M
<i>M. nivalis</i>	2.06 (7)	102.74%	Sardinia	9	France, Spain, and Italy S of 45°N, E of 0°E	12	M
<i>M. nivalis</i>	2.06 (7)	104.57%	Sjaelland	9	Denmark, Germany, and Sweden, 53°60°N	5	M
<i>Mustela putorius</i>	2.84 (7)	102.05%	Britain	13	France N of 49°N, Netherlands and Belgium	47	F
<i>M. putorius</i>	2.84 (7)	99.19%	Sjaelland	8	Denmark (Jutland)	8	F
<i>M. putorius</i>	3.05 (7)	100.09%	Britain	38	France N of 49°N, Netherlands and Belgium	82	M
<i>M. putorius</i>	3.05 (7)	99.64%	Sjaelland	16	Denmark (Jutland)	17	M
<i>Mustela sibirica</i>	2.60 (2)	86.43%	Honshu	13	E Asia, 30°45°N, E of 115°E	6	F
<i>M. sibirica</i>	2.89	91.51%	Honshu	87	E Asia, 30°45°N, E of 115°E	7	M
<i>M. sibirica</i>	2.89	103.84%	Kyushu	5	Honshu	87	M
<i>M. sibirica</i>	2.89	98.15%	Sado	9	Honshu	87	M
<i>M. sibirica</i>	2.89	95.43%	Shikoku	5	Honshu	87	M
<i>Mustela vison</i>	2.89	99.33%	Baranof	13	Alaska S of 61°N, E of 150°W	11	F
<i>M. vison</i>	2.89	98.02%	Chichagof	7	Alaska S of 61°N, E of 150°W	11	F
<i>M. vison</i>	2.89	100.12%	Nunivak	10	Alaska, 55°65°N, W of 157°W	7	F
<i>M. vison</i>	2.89	99.36%	Vancouver Island	19	BC S of 53°N, W of 121°W	9	F
<i>M. vison</i>	3.12	99.15%	Baranof	29	Alaska S of 61°N, E of 150°W	14	M
<i>M. vison</i>	3.12	98.70%	Chichagof	8	Alaska S of 61°N, E of 150°W	14	M
<i>M. vison</i>	3.12	97.51%	Nunivak	11	Alaska, 55°65°N, W of 157°W	32	M
<i>M. vison</i>	3.12	104.39%	Vancouver Island	19	BC S of 53°N, W of 121°W	8	M
<i>Nyctereutes procyonoides</i>	3.69	98.98%	Kyushu	5	Honshu	40	M
<i>Paguma larvata</i>	3.47	93.93%	Borneo	9	Malaya S of 9°N	6	F
<i>P. larvata</i>	3.47	101.46%	Sumatra	9	Malaya S of 9°N	6	F

<i>P. larvata</i>	3.78 (4)	92.00%	Borneo	6	Malaya S of 9°N	6	M
<i>P. larvata</i>	3.78 (4)	101.29%	Sumatra	5	Malaya S of 9°N	6	M
<i>Panthera tigris</i>	5.08 (3)	102.23%	Java	6	Sumatra	6	M
<i>P. tigris</i>	5.34 (3)	96.07%	Sumatra	6	Malaya, Vietnam, and Thailand S of 17°S	7	M
<i>Paradoxurus hermaphroditus</i>	3.51 (6)	94.94%	Borneo	11	Malaya and Thailand S of 9°N	18	F
<i>P. hermaphroditus</i>	3.51 (6)	108.14%	Java	30	Sumatra	17	F
<i>P. hermaphroditus</i>	3.51 (6)	100.92%	Sumatra	15	Malaya and Thailand S of 9°N	18	F
<i>P. hermaphroditus</i>	3.52 (1)	92.19%	Bali	6	Java	14	M
<i>P. hermaphroditus</i>	3.52 (1)	93.58%	Borneo	23	Malaya and Thailand S of 9°N	24	M
<i>P. hermaphroditus</i>	3.52 (1)	105.02%	Java	14	Sumatra	17	M
<i>P. hermaphroditus</i>	3.52 (1)	97.82%	Palawan	5	Borneo	23	M
<i>P. hermaphroditus</i>	3.52 (1)	101.99%	Sumatra	17	Malaya and Thailand S of 9°N	24	M
<i>P. hermaphroditus</i>	3.52 (1)	98.58%	Terutau	7	Malaya and Thailand S of 9°N	24	M
<i>Procyon lotor</i>	3.81 (6)	96.41%	Vancouver Island	14	Washington N of 46°N, W of 120°W	5	F
<i>P. lotor</i>	3.93 (6)	93.41%	No name key	5	Florida	19	M
<i>P. lotor</i>	3.93 (6)	96.62%	Vancouver Island	16	Washington N of 46°N, W of 120°W	5	M
<a href="#">Urocyon littoralis 1</a>	3.50 (6)	81.60%	San Clemente	5	Baja California and California, 28°37°N	9	F
<a href="#">Urocyon littoralis 1</a>	3.59 (6)	91.41%	Santa Catalina	5	Baja California S of 31°N	5	M
<a href="#">Urocyon littoralis 1</a>	3.59 (6)	81.64%	Santa Rosa	6	Baja California and California, 30°37°N	17	M
<i>Ursus americanus</i>	5.19 (6)	98.25%	Kuiu	6	Kupreanof	5	M
<i>U. americanus</i>	5.19 (6)	99.31%	Kupreanof	5	Alaska S of 61°N, E of 136°W	9	M
<i>U. americanus</i>	5.19 (6)	98.33%	Vancouver Island	6	BC S of 55°N, W of 122°W	7	M
<i>Ursus arctos</i>	5.48 (1)	97.38%	Admiralty	18	Alaska and BC, 54°61°N, 127°150°W	12	F
<i>U. arctos</i>	5.48 (1)	99.86%	Chichagof	9	Alaska and BC, 54°61°N, 127°150°W	12	F
<i>U. arctos</i>	5.48 (1)	100.61%	Kodiak	12	Alaska S of 62°N, 149°159°W	24	F
<i>U. arctos</i>	5.65 (1)	95.20%	Admiralty	34	Alaska and BC, 54°61°N, 127°150°W	5	M
<i>U. arctos</i>	5.65 (1)	97.37%	Chichagof	11	Alaska and BC, 54°61°N, 127°150°W	5	M
<i>U. arctos</i>	5.65 (1)	103.93%	Kodiak	8	Alaska S of 62°N, 149°159°W	13	M
<i>Viverra zibetha</i>	3.87 (6)	101.31%	Sulawesi	6	Borneo	40	M
<i>Viverricula indica</i>	3.41	93.52%	Hainan	8	Laos, Vietnam, and China, 15°26°N, E of 102°E	12	F
<i>V. indica</i>	3.41	91.75%	Taiwan	6	China, 23°26°N, E of 113°E	11	F
<i>V. indica</i>	3.47 (6)	95.30%	Hainan	5	Laos, Vietnam, and China, 15°26°N, E of 102°E	22	M
<i>V. indica</i>	3.47 (6)	98.69%	Sri Lanka	10	India S of 23°N	6	M
<i>V. indica</i>	3.47 (6)	94.96%	Taiwan	7	China, 23°26°N, E of 113°E	13	M
<i>Vulpes vulpes</i>	3.74	101.00%	Britain	23	Belgium	18	F
<i>V. vulpes</i>	3.74	98.70%	Ireland	45	Britain	23	F
<i>V. vulpes</i>	3.63 (3)	102.58%	Newfoundland	9	Labrador, NB, NS; Maine E of 70°W	9	F
<i>V. vulpes</i>	3.85	102.08%	Britain	29	Belgium	21	M
<i>V. vulpes</i>	3.85	99.99%	Ireland	51	Britain	29	M
<i>V. vulpes</i>	3.7	101.94%	Newfoundland	6	Labrador, NB, NS; Maine E of 70°W	18	M
<i>V. vulpes</i>	3.7	105.41%	Tukarak	7	Ontario and Quebec, 50°60°N, 76°85°W	10	M

Note: Size (relative) is the relative CBL of the insular population (as a fraction of the mainland value of the mainland population).

1 Interspecific comparisons (see text).

Sources for the mass data: 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, the body mass data are based on tag data for specimens measured in this study.

BC is British Columbia. Malaya is the Malay peninsula. NB is New Brunswick. NS is Nova Scotia.

Table 2

Island-mainland comparisons (upper canine diameter)

Species	Log mass (g)	Size (relative)	Island	n	Mainland	n	Sex
<i>Alopex lagopus</i>	3.42	99.72%	St. Lawrence	26	Alaska W of 156°W	32	F
<i>A. lagopus</i>	3.42	93.47%	St. Matthew	9	Alaska W of 156°W	32	F
<i>A. lagopus</i>	3.53	99.85%	St. Lawrence	36	Alaska W of 156°W	30	M
<i>A. lagopus</i>	3.53	93.49%	St. Matthew	7	Alaska W of 156°W	30	M
<i>Aonyx cinerea</i>	3.48 (3)	103.65%	Java	14	Sumatra	8	F
<i>A. cinerea</i>	3.48 (3)	100.04%	Borneo	8	Malaya S of 9°N	6	M
<i>A. cinerea</i>	3.48 (3)	100.44%	Java	20	Sumatra	5	M
<i>A. cinerea</i>	3.48 (3)	101.20%	Sumatra	5	Malaya S of 9°N	6	M
<i>Arctogalidia trivirgata</i>	3.38 (4)	99.27%	Borneo	25	Malaya S of 7°N	7	M
<i>Canis aureus</i>	4.05 (4)	101.89%	Sri Lanka	5	India S of 19°N	11	M
<i>Canis lupus</i>	4.52 (4)	97.67%	Prince of Wales	16	Alaska and BC, 54°61'N, 127°143'W	11	F
<i>C. lupus</i>	4.52 (4)	93.18%	Vancouver Island	18	BC S of 55°N, W of 122°W	7	F
<i>C. lupus</i>	4.54 (4)	93.72%	Prince of Wales	6	Alaska and BC, 54°61'N, 127°147'W	12	M
<i>C. lupus</i>	4.54 (4)	94.92%	Vancouver Island	28	BC and Washington, 46°55'N, W of 122°W	12	M
<i>Felis bengalensis</i>	3.35 (4)	90.74%	Borneo	9	Malaya and Thailand S of 7°N	6	F
<i>F. bengalensis</i>	3.35 (4)	99.41%	Hainan	5	Vietnam and China, 16°26'N, E of 105°E	5	F
<i>F. bengalensis</i>	3.35 (4)	96.60%	Java	22	Sumatra	10	F
<i>F. bengalensis</i>	3.35 (4)	95.46%	Sumatra	10	Malaya and Thailand S of 7°N	6	F
<i>F. bengalensis</i>	3.52 (4)	93.64%	Bali	6	Java	19	M
<i>F. bengalensis</i>	3.52 (4)	90.73%	Borneo	14	Malaya and Thailand S of 15°N	7	M
<i>F. bengalensis</i>	3.52 (4)	89.09%	Hainan	5	Vietnam and China, 16°26'N, E of 103°E	8	M
<i>F. bengalensis</i>	3.52 (4)	96.23%	Java	19	Sumatra	8	M
<i>F. bengalensis</i>	3.52 (4)	100.25%	Palawan	5	Borneo	14	M
<i>F. bengalensis</i>	3.52 (4)	93.91%	Sumatra	8	Malaya and Thailand S of 15°N	7	M
<i>Felis concolor</i>	4.63 (4)	99.40%	Vancouver Island	12	BC and Washington, 46°54'N, W of 121°W	5	F
<i>F. concolor</i>	4.81 (4)	104.31%	Vancouver Island	11	BC and Washington, 46°51'N, W of 122°W	6	M
<i>Felis planiceps</i>	3.20 (4)	98.90%	Borneo	9	Malaya S of 9°N	9	M
<i>Felis silvestris</i>	3.63 (1)	93.44%	Britain	12	Belgium and France N of 48°N	6	F
<i>F. silvestris</i>	3.70 (1)	99.28%	Britain	21	Belgium and France N of 47°N	5	M
<i>Herpestes smithii</i>	3.11 (1)	93.45%	Sri Lanka	5	India S of 22°N	5	F
<i>Herpestes urva</i>	3.3 (1)	98.26%	Taiwan	7	China, 25°27'N, E of 118°E	6	F
<i>Herpestes vitticollis</i>	3.46 (4)	103.65%	Sri Lanka	7	India S of 12°N	5	M
<i>Lutra canadensis</i>	3.91	105.87%	Vancouver Island	7	BC and Washington, 47°55'N, W of 124°W	8	F
<i>Lutra lutra</i>	3.83 (4)	98.42%	Britain	7	Belgium and France N of 47°N	6	F
<i>L. lutra</i>	3.83 (4)	95.92%	Ireland	19	Britain	7	F
<i>L. lutra</i>	3.83 (4)	96.46%	Sri Lanka	8	India S of 26°N	5	F
<i>L. lutra</i>	4.00 (4)	107.92%	Britain	10	Belgium, Netherlands, and France N of 47°N	5	M
<i>L. lutra</i>	4.00 (4)	96.92%	Ireland	19	Britain	10	M
<i>Martes americana</i>	2.8	99.04%	Chichagof	32	Alaska and BC, 54°61'N, 129°135'W	22	F
<i>M. americana</i>	2.8	106.70%	Louise Island	8	BC, 50°55'N, W of 126°W	14	F
<i>M. americana</i>	2.8	102.53%	Mitkof	15	Alaska and BC, 54°61'N, 129°135'W	22	F
<i>M. americana</i>	2.8	106.77%	Moresby	15	BC, 50°55'N, W of 126°W	14	F
<i>M. americana</i>	2.8	94.93%	Prince of Wales	7	Alaska and BC, 54°61'N, 129°135'W	22	F
<i>M. americana</i>	2.8	102.72%	Vancouver Island	80	BC and Washington, 47°55'N, W of 122°W	28	F
<i>M. americana</i>	3.14	98.90%	Chichagof	49	Alaska and BC, 54°61'N, 127°147'W	29	M
<i>M. americana</i>	3.14	107.53%	Louise Island	6	BC, 50°55'N, W of 125°W	31	M
<i>M. americana</i>	3.14	104.15%	Mitkof	26	Alaska and BC, 54°61'N, 127°147'W	29	M
<i>M. americana</i>	3.14	109.15%	Moresby	30	BC, 50°55'N, W of 125°W	31	M
<i>M. americana</i>	3.14	96.96%	Prince of Wales	11	Alaska and BC, 54°61'N, 127°147'W	29	M
<i>M. americana</i>	3.14	107.53%	Vancouver Island	69	BC and Washington, 49°51'N, W of 122°W	27	M
<i>Martes flavigula</i>	3.40 (3)	93.96%	Borneo	20	Malaya Burma and Thailand S of 13°N	12	F
<i>M. flavigula</i>	3.40 (3)	92.47%	Borneo	9	Malaya Burma and Thailand S of 15°N	5	M
<i>M. flavigula</i>	3.40 (3)	94.18%	Sumatra	6	Malaya Burma and Thailand S of 15°N	5	M
<i>Martes foina</i>	3.13	97.39%	Sjaelland	10	Denmark (Jutland)	6	M

<i>Martes martes</i>	3.22 (5)	101.65%	Britain	7	Belgium and France N of 48°N	23	M
<i>M. martes</i>	3.22 (5)	95.50%	Ireland	12	Britain	7	M
<i>M. martes</i>	3.22 (5)	95.44%	Sjaelland	9	Denmark (Jutland)	8	M
<i>Meles meles</i>	4.00 (5)	92.47%	Britain	17	Belgium, Netherlands, and France N of 48°N	10	F
<i>M. meles</i>	4.00 (5)	104.54%	Ireland	28	Britain	17	F
<i>M. meles</i>	4.00 (5)	100.38%	Sjaelland	21	Denmark (Jutland)	81	F
<i>M. meles</i>	4.06 (5)	101.78%	Britain	17	Belgium, Netherlands, and France N of 48°N	11	M
<i>M. meles</i>	4.06 (5)	97.44%	Ireland	20	Britain	17	M
<i>M. meles</i>	4.06 (5)	103.20%	Sjaelland	21	Denmark (Jutland)	69	M
<i>Melogale moschata</i>	2.91	97.94%	Hainan	8	Vietnam and China, 22°26'N, E of 103°E	5	F
<i>M. moschata</i>	2.91	107.42%	Taiwan	26	China S of 30°N, E of 113°E	6	F
<i>M. moschata</i>	2.9	105.17%	Hainan	5	Laos, Vietnam, and China, 21°26'N, E of 102°E	10	M
<i>M. moschata</i>	2.9	99.98%	Taiwan	20	China S of 30°N, E of 113°E	6	M
<i>Mustela erminea</i>	2.32	106.66%	Britain	56	Belgium	47	F
<i>M. erminea</i>	2.32	86.69%	Ireland	26	Britain	56	F
<i>M. erminea</i>	1.91	95.49%	Mitkof	12	Alaska and BC, 55°61'N, 127°150'W	10	F
<i>M. erminea</i>	1.91	107.31%	Newfoundland	10	SE Canada and Maine, 44°54'N, E of 70°W	34	F
<i>M. erminea</i>	2.32	103.05%	Sjaelland	14	Denmark (Jutland)	8	F
<i>M. erminea</i>	1.91	91.95%	Vancouver Island	9	BC and Washington, 49°55'N, W of 122°W	32	F
<i>M. erminea</i>	2.56	110.09%	Britain	71	Belgium	45	M
<i>M. erminea</i>	2.56	95.77%	Ireland	60	Britain	71	M
<i>M. erminea</i>	2.35	101.73%	Kodiak	10	Alaska S of 61°N, 149°159'W	7	M
<i>M. erminea</i>	2.35	91.74%	Mitkof	26	Alaska and BC, 54°61'N, 127°147'W	36	M
<i>M. erminea</i>	2.35	105.04%	Newfoundland	47	SE Canada and Maine, 44°54'N, E of 70°W	92	M
<i>M. erminea</i>	2.35	98.22%	Prince of Wales	9	Alaska and BC, 54°61'N, 127°147'W	36	M
<i>M. erminea</i>	2.56	101.37%	Sjaelland	18	Denmark (Jutland)	7	M
<i>M. erminea</i>	2.35	100.19%	Tukarak	13	Ontario and Quebec, 50°60'N, 75°90'W	33	M
<i>M. erminea</i>	2.35	77.82%	Vancouver Island	18	BC and Washington, 48°55'N, W of 122°W	45	M
<i>Mustela nivalis</i>	1.77 (5)	100.23%	Britain	38	Belgium	122	F
<i>M. nivalis</i>	2.06 (5)	106.15%	Britain	150	Belgium	120	M
<i>M. nivalis</i>	2.06 (5)	98.63%	Sardinia	10	France, Spain, and Italy S of 45°N, E of 0	11	M
<i>Mustela putorius</i>	2.84 (5)	96.22%	Britain	16	Belgium	48	F
<i>M. putorius</i>	2.84 (5)	95.12%	Sjaelland	8	Denmark (Jutland)	10	F
<i>M. putorius</i>	3.05 (5)	93.80%	Britain	45	Belgium	76	M
<i>M. putorius</i>	3.05 (5)	95.74%	Sjaelland	16	Denmark (Jutland)	17	M
<i>Mustela sibirica</i>	2.6 (2)	88.43%	Honshu	13	E Asia, 30°39'N, E of 116°E	9	F
<i>M. sibirica</i>	2.89	92.64%	Honshu	97	E Asia, 30°46'N, E of 115°E	7	M
<i>M. sibirica</i>	2.89	103.29%	Kyushu	5	Honshu	97	M
<i>M. sibirica</i>	2.89	96.42%	Sado	8	Honshu	97	M
<i>M. sibirica</i>	2.89	92.77%	Shikoku	6	Honshu	97	M
<i>Mustela vison</i>	2.89	102.27%	Baranof	13	Alaska, 55°61'N, 132°150'W	11	F
<i>M. vison</i>	2.89	100.04%	Chichagof	5	Alaska, 55°61'N, 132°150'W	11	F
<i>M. vison</i>	2.89	108.87%	Vancouver Island	18	BC S of 55°N, W of 123°W	6	F
<i>M. vison</i>	3.12	106.02%	Baranof	27	Alaska and BC, 55°61'N, 127°150'W	15	M
<i>M. vison</i>	3.12	93.40%	Nunivak	9	Alaska, 55°62'N, W of 157°W	28	M
<i>M. vison</i>	3.12	104.59%	Vancouver Island	21	BC S of 55°N, W of 122°W	7	M
<i>Nyctereutes procyonoides</i>	3.69	96.29%	Kyushu	6	Honshu	50	M
<i>N. procyonoides</i>	3.69	99.12%	Okushiri Island	6	Honshu	50	M
<i>Paguma larvata</i>	3.47	90.40%	Borneo	11	Malaya and Thailand S of 9°N	7	F
<i>P. larvata</i>	3.47	103.63%	Sumatra	9	Malaya and Thailand S of 9°N	7	F
<i>Panthera pardus</i>	4.48 (4)	99.11%	Sri Lanka	9	India S of 28°N	7	M
<i>Panthera tigris</i>	5.08 (3)	104.23%	Java	7	Sumatra	6	M
<i>Paradoxurus hermaphroditus</i>	3.51 (4)	93.23%	Borneo	11	Malaya and Thailand S of 8°N	13	F
<i>P. hermaphroditus</i>	3.51 (4)	104.88%	Java	30	Sumatra	14	F
<i>P. hermaphroditus</i>	3.51 (4)	106.15%	Palawan	5	Borneo	11	F
<i>P. hermaphroditus</i>	3.51 (4)	104.86%	Sumatra	13	Malaya and Thailand S of 8°N	13	F
<i>P. hermaphroditus</i>	3.52 (1)	93.32%	Bali	5	Java	24	M
<i>P. hermaphroditus</i>	3.52 (1)	90.28%	Borneo	23	Malaya and Thailand S of 10°N	25	M
<i>P. hermaphroditus</i>	3.52 (1)	102.76%	Java	24	Sumatra	15	M
<i>P. hermaphroditus</i>	3.52 (1)	99.53%	Palawan	8	Borneo	23	M
<i>P. hermaphroditus</i>	3.52 (1)	99.64%	Sumatra	15	Malaya and Thailand S of 10°N	25	M
<i>P. hermaphroditus</i>	3.52 (1)	97.48%	Terutau	10	Malaya and Thailand S of 10°N	25	M

<i>Procyon lotor</i>	3.81 (4)	99.19%	Elliott's key	5	Florida	19	F
<i>P. lotor</i>	3.93 (4)	102.66%	Big pine key	5	Florida	18	M
<i>P. lotor</i>	3.93 (4)	95.92%	Vancouver Island	17	Washington N of 46°N, W of 121°W	5	M
<a href="#">Urocyon littoralis 1</a>	3.50 (4)	97.90%	San Clemente	6	Baja California and California, 28°37'N	15	F
<a href="#">Urocyon littoralis 1</a>	3.59 (4)	93.03%	Santa Catalina	5	Baja California S of 31°N	8	M
<a href="#">Urocyon littoralis 1</a>	3.59 (4)	95.72%	Santa Rosa	6	Baja California and California, 30°37'N	20	M
<i>Ursus americanus</i>	5.19 (4)	100.32%	Vancouver Island	5	BC S of 55°N, W of 122°W	5	M
<i>Ursus arctos</i>	5.48 (1)	98.97%	Admiralty	7	Alaska and BC, 55°61'N, 127°150'W	7	F
<i>U. arctos</i>	5.48 (1)	100.40%	Chichagof	6	Alaska and BC, 55°61'N, 127°150'W	7	F
<i>U. arctos</i>	5.48 (1)	100.45%	Kodiak	9	Alaska S of 62°N, 149°162'W	14	F
<i>U. arctos</i>	5.65 (1)	93.18%	Admiralty	15	Alaska and BC, 55°63'N, 129°151'W	6	M
<i>U. arctos</i>	5.65 (1)	96.66%	Chichagof	7	Alaska and BC, 55°63'N, 129°151'W	6	M
<i>U. arctos</i>	5.65 (1)	102.89%	Kodiak	7	Alaska S of 61°N, 149°162'W	10	M
<i>Viverra zangalla</i>	3.87 (4)	102.95%	Sulawesi	7	Borneo	37	M
<i>Viverricula indica</i>	3.41	90.43%	Hainan	6	Vietnam and China, 21°26'N, E of 106°E	11	F
<i>V. indica</i>	3.41	87.01%	Taiwan	6	China, 23°26'N, E of 113°E	10	F
<i>V. indica</i>	3.47 (4)	101.40%	Sri Lanka	11	India S of 15°N	5	M
<i>V. indica</i>	3.47 (4)	90.28%	Taiwan	7	China, 23°26'N, E of 113°E	11	M
<i>Vulpes vulpes</i>	3.74	103.30%	Britain	19	Belgium and France N of 48°N	18	F
<i>V. vulpes</i>	3.74	96.21%	Ireland	54	Britain	19	F
<i>V. vulpes</i>	3.63 (3)	107.05%	Newfoundland	10	SE Canada and Maine, 44°54'N, E of 70°W	10	F
<i>V. vulpes</i>	3.85	109.13%	Britain	27	Belgium and France N of 48°N	29	M
<i>V. vulpes</i>	3.85	95.48%	Ireland	72	Britain	27	M
<i>V. vulpes</i>	3.7	111.16%	Newfoundland	6	SE Canada and Maine, 44°54'N, E of 70°W	22	M

Note: Size (relative) is the relative upper canine diameter of the insular population (as a fraction of the mainland value of the mainland population).

### 1 Interspecific comparisons (see text).

Sources for the mass data:

Creel and Macdonald 1995 (1), Johnson et al. 2000 (2), Nowak 1999 (3), Silva and Downing 1995 (4), and Weckerly 1998 (5).

Where no source is given, the body mass data are based on tag data for specimens measured in this study.

BC is British Columbia. Malaya is the Malay peninsula.

Table 3

## Island-mainland comparisons (M1)

Species	Log mass (g)	Size (relative)	Island	n	Mainland	n	Sex
<i>Alopex lagopus</i>	3.42	99.27%	St. Lawrence	44	Alaska W of 156°W	33	F
<i>A. lagopus</i>	3.42	94.82%	St. Matthew	8	Alaska W of 156°W	33	F
<i>A. lagopus</i>	3.42	99.72%	Flaherty	6	Quebec N of 55°N	22	M
<i>A. lagopus</i>	3.53	100.06%	St. Lawrence	49	Alaska W of 156°W	36	M
<i>A. lagopus</i>	3.53	96.87%	St. Matthew	7	Alaska W of 156°W	36	M
<i>Aonyx cinerea</i>	3.48 (4)	102.45%	Java	14	Sumatra	8	F
<i>A. cinerea</i>	3.48 (4)	104.74%	Borneo	7	Malaya and Thailand S of 9°N	6	M
<i>A. cinerea</i>	3.48 (4)	98.64%	Java	19	Sumatra	5	M
<i>A. cinerea</i>	3.48 (4)	105.43%	Sumatra	5	Malaya and Thailand S of 9°N	6	M
<i>Arctogalidia trivirgata</i>	3.38 (5)	108.33%	Borneo	25	Malaya	5	M
<i>Canis aureus</i>	4.05 (5)	99.22%	Sri Lanka	5	India S of 19°N	12	M
<i>Canis lupus</i>	4.52 (5)	98.66%	Kuiu	5	Kupreanof	6	F
<i>C. lupus</i>	4.52 (5)	99.97%	Kupreanof	6	Alaska and BC, 54°61'N, 127°146'W	17	F
<i>C. lupus</i>	4.52 (5)	98.12%	Prince of Wales	20	Alaska and BC, 54°61'N, 127°146'W	17	F
<i>C. lupus</i>	4.52 (5)	96.86%	Vancouver Island	26	BC S of 55°N, W of 122°W	12	F
<i>C. lupus</i>	4.54 (5)	96.47%	Prince of Wales	11	Alaska and BC, 54°61'N, 127°147'W	15	M
<i>C. lupus</i>	4.54 (5)	96.05%	Vancouver Island	36	BC S of 55°N, W of 122°W	12	M
<i>Felis bengalensis</i>	3.35 (5)	90.87%	Borneo	9	Malaya and Thailand S of 7°N	5	F
<i>F. bengalensis</i>	3.35 (5)	96.93%	Java	21	Sumatra	9	F
<i>F. bengalensis</i>	3.35 (5)	93.15%	Sumatra	9	Malaya and Thailand S of 7°N	5	F
<i>F. bengalensis</i>	3.52 (5)	95.10%	Bali	6	Java	21	M
<i>F. bengalensis</i>	3.52 (5)	88.99%	Hainan	5	Laos, Vietnam, and China, 15°26'N, E of 102°E	11	M
<i>F. bengalensis</i>	3.52 (5)	101.26%	Java	18	Sumatra	5	M
<i>F. bengalensis</i>	3.52 (5)	90.97%	Palawan	5	Borneo	15	M
<i>Felis concolor</i>	4.63 (5)	102.53%	Vancouver Island	14	BC and Washington, 45°55'N, W of 121°W	9	F
<i>F. concolor</i>	4.81 (5)	102.85%	Vancouver Island	11	BC and Washington, 45°55'N, W of 121°W	5	M
<i>Felis lynx</i>	3.94	95.62%	Newfoundland	31	Main, Labrador, and Quebec E of 70°N	5	M
<i>Felis planiceps</i>	3.20 (5)	98.39%	Borneo	9	Malaya	9	M
<i>Felis silvestris</i>	3.63 (2)	93.06%	Britain	12	France N of 47°N and Belgium	5	F
<i>F. silvestris</i>	3.70 (2)	94.93%	Britain	19	France N of 47°N and Belgium	9	M
<i>Herpestes smithii</i>	3.11 (1)	104.49%	Sri Lanka	5	India S of 24°N	5	F
<i>H. smithii</i>	3.32 (1)	105.41%	Sri Lanka	5	India S of 19°N	8	M
<i>Herpestes urva</i>	3.30 (2)	95.85%	Taiwan	8	China S of 27°N, E of 118°E	6	F
<i>Herpestes vitticollis</i>	3.46 (5)	94.65%	Sri Lanka	6	India S of 12°N	5	M
<i>Lontra canadensis</i>	3.91	108.68%	Vancouver Island	8	BC and Washington, 45°55'N, W of 121°W	15	F
<i>L. canadensis</i>	3.93	104.12%	Baranof	7	Alaska and BC, 54°61'N, 126°136'W	5	M
<i>L. canadensis</i>	3.93	101.41%	Prince of Wales	5	Alaska and BC, 54°61'N, 127°150'W	5	M
<i>L. canadensis</i>	3.93	104.48%	Vancouver Island	6	BC and Washington, 45°55'N, W of 121°W	21	M
<i>Lutra lutra</i>	3.83 (5)	95.27%	Britain	7	France N of 47°N and Belgium	6	F
<i>L. lutra</i>	3.83 (5)	99.71%	Ireland	19	Britain	7	F
<i>L. lutra</i>	4.00 (5)	101.78%	Ireland	19	Britain	7	M
<i>Martes americana</i>	2.8	103.97%	Chichagof	32	Alaska and BC, 54°59'N, 129°135'W	22	F
<i>M. americana</i>	2.8	106.00%	Mitkof	15	Alaska and BC, 54°61'N, 127°136'W	22	F
<i>M. americana</i>	2.8	112.91%	Moresby	15	Alaska and BC, 50°56'N, W of 126°W	23	F
<i>M. americana</i>	2.8	102.15%	Prince of Wales	6	Alaska and BC, 54°61'N, 127°136'W	22	F
<i>M. americana</i>	2.8	103.12%	Vancouver Island	84	BC and Washington, 46°55'N, W of 121°W	41	F
<i>M. americana</i>	3.14	102.65%	Chichagof	50	Alaska and BC, 54°60'N, 127°136'W	29	M
<i>M. americana</i>	3.14	105.82%	Mitkof	25	Alaska and BC, 54°61'N, 127°136'W	29	M
<i>M. americana</i>	3.14	113.78%	Moresby	31	Alaska and BC, 50°56'N, W of 126°W	30	M
<i>M. americana</i>	3.14	104.31%	Prince of Wales	11	Alaska and BC, 54°61'N, 127°136'W	29	M
<i>M. americana</i>	3.14	104.50%	Vancouver Island	121	BC and Washington, 46°55'N, W of 121°W	82	M
<i>Martes flavigula</i>	3.40 (4)	91.88%	Borneo	18	Malaya and Thailand S of 8°N	9	F
<i>M. flavigula</i>	3.53 (5)	118.61%	Java	5	Borneo	18	F
<i>Martes foina</i>	3.13	97.97%	Sjaelland	11	Denmark (Jutland)	6	M
<i>Martes martes</i>	3.22(6)	101.06%	Ireland	12	Britain	7	M
<i>M. martes</i>	3.22(6)	100.63%	Britain	7	France N of 48°N and Belgium	25	M
<i>M. martes</i>	3.22(6)	97.57%	Sjaelland	9	Denmark (Jutland)	7	M
<i>Meles meles</i>	4.00 (6)	99.52%	Britain	17	France N of 48°N Netherlands and Belgium	11	F
<i>M. meles</i>	4.00 (6)	103.26%	Ireland	11	Britain	17	F
<i>M. meles</i>	4.00 (6)	103.56%	Sjaelland	20	Denmark (Jutland)	78	F
<i>M. meles</i>	4.06 (6)	101.21%	Britain	24	France N of 48°N Netherlands and Belgium	16	M
<i>M. meles</i>	4.06 (6)	99.63%	Ireland	10	Britain	24	M
<i>M. meles</i>	4.06 (6)	101.59%	Sjaelland	22	Denmark (Jutland)	66	M
<i>Melogale moschata</i>	2.91	95.48%	Hainan	8	Vietnam and China, 22°26'N, E of 103°E	6	F
<i>M. moschata</i>	2.91	99.42%	Taiwan	20	China S of 30°N, E of 113°E	6	F
<i>M. moschata</i>	2.9	101.33%	Hainan	5	Laos, Vietnam, and China, 15°26'N, E of 102°E	9	M
<i>Mustela erminea</i>	2.32	105.44%	Britain	57	Belgium	49	F
<i>M. erminea</i>	2.32	87.94%	Ireland	37	Britain	57	F
<i>M. erminea</i>	1.91	103.21%	Mitkof	13	Alaska and BC, 54°59'N, 127°136'W	14	F
<i>M. erminea</i>	1.91	106.98%	Newfoundland	10	Canada E of 69°W, 45°54'N	32	F
<i>M. erminea</i>	2.32	96.75%	Sjaelland	21	Denmark (Jutland)	8	F
<i>M. erminea</i>	1.91	101.39%	Tukarak	12	Ontario and Quebec, 51°55'N, 77°90'W	5	F
<i>M. erminea</i>	1.91	102.91%	Vancouver Island	10	BC and Washington, 46°55'N, W of 122°W	39	F
<i>M. erminea</i>	2.69	105.85%	Britain	71	Belgium, Netherlands	48	M
<i>M. erminea</i>	2.69	93.42%	Ireland	75	Britain	71	M
<i>M. erminea</i>	2.35	97.22%	Kodiak	11	Alaska S of 61°N, 149°159'W	8	M
<i>M. erminea</i>	2.35	95.95%	Mitkof	25	Alaska and BC, 54°61'N, 127°135'W	27	M
<i>M. erminea</i>	2.35	107.54%	Newfoundland	51	Canada E of 69°W, 44°54'N	59	M
<i>M. erminea</i>	2.35	102.26%	Prince of Wales	9	Alaska and BC, 54°61'N, 127°136'W	27	M
<i>M. erminea</i>	2.69	100.23%	Sjaelland	21	Denmark, Germany, and Sweden, 53°60'N	12	M

<i>M. erminea</i>	2.35	101.98%	Tukarak	13	Ontario and Quebec, 50°57'N, 77°90'W	19	M
<i>M. erminea</i>	2.35	92.09%	Vancouver Island	18	BC and Washington, 46°55'N, W of 122°W	59	M
<i>Mustela nivalis</i>	1.77 (6)	101.81%	Britain	37	Belgium	85	F
<i>M. nivalis</i>	2.06 (6)	105.40%	Britain	120	Belgium	157	M
<i>M. nivalis</i>	2.06 (6)	99.05%	Sardinia	11	France and Italy S of 45°N	10	M
<i>Mustela putorius</i>	2.84 (6)	97.82%	Britain	14	France N of 49°N, Netherlands and Belgium	67	F
<i>M. putorius</i>	2.84 (6)	93.91%	Sjaelland	8	Denmark (Jutland)	10	F
<i>M. putorius</i>	3.05 (6)	94.18%	Britain	45	France N of 49°N, Netherlands and Belgium	98	M
<i>M. putorius</i>	3.05 (6)	97.37%	Sjaelland	16	Denmark (Jutland)	17	M
<i>Mustela sibirica</i>	2.60 (3)	83.98%	Honshu	12	E Asia, 30°50'N, E of 116°E	13	F
<i>M. sibirica</i>	2.89	86.33%	Honshu	101	E Asia, 30°50'N, E of 116°E	19	M
<i>M. sibirica</i>	2.89	106.02%	Kyushu	5	Honshu	101	M
<i>M. sibirica</i>	2.89	100.24%	Sado	8	Honshu	101	M
<i>M. sibirica</i>	2.89	98.26%	Shikoku	6	Honshu	101	M
<i>Mustela vison</i>	2.89	102.35%	Baranof	12	Alaska S of 61°N, E of 150°W	11	F
<i>M. vison</i>	2.89	101.90%	Chichagof	6	Alaska S of 61°N, E of 150°W	9	F
<i>M. vison</i>	2.89	94.26%	Nunivak	10	Alaska, 55°62'N, W of 157°W	6	F
<i>M. vison</i>	2.89	103.54%	Vancouver Island	19	BC, 49°54'N, W of 121°W	13	F
<i>M. vison</i>	3.12	104.03%	Baranof	28	Alaska S of 61°N, E of 150°W	13	M
<i>M. vison</i>	3.12	101.99%	Chichagof	6	Alaska S of 61°N, E of 150°W	12	M
<i>M. vison</i>	3.12	94.47%	Nunivak	12	Alaska, 55°66'N, W of 157°W	33	M
<i>M. vison</i>	3.12	110.02%	Vancouver Island	19	BC, 49°54'N, W of 121°W	12	M
<i>Nyctereutes procyonoides</i>	3.69	96.58%	Kyushu	6	Honshu	59	M
<i>Paguma larvata</i>	3.47	90.95%	Borneo	7	Malaya and Thailand S of 9°N	7	F
<i>P. larvata</i>	3.47	94.60%	Sumatra	6	Malaya and Thailand S of 9°N	7	F
<i>Panthera tigris</i>	5.34 (4)	99.49%	Java	5	Sumatra	8	M
<i>P. tigris</i>	5.08 (4)	95.75%	Sumatra	8	Indochina S of 17°N	7	M
<i>Paradoxurus hermaphroditus</i>	3.51 (5)	94.42%	Borneo	9	Malaya and Thailand S of 8°N	7	F
<i>P. hermaphroditus</i>	3.51 (5)	107.28%	Java	31	Sumatra	14	F
<i>P. hermaphroditus</i>	3.51 (5)	111.20%	Palawan	5	Borneo	9	F
<i>P. hermaphroditus</i>	3.51 (5)	102.84%	Sumatra	13	Malaya and Thailand S of 8°N	7	F
<i>P. hermaphroditus</i>	3.52 (2)	90.00%	Bali	5	Java	21	M
<i>P. hermaphroditus</i>	3.52 (2)	88.44%	Borneo	22	Malaya and Thailand S of 8°N	18	M
<i>P. hermaphroditus</i>	3.52 (2)	109.85%	Java	21	Sumatra	15	M
<i>P. hermaphroditus</i>	3.52 (2)	104.26%	Palawan	6	Borneo	22	M
<i>P. hermaphroditus</i>	3.52 (2)	97.93%	Sumatra	15	Malaya and Thailand S of 9°N	18	M
<i>P. hermaphroditus</i>	3.52 (2)	95.04%	Terutau	7	Malaya S of 13°N	20	M
<i>Procyon lotor</i>	3.81 (5)	99.37%	Elliott's key	5	Florida	21	F
<i>P. lotor</i>	3.93 (5)	93.20%	Big Pine key	5	Florida	18	M
<i>P. lotor</i>	3.93 (5)	90.17%	No name key	5	Florida	18	M
<i>Urocyon littoralis</i> 1	3.50 (5)	89.33%	San Clemente	6	Baja California and California, 28°37'N	15	F
<i>Urocyon littoralis</i> 1	3.59 (5)	93.10%	Santa Catalina	6	Baja California S of 31°N	8	M
<i>Urocyon littoralis</i> 1	3.59 (5)	87.63%	Santa Rosa	6	Baja California and California, 30°37'N	19	M
<i>Ursus americanus</i> 2	5.19 (5)	97.26%	Kuiu	7	Kupreanof	6	M
<i>Ursus americanus</i> 2	5.19 (5)	102.21%	Kupreanof	6	Alaska and BC, 54°62'N, 131°150'W	10	M
<i>Ursus americanus</i> 2	5.19 (5)	100.30%	Vancouver Island	8	BC S of 55°N, W of 122°W	6	M
<i>Ursus arctos</i> 2	5.48 (2)	99.02%	Admiralty	18	Alaska and BC, 54°61'N, 127°150'W	9	F
<i>Ursus arctos</i> 2	5.48 (2)	97.34%	Chichagof	9	Alaska and BC, 54°61'N, 127°150'W	9	F
<i>Ursus arctos</i> 2	5.48 (2)	98.28%	Kodiak	13	Alaska S of 61°N, 149°159'W	18	F
<i>Ursus arctos</i> 2	5.65 (2)	95.38%	Admiralty	33	Alaska and BC, 54°61'N, 127°150'W	6	M
<i>Ursus arctos</i> 2	5.65 (2)	88.45%	Baranof	5	Alaska and BC, 54°61'N, 127°150'W	6	M
<i>Ursus arctos</i> 2	5.65 (2)	93.08%	Chichagof	13	Alaska and BC, 54°61'N, 127°150'W	6	M
<i>Ursus arctos</i> 2	5.65 (2)	99.77%	Kodiak	9	Alaska S of 61°N, 149°159'W	8	M
<i>Viverra zibetha</i>	3.87 (5)	91.00%	Sulawesi	6	Borneo	37	M
<i>Viverricula indica</i>	3.41	97.31%	Hainan	8	Vietnam and China, 15°26'N, E of 102°E	13	F
<i>V. indica</i>	3.41	95.38%	Taiwan	6	China, 23°26'N, E of 113°E	11	F
<i>V. indica</i>	3.47 (5)	96.34%	Sri Lanka	12	India S of 22°N	6	M
<i>V. indica</i>	3.47 (5)	97.25%	Taiwan	7	China 23°26'N, E of 113°E	15	M
<i>Vulpes vulpes</i>	3.74	103.42%	Britain	20	Belgium and France N of 48°N	22	F
<i>V. vulpes</i>	3.74	96.49%	Ireland	86	Britain	20	F
<i>V. vulpes</i>	3.63 (4)	107.08%	Newfoundland	12	SE Canada and Maine S of 55°N, E of 70°W	11	F
<i>V. vulpes</i>	3.85	103.34%	Britain	30	Belgium and France N of 48°N	32	M
<i>V. vulpes</i>	3.74 (1)	99.26%	Honshu	7	E Asia, 30°45'N, E of 115°E	5	M
<i>V. vulpes</i>	3.85	95.64%	Ireland	101	Britain	30	M
<i>V. vulpes</i>	3.7	106.69%	Newfoundland	7	SE Canada and Maine S of 55°N, E of 70°W	23	M

Note: Size (relative) is the relative  $M_1$  length of the insular population (as a fraction of the mainland value of the mainland population).

1 Interspecific comparisons (see text).

2 For *Ursus*, the tooth measured was M2 rather than M1.

Sources for the mass data:

Abe 1994 (1), Creel and Macdonald 1995 (2), Johnson et al. 2000 (3),

Nowak 1999 (4), Silva and Downing 1995 (5), and Weckerly 1998 (6).

Where no source is given, the body mass data are from tag data of specimens measured in this study.

BC is British Columbia. Malaya is the Malay peninsula.