

Insular Carnivore Biogeography: Island Area and Mammalian Optimal Body Size

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ABSTRACT: Patterns of size variation in insular mammals have been used to support the claim that mammals have a single optimal body size. This hypothesis enjoys wide support, despite having been questioned on both theoretical and empirical grounds. It is claimed that species of optimal size maintain the highest population densities. Therefore these species are thought to inhabit the smallest islands, where larger and smaller species are generally absent. We sought such a pattern by testing how area affects the body sizes of the largest and smallest carnivore species on islands. Using data on carnivores from 322 islands, we found that the sizes of carnivores on small islands tend to be close to the order's mode. Furthermore, we found that the size distribution of carnivore species that inhabit islands resembles that of those whose range is entirely continental. We conclude that insular carnivores provide no support for theories proposing a single optimal size, and we suspect such theories are also flawed on theoretical grounds.

Keywords: Carnivora, islands, island area, optimal body size.

Mammals come in many sizes, from 2-g shrews and bats to blue whales (*Balaenoptera musculus*) nearly six orders of magnitude larger (Nowak 1999). However, not all sizes are equally common. The frequency distribution of mammalian body sizes is highly skewed, with a conspicuous mode in the small size range at about 25 g (Gardezi and da Silva 1999). Although other lower peaks are found at

higher masses (Bourliere 1975; Alroy 1998, 2003; Lovegrove and Haines 2004), there is no denying that there are more species of fairly small mammals than there are species of either larger or smaller ones (Blackburn and Gaston 1998; Smith et al. 2004).

A similarly shaped size distribution for animals in general (Blackburn and Gaston 1994; Purvis et al. 2003) led Hutchinson and MacArthur (1959) to try to explain the abundance of small animals by claiming that such species perceive the environment as coarser grained compared with the perception of larger ones, thus enabling them to occupy more niches. Stanley (1973) stressed the importance of constraints on minimum size to account for the scarcity of species in the very smallest size classes. At the same time, he argued against a misleading interpretation of Cope's rule, according to which larger is always better. According to Stanley (1973), the abundance of relatively small species is a consequence of higher rates of speciation at these sizes. He concluded that the disadvantages of increased size, that is, the higher risk of extinction, cause the observed pattern. Gould (1988) likewise emphasized the existence of a stable modal body size throughout the history of various clades.

Maiorana (1990) suggested that the modal size is adaptive in itself. She claimed that an intermediate size may be optimal for obtaining and processing energy as well as for allocating the largest proportion of energy to reproduction. Maiorana (1990) attributed deviations from the modal size to competition and predation and suggested that lower levels of both selective pressures on islands may explain the tendency of insular mammals to converge on an intermediate size (Van Valen 1973; Lomolino 1985; but see Meiri et al. 2004a). Damuth (1993) also claimed that intermediate masses are optimal, and he explicitly defined what this optimum mass is: 1,000 g. He maintained that the optimal size is the size at which species are able to control the greatest proportion of available energy. Damuth (1993) found that in guilds of mostly small mammals (the largest members of which weigh about 1 kg), it is the larger species that control most energy. However, it is small members that control most of the energy in guilds of

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mostly large mammals (guilds where the smaller species weigh about 1 kg). Damuth (1993) therefore concluded that it is at about 1 kg that species control most energy in most dietary groups.

That same year, Brown and his colleagues also claimed the existence of an optimal intermediate size of terrestrial mammals at 100 g (Brown et al. 1993), arguing that this value is close to the mammalian modal size. Brown et al. (1993) suggested that mammals of about 100 g are most efficient in converting energy into offspring production and that the modal size is a consequence of the higher fitness of optimal-sized mammals. Brown et al. (1996, p. 1073) proposed that their model predicts the optimal size for a clade in the absence of resource limitation.

Both Damuth (1993) and Brown et al. (1993) saw their conclusion—a single optimal body size for all terrestrial mammals—as supported by the size patterns of insular mammals (e.g., Foster 1964; Lomolino 1985). However, resource limitation is thought by some to be of major importance for size evolution on islands (Heaney 1978; Lomolino 1985); if true, this would be at odds with one of the model's assumptions (Brown et al. 1996). Brown et al. (1993) and Damuth (1993) argued that competition causes deviations from optimal size and that reduced competition on islands leads to evolution toward the optimal size there. Maurer et al. (1992) suggested that 250 g is approximately the body mass at which, according to Lomolino's (1985) data, island forms tend not to diverge from their mainland relatives. Brown et al. (1993) suggested that the similarity of 250 g to 100 g lends empirical support to their model (but see Blackburn and Gaston 1996; Meiri et al. 2004a).

Another study believed to support this model is that of Marquet and Taper (1998, cited as an unpublished manuscript by Brown et al. [1993]). These authors regressed the logarithm of island area on the logarithms of the sizes of both the largest and the smallest mammals in mountaintop "islands" in the American Southwest, on land-bridge islands in the Sea of Cortéz, and on seven continents (Marquet and Taper 1998). They found that the two regression lines intersect at 1.71 (Marquet and Taper 1998), corresponding to a mass of 51 g (Meiri et al. 2004a). Boback and Guyer (2003), analyzing a sample of insular snakes, found qualitatively similar regression lines, converging at a size very similar to the one actually found on one-species islands. Theoretically, the convergence is predicted by the species-area relationship, because drawing a larger number of species at random from the regional species pool will result in a wider size range on larger islands (Blackburn and Gaston 1996). Marquet and Taper (1998) performed a bootstrap analysis, showing that slopes predicted from such a random process are significantly

steeper than those actually observed, with the lines intersecting at about 100 g rather than the observed 50 g.

Kelt and Van Vuren (1999, 2001) advanced another line of evidence in support of an optimal size at about 100 g; they found that the minimum mammalian home ranges decrease with mass up to about 100 g and increase as mass increases beyond this point. Marquet and Taper (1998) assert that it is this tendency of 100-g mammals to have the smallest ranges that is adaptive. They suggested that, as population size is inversely correlated with extinction probability, the smaller the geographical area inhabited by a population, the more likely it is to go extinct. Citing these data and those of Brown and Maurer (1989), Marquet and Taper (1998) predicted that, on the smallest islands, only mammals close to the optimal size (i.e., those with the smallest home range) will persist. Wassersug et al. (1979) accounted for the evolution of insular dwarves by a similar argument.

According to these theories, the course of evolution can go either way, but populations evolving toward the "wrong" size are more likely to go extinct (Roth 1992; but see Wilkinson and O'Regan 2003 for an example where a larger species further away from the optimum is more likely to persist on small islands). The only additional test using Marquet and Taper's (1998) logic, conducted by Burness et al. (2001), supported their conclusion regarding the relationship between home range and island area, at least for the largest species.

Despite much criticism, the notion of a single body mass optimum for a given taxon still enjoys a respectable reputation in recent works (e.g., Ginsberg 2000; Roy et al. 2000; Boback and Guyer 2003; Clarke 2003; Raia et al. 2003; Scott et al. 2003; Etienne and Olff 2004). This may be due to its apparent success in using simple physiological allometries to predict evolutionary and ecological phenomena such as modal body sizes and the direction of size evolution on islands (see also Blackburn and Gaston 1994). Empirical support for the two models (Brown et al. 1993; Damuth 1993) was found in patterns of size evolution on islands at both the intra- (Lomolino 1985) and interspecific levels (Marquet and Taper 1998).

At the intraspecific level, we have shown (Meiri et al. 2004a) that the model is not supported. We now aim to test predictions stemming from the interspecific pattern described by Marquet and Taper (1998). We ask if carnivore species tend to approach a particular size on small islands or if the size of carnivores on the smallest islands can be predicted by a random draw from the appropriate species pool. Carnivores are suitable for such a study because they 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), making them an adequate

model for mammals as a whole, despite a minority of species smaller than 100 g. That this size is within the range of carnivore sizes makes this clade appropriate for such a study, in that the model predicts that species in this size class will be relatively more abundant on islands than if species were drawn randomly from a global pool, with the number of species drawn for each site the number actually present at that site. Insular carnivores inhabit continental-shelf islands almost exclusively (Alcover and McMinn 1994), thus forming precisely the type of relaxation faunas predicted to show the pattern reported by Marquet and Taper (1998).

Material and Methods

Carnivore Biogeography

For each island on which carnivores occur naturally, we recorded island area and carnivore richness. We obtained data on island areas from the literature (e.g., Lawlor 1982; Heaney 1986), from the United Nations Environment Programme Web site (<http://islands.unep.ch/isldir.htm>), and from E. Meijaard and J. Calder (personal communication, 2003). In other cases, island area was obtained from a computerized Geographic Information Systems map of the world.

We compiled data on carnivore occurrence on islands from museum specimens and from the literature. Carnivore species said to occupy an island by any source were counted as present, unless specifically marked as absent by another source. We followed the taxonomy of Nowak (1999) and excluded marine species (*Enhydra lutris*, *Ursus maritimus*). We disregarded all known cases of historic introductions but did use data on species whose status as introduced is difficult to establish (e.g., the five strictly insular species of raccoons: *Procyon*, Zeweloff 2003; viverrids east of Wallace's line: e.g., *Paradoxurus hermaphroditus*, Meijaard 2003). Carnivores known to have gone extinct on an island during historic times were counted as extant (e.g., *Ursus arctos* on Britain; Yalden 1999). Because of uncertainties as to the extent of carnivore movement over sea ice in northern latitudes, we limited our analysis to islands south of the Arctic Circle.

Body Mass

We compiled a list of the masses of all wild terrestrial carnivores (table A1 in the appendix in the online edition of the *American Naturalist*), obtaining masses from museum specimen labels or from the literature if weight data were missing. Both these methods are flawed (see an excellent discussion in Smith and Jungers 1997), especially the latter, where sometimes the primary sources for mass

data are not even acknowledged. Carnivores, more than the primates discussed by Smith and Jungers (1997), present an additional problem: geographic variation, which is often very pronounced in carnivores (Meiri et al. 2004b). Because the mass within a species of carnivore often varies more than twofold over its geographic range, we used the midpoint of the mass range as an estimate wherever possible (with museum data and with sources reporting masses of individuals; e.g., Silva and Downing 1995). The use of the midpoint avoids the problem of excessively weighting easily obtainable data. We used only wild-caught adult specimens (those with complete closure of the dorsal sutures of the skull) for calculations of masses of museum specimens. A list of individual specimen masses is available from S. Meiri. We were unable to obtain mass data for nine species. For eight of these species, we estimated mass based on body length (Silva 1998), skull length (CBL; Von den Driesch 1976), or the length of the lower carnassial (Van Valkenburgh 1990; table A1). For the ninth species, *Procyon minor*, we used mass of *Procyon lotor* from Georgia (Silva and Downing 1995) because this raccoon is similar in size to those of the southeastern United States (Helgen and Wilson 2003).

Sexual size dimorphism, with males larger than females, is pronounced in many carnivores (Gittleman and Van Valkenburgh 1997; Dayan and Simberloff 1998; Weckerly 1998). It can therefore be argued that we should use masses of females from the smallest species and of males from the largest. Mass data, however, are often missing for the separate sexes. More importantly, studies relevant to the question we ask (e.g., those that study basal metabolic rate, home range size, etc.) invariably use species-specific averages rather than female or male mass, including both models of optimal size discussed here (Brown et al. 1993; Damuth 1993) and data used to support them (Marquet and Taper 1998). Moreover, the two sexes cannot be regarded as independent data points, in either the statistical sense (Smith 1994) or the biological (home range, viable population) one. We therefore used the average of the minimum mass of the smallest sex and the maximum mass of the larger sex where such data were available. Otherwise, we averaged the mean masses of the sexes. When no mass estimate was available for both sexes, we used average species mass.

The smallest carnivores on many of the islands were *Mustela erminea* and *Mustela nivalis*. Because both these Holarctic species are usually smaller in North America than in Eurasia, we used different mass estimates for these species in Nearctic and Palearctic regions. Based on specimens we have examined, we use 41.5 g and 82.5 g as the mass of *M. nivalis* and 182 g and 264 g as the mass of *M. erminea* in the Nearctic and Palearctic regions, respectively.

Analysis

We first checked if size determines whether different carnivore species are prevented from inhabiting islands. We did so by comparing the mass frequency distribution of all carnivores inhabiting at least one island to that for species that are strictly continental. If carnivores much larger than 100 g are at a disadvantage on islands, we predict that such species will be more likely to be excluded from the insular environment, whereas small species will be more likely to inhabit islands. To investigate whether large carnivores inhabit only large islands, whereas small carnivores can be found on both large and small islands, we regressed body mass on the area of the smallest island on which a particular species occurs.

We then determined both the largest and the smallest carnivore species occurring on each island and correlated sizes of both species with the logarithm of island area (in square kilometers). According to the physiologically based optimal body size theory (Brown et al. 1993; Marquet and Taper 1998), because most carnivores are larger than 100 g, only members of the smallest species are predicted to occur on very small islands. This model predicts that the correlation between size and area will be positive for the largest carnivore species on islands, but because the smallest carnivores are near the proposed optimal size of 100 g, all islands regardless of their area will have as their smallest carnivore species one of the smallest carnivores in the regional assemblage. Thus, the size of the smallest carnivore should be independent of island area.

We therefore separately regressed the masses of both the smallest and largest carnivore on each island against island area. We then calculated the intersection point of these two regression lines (following Marquet and Taper 1998). The optimal size model predicts that these lines will intersect at 100 g.

To see whether the result of this analysis differs from those expected by chance, we drew at random for each island the same number of carnivores actually occurring on it from the global species pool. We then found the largest and smallest mass of each draw and regressed both the smallest masses and the largest ones on actual island area for all islands in our sample. We then found the mass at which the two lines intersect. This procedure was repeated 10,000 times. We compared the frequency distribution of masses thus obtained to the result obtained with the real data.

Results

A frequency distribution of all sizes of all carnivore species occurring on islands (aside from introduced species) versus those never occurring on islands without human as-

sistance is depicted in figure 1. The latter two distributions differ significantly from one another (Kolmogorov-Smirnov two-sample test, $D = 0.177$, $P < .05$). The average mass of insular carnivore species (3,544 g) is higher (i.e., farther away from 100 g) than that of strictly continental ones (2,745 g), although this difference is only marginally significant (Mann-Whitney U -test, $U = 6,199$, $P = .053$). The average mass in the order is 3,159 g. Furthermore, there is no correlation between the mass of a carnivore species and the area of the smallest island that it inhabits ($n = 132$, $r = -0.107$, $P = .22$).

The smallest and largest carnivore species on all 322 islands are listed in table A2 in the online edition of the *American Naturalist* (a list of all the carnivores occurring on each of these islands is available from S. Meiri). Figure 2 shows the correlations between the logarithm of island area (on the ordinate) and the logarithms of both the largest and the smallest carnivore masses (on the abscissa; following Marquet and Taper 1998). Both correlations are significant ($n = 322$; smallest carnivores, $r = -0.226$, $P < .001$; largest carnivores, $r = 0.430$, $P < .001$). The equations for the linear correlation are $y = -0.301x + 3.617$ for the smallest carnivores and $y = 0.517x + 0.641$ for the largest ones. The intersection of these two lines is at $x = 3.64$, corresponding to a mass of 4,363 g. This size is slightly higher than the order's modal size class. The two lines intersect at an area of 333 km². Therefore, on smaller islands, carnivore mass cannot be predicted from these equations. For the 148 such islands in our database, the modal size class of the smallest carnivores is the 1,585–4,000-g one (40 islands). The modal size class of the largest carnivores in those islands is 4–10-kg (53 islands). These two size classes, with 38 and 37 islands, respectively, are the modal mass categories for the 118 islands that have a single carnivore species.

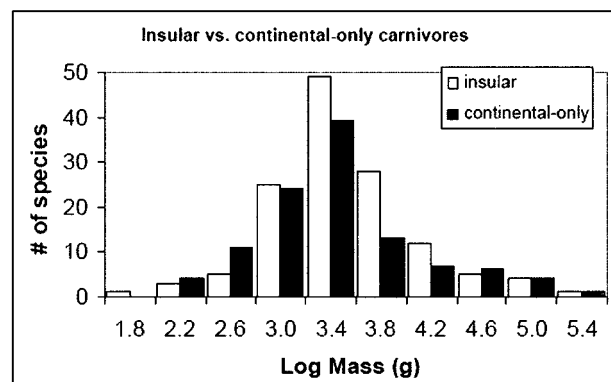


Figure 1: Mass distribution of carnivores. Shaded bars = carnivores not naturally occurring on islands. Unshaded bars = carnivores naturally occurring on islands.

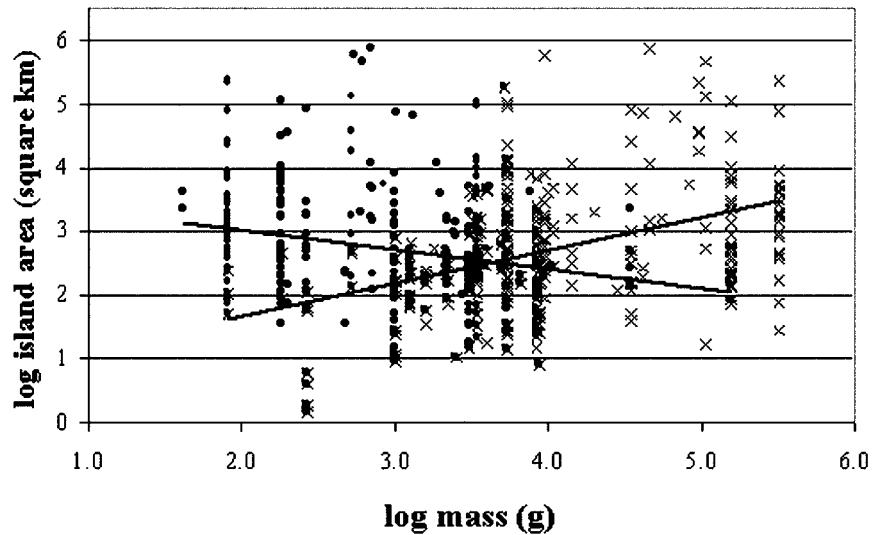


Figure 2: Correlations between the logarithm of island area (in square kilometers) and the logarithm of body mass (in grams) of the smallest and largest carnivores on all islands in table A2 in the online edition of the *American Naturalist*. A dot represents the smallest carnivore on each island (descending line is a product-moment correlation best-fit line). An X represents the largest carnivore on each island (ascending line is a product-moment correlation best-fit line).

Both carnivore richness and size range (calculated as the ratio of the largest to the smallest carnivore masses) increase with island size: the species-area relationship is $y = 0.583x^{0.218}$ ($R^2 = 0.374$). The mass range increases with area as $y = 0.363x^{0.529}$ ($R^2 = 0.204$), and $y = 3.44x^{0.342}$ when islands inhabited by only one carnivore species (i.e., those with a mass range of 1) are omitted.

Results of the bootstrap procedure are presented in figure 3. The mean size in 10,000 simulated runs is 3.494, corresponding to a mass of 3,122 g. This value is lower than the size where the two correlation lines converge. None of the bootstrap values is as large as the 4,363 g actually obtained.

For fitted regression lines for different archipelagoes (18 archipelagoes with $n > 4$ islands) separately, the average mass at which the two regression lines intersect is 20,450 g when one anomalous result (south Alaska, where the largest carnivore on all islands is *Ursus arctos*) is omitted. In only one archipelago (the west Mediterranean) do the regression lines intersect at a mass (171 g) within the range advocated in support of the model (80–250 g; see discussion in Blackburn and Gaston 1996).

Discussion

We find no evidence to support the optimal size model in our data. Species inhabiting islands are no closer to 100 g or 1 g than are strictly continental species, and small

islands are inhabited by modal-sized species rather than by species closer in mass to the proposed optima.

It seems that carnivores absent from islands are nearly always those that do not even reach the coastal areas (e.g., *Felis jacobita*, *Mustela nigripes*, *Osbornictis piscivora*, *Panthera uncia*) or, more frequently, those found in island-poor environments (e.g., Africa, eastern South America). In our opinion, the only carnivore species we would have expected to find on islands (species that inhabit continental areas adjacent to islands on which carnivores are known to occur) but do not are probably the kit and swift foxes (*Vulpes macrotis*, *Vulpes velox*). Their masses are within the modal size category of insular carnivores (fig. 1). Therefore, we believe that carnivores are not excluded from insular environments because they are the wrong size (and indeed, the entire range of terrestrial mammal sizes, from elephants to pygmy shrews, is represented on the island of Sri Lanka; Nowak 1999).

If a body mass of 100 g were advantageous, we would predict that the smallest carnivore in an assemblage would be present on the smallest islands while larger species would not, because carnivores are nearly always larger than 100 g. Therefore, as Marquet and Taper (1998) found, the regression lines should intersect near this size. In fact, the regression lines describing the relationship of the extreme sizes of carnivores and island area cross at the modal size class of the order, more than an order of magnitude larger than the predicted mass. This size is also the most common on the smallest islands, as expected if colonization were

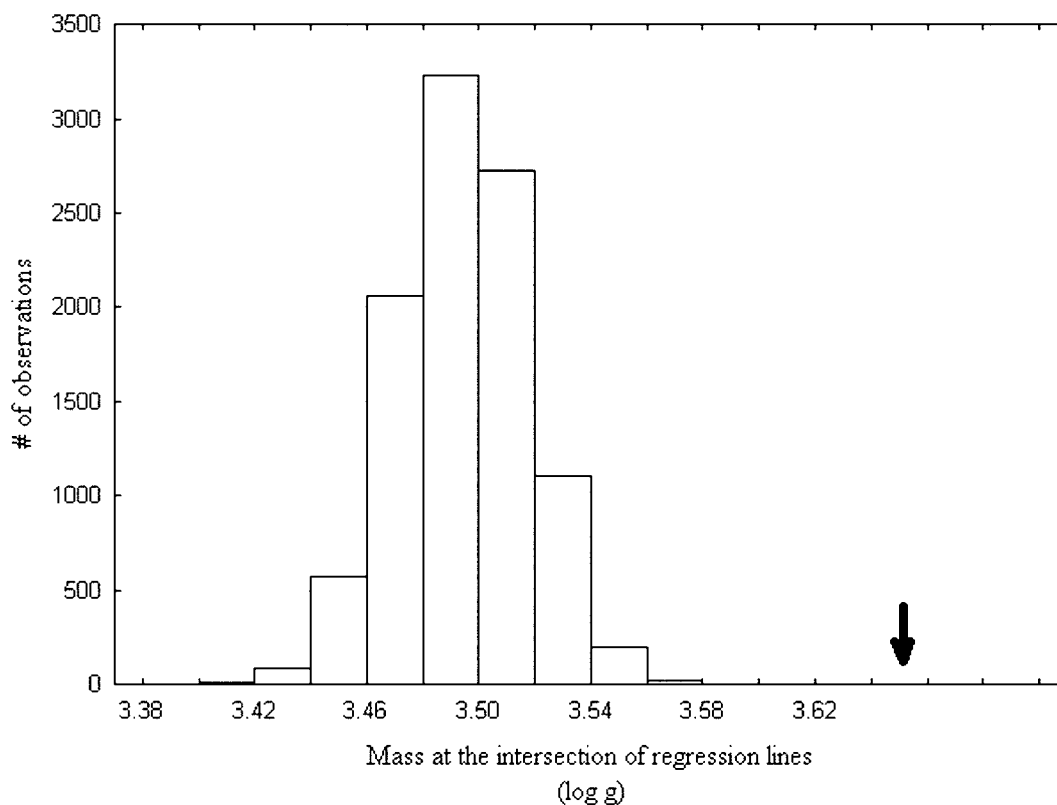


Figure 3: Results of a bootstrap analysis. The abscissa represents the logarithm of body mass (in grams) at the intersection of two correlation lines: that of (log) mass of the smallest carnivore on each island and (log) island area and that of (log) mass of the largest carnivore on each island and (log) island area. The ordinate is the frequency of such observations in a bootstrap procedure repeated 10,000 times. The arrow points to the actual value.

random in relation to size (Blackburn and Gaston 1996). Our bootstrap analysis actually implies that carnivores inhabiting small islands are significantly larger than expected by chance. The tendency of large mammals to have wide geographic distributions (Brown 1995) may explain both this result and the fact that species of carnivores that inhabit insular environments are on average larger than strictly continental ones.

Our results imply that carnivore colonization and extinction patterns on islands are to a large extent independent of size. It is not uncommon to find the largest carnivore in a regional species pool on small islands, and often the smallest carnivore (i.e., the one closest to 100 g) does not inhabit such islands. While *Mustela nivalis* is indeed quite ubiquitous on Palearctic islands (islands near Britain notwithstanding), it is nearly always absent from Nearctic ones. In tropical areas, the smallest carnivores (e.g., *Mustela lutreolina* in Southeast Asia, *Lyncodon patagonicus* in South America, and *Helogale parvula* in Africa)

are remarkable in their absence from small islands (the latter two are strictly continental).

The theory of a single optimal size for mammals has generated much controversy. Brown et al.'s (1993) model attracted criticism on theoretical grounds. It was claimed that the model ignores mortality and that exponents used in building it are unrealistic (Kozłowski 1996; cf. Brown et al. 1996), that it maximizes power instead of efficiency (Chown and Gaston 1997), and that it uses the wrong units, mixing reproductive output and conversion rate (Perrin 1998). It was claimed that it is internally inconsistent (Bokma 2001), that it ignores important aspects of time allocation, and that it mixes individual with population estimates (Kozłowski 2002; but see Brown et al. 1996). Blackburn and Gaston (1996) forcefully argued that different subtaxa may have different optima—that modal does not mean best. They also showed that evidence cited in support of the model actually spans a fairly wide range of sizes (see also Meiri et al. 2004a).

Empirical analyses of life-history traits of bats (Jones and Purvis 1997) and insectivores (Symonds 1999) failed to support the model, which also failed to predict the modal body size of diprotodont marsupials (Chown and Gaston 1997). Similarly, we found no tendency for evolution toward an optimum size in insular carnivores (Meiri et al. 2004a).

Could it be that, with respect to the optimal size, carnivores differ in some way from other mammals, as do the mostly carnivorous bats and insectivores (Jones and Purvis 1997; Symonds 1999)? Marquet et al. (1995) found different allometries of population density in herbivorous, omnivorous, and carnivorous mammals (however, carnivorous and insectivorous mammals have negative allometries, suggesting that small species control the most energy). The scaling of home range for carnivorous mammals has similar slopes to those of omnivorous and herbivorous ones (Kelt and Van Vuren 2001). The higher intercepts of the former should reflect differing densities of food for these groups (McNab 1963; Kelt and Van Vuren 2001). This fact implies that carnivores may be absent from the smallest islands (Heaney 1984), not that the optimal size of carnivorous mammals should differ from that of herbivores.

The shape of the function relating home ranges to mass of carnivores is very similar to that for all mammals (data provided by D. A. Kelt), fitting an oblong polygonal area with a minimum range size at masses slightly above the minimum mass. The mass at this minimum range for carnivores (Kelt and Van Vuren 2001), however, is higher than that of all mammals, by about an order of magnitude (the smallest ranges are for the ~700-g introduced *Herpestes javanicus* [Nellis and Everard 1983] and the ~2,100-g *Genetta tigrina* [Ikeda et al. 1982]). The smallest mammalian home ranges nearly always belong to fossorial rodents of ~100 g (Kelt and Van Vuren 1999).

Therefore, most empirical evidence for an optimal size at 100 g rests on the slender shoulders of rodents. Rodents of 100 g are extremely abundant and 100-g marsupials, insectivores, and bats fairly so (Gardezi and da Silva 1999). The latter three taxa were found not to conform to the predictions of this hypothesis (Chown and Gaston 1997; Jones and Purvis 1997; Symonds 1999). For carnivores, 100 g seems more like a constraint on size rather than an optimum (see discussion on the smallest carnivores in King 1989).

Within herbivorous mammals, a mass of 100 g is rare except in rodents. It is absent in ungulates, often limited to large sizes by the requirement for efficient fermentation of plant material in hindgut fermenters (Proboscidea, Perissodactyla) and ruminants. Marine mammals (Sirenia, Cetacea, Pinnipedia) are also uniformly large. We do not believe that it is competition with rodents that keeps these

and other mammals (e.g., Xenarthra) from attaining a mass of 100 g, but that 100 g is not optimal for those taxa (Blackburn and Gaston 1996), whereas the optimal size model predicts every mammalian subclade to have the same size distribution and mode (Purvis et al. 2003). Neither do we believe that our results indicate that carnivores have an optimal size of their own (be that at the modal size, modal size of insular carnivores, intersection point of the regression line, or otherwise). In this diverse assemblage, each species is probably well adapted to its particular niche.

We therefore believe that what needs to be explained is not why the 100-g class is so common in mammals or why mammals with the smallest home ranges tend to be close to 100 g in mass but why these patterns obtain for rodents. Other mammalian taxa simply do not converge on this size either intraspecifically (Meiri et al. 2004a) or interspecifically (Alroy 1998; this study).

Why do we see the pattern observed by Marquet and Taper (1998)? At the continental scale, we believe no real pattern is apparent. The fact that North America and Europe have no elephants surely does not mean that they cannot exist there—in fact, a large proboscidean clade inhabited both continents as late as the end of the last ice age. Furthermore, elephants inhabit Sri Lanka (65,000 km²) today, so their absence from larger landmasses does not mean areal size is a restrictive factor. Likewise, Roth (1992) argued that Sicily (25,460 km²) could have harbored a population of 3,000 15-ton elephants. As for the smallest end of the spectrum, Y. Mandelik (unpublished data) calculated the density of one of the world's smallest mammals, the 2.5-g (Nowak 1999) *Suncus etruscus* as 16 individuals per hectare in the Judean foothills. As Marquet and Taper (1998) themselves pointed out, for the smallest mammals, continental size is not restrictive. It even seems that, given suitable habitat, mammals weighing much less than 100 g can probably maintain viable populations on very small islands indeed. Another important matter in this regard is actual density. Marquet and Taper (1998) derived their equations from the area required per average individual within a species of a particular size. However, their equations are correct only for strictly territorial species, with zero overlap between neighboring territories. As Case (1978) pointed out, the question of territoriality is important in accounting for body size patterns in insular mammals.

Density compensation and overcompensation (MacArthur et al. 1972; Dunham et al. 1978; Gliwicz 1980; Brown and Lomolino 1998) can also “allow” more animals to inhabit a given area than theory (Marquet and Taper 1998) might imply (Blackburn and Gaston 1996). If territoriality and density compensation are not independent of mass it might not be 100-g mammals that have the

highest population densities on islands. Finally, there simply are not enough paleontological data to support the notion that populations of animals in the “wrong” size range go extinct on islands (Roth 1992).

We think that the main question to be answered is, Can all mammalian species be assumed to have a single optimal mass (Blackburn and Gaston 1996)? We believe that, both on empirical and conceptual grounds, defining one optimal size for a diverse assemblage such as the class Mammalia is unwarranted. Optimal size can and does vary even within single species in response to many factors such as climate (Meiri and Dayan 2003), resource availability, and community composition (Dayan and Simberloff 1998). It can vary between the sexes (generating sexual size dimorphism) and with time (Yom-Tov 2003). We do not think a 100-g rodent is in any way more “optimal” or fit than a 3-g shrew, a 200,000-g deer, or a 5,500-g fox. These animals are all adapted to their particular life-history characteristics, environments, and feeding habits (Blackburn and Gaston 1996). Evolution is not about an optimization to an unchanging single mode but about grasping temporally changing and always context-dependent opportunities.

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Appendix from S. Meiri et al., ‘Insular Carnivore Biogeography: Island Area and Mammalian Optimal Body Size’ (Am. Nat., vol. 165, no. 4, p. 505)

Carnivore Species Data

Table A1
Carnivore biogeography and body masses

| Species | Log mass (g) | Source | Occurs on |
|----------------------------------|--------------|----------------------------|------------------------|
| <i>Acinonyx jubatus</i> | 4.70 | Kingdon 1997 | Continents only |
| <i>Ailuropoda melanoleuca</i> | 5.07 | Nowak 1999 | Continents only |
| <i>Ailurus fulgens</i> | 3.69 | Silva and Downing 1995 | Continents only |
| <i>Alopex lagopus</i> | 3.48 | This study | Continents and islands |
| <i>Aonyx capensis</i> | 4.10 | Silva and Downing 1995 | Continents only |
| <i>Aonyx cinerea</i> | 3.48 | Nowak 1999 | Continents and islands |
| <i>Aonyx congica</i> | 4.30 | Kingdon 1997 | Continents and islands |
| <i>Arctictis binturong</i> | 4.16 | Kanchanasakha et al. 1998 | Continents and islands |
| <i>Arctogalidia trivirgata</i> | 3.35 | Kanchanasakha et al. 1998 | Continents and islands |
| <i>Arctonyx collaris</i> | 4.02 | Kanchanasakha et al. 1998 | Continents and islands |
| <i>Atelocynus microtis</i> | 3.98 | Nowak 1999 | Continents only |
| <i>Atilax paludinosus</i> | 3.56 | Kingdon 1997 | Continents and islands |
| <i>Bassaricyon alleni</i> | 3.09 | Smith et al. 2003 | Continents only |
| <i>Bassaricyon beddardi</i> | 3.09 | Nowak 1999 | Continents only |
| <i>Bassaricyon gabbii</i> | 2.90 | Kays 2000 | Continents only |
| <i>Bassaricyon lasius</i> | 3.09 | Nowak 1999 | Continents only |
| <i>Bassaricyon pauli</i> | 3.09 | Nowak 1999 | Continents only |
| <i>Bassariscus astutus</i> | 3.00 | Egi 2001 | Continents and islands |
| <i>Bassariscus sumichrasti</i> | 3.04 | Reid 1997 | Continents only |
| <i>Bdeogale crassicauda</i> | 3.23 | Kingdon 1997 | Continents and islands |
| <i>Bdeogale jacksoni</i> | 3.40 | Kingdon 1997 | Continents only |
| <i>Bdeogale nigripes</i> | 3.44 | Kingdon 1997 | Continents only |
| <i>Canis adustus</i> | 3.98 | Kingdon 1997 | Continents only |
| <i>Canis aureus</i> | 3.96 | This study | Continents and islands |
| <i>Canis latrans</i> | 4.03 | This study | Continents and islands |
| <i>Canis lupus</i> | 4.54 | This study | Continents and islands |
| <i>Canis mesomelas</i> | 3.93 | Kingdon 1997 | Continents only |
| <i>Canis rufus</i> | 4.45 | Alderton 1994 | Continents and islands |
| <i>Canis simensis</i> | 4.14 | Kingdon 1997 | Continents only |
| <i>Cerdocyon thous</i> | 3.79 | Redford and Eisenberg 1992 | Continents and islands |
| <i>Chrotogale owstoni</i> | 3.40 | Kanchanasakha et al. 1998 | Continents only |
| <i>Chrysocyon brachiurus</i> | 4.37 | Silva and Downing 1995 | Continents only |
| <i>Civettictis civetta</i> | 4.13 | Kingdon 1997 | Continents and islands |
| <i>Conepatus chinga</i> | 3.30 | Silva and Downing 1995 | Continents only |
| <i>Conepatus humboldti</i> | 3.01 | Weckerly 1998 | Continents and islands |
| <i>Conepatus leuconotus</i> | 3.01 | Weckerly 1998 | Continents only |
| <i>Conepatus mesoleucus</i> | 3.36 | Van Valkenburgh 1990 | Continents only |
| <i>Conepatus semistriatus</i> | 3.39 | Reid 1997 | Continents and islands |
| <i>Crocuta crocuta</i> | 4.81 | Kingdon 1997 | Continents only |
| <i>Crossarchus alexandri</i> | 3.18 | Kingdon 1997 | Continents only |
| <i>Crossarchus ansorgei</i> | 3.00 | Macdonald 1984 | Continents only |
| <i>Crossarchus obscurus</i> | 3.10 | Kingdon 1997 | Continents only |
| <i>Crossarchus platycephalus</i> | 3.10 | Kingdon 1997 | Continents only |
| <i>Cryptoprocta ferox</i> | 3.98 | Nowak 1999 | Islands only |

Table A1 (Continued)

| Species | Log mass (g) | Source | Occurs on |
|-------------------------------|--------------|----------------------------|------------------------|
| <i>Cuon alpinus</i> | 4.20 | Nowak 1999 | Continents and islands |
| <i>Cynictis penicillata</i> | 2.79 | Kingdon 1997 | Continents only |
| <i>Cynogale bennettii</i> | 3.60 | Kanchanasakha et al. 1998 | Continents and islands |
| <i>Cynogale lowei</i> | 3.60 | Helin et al. 1999 | Continents only |
| <i>Diplogale hosei</i> | 3.38 | Mass estimate ^a | Islands only |
| <i>Dologale dybowskii</i> | 2.51 | Kingdon 1997 | Continents only |
| <i>Dusicyon australis</i> | 4.20 | Mass estimate ^a | Islands only |
| <i>Eira barbara</i> | 3.62 | Van Valkenburgh 1990 | Continents and islands |
| <i>Eupleres goudotti</i> | 3.48 | Nowak 1999 | Islands only |
| <i>Felis aurata</i> | 4.02 | Nowak 1999 | Continents only |
| <i>Felis badia</i> | 3.54 | Sunquist and Sunquist 2002 | Islands only |
| <i>Felis bengalensis</i> | 3.60 | Kanchanasakha et al. 1998 | Continents and islands |
| <i>Felis bieti</i> | 3.74 | Helin et al. 1999 | Continents only |
| <i>Felis canadensis</i> | 3.94 | This study | Continents and islands |
| <i>Felis caracal</i> | 4.06 | This study | Continents only |
| <i>Felis chaus</i> | 3.85 | Sunquist and Sunquist 2002 | Continents and islands |
| <i>Felis colocolo</i> | 3.43 | Sunquist and Sunquist 2002 | Continents only |
| <i>Felis concolor</i> | 4.62 | This study | Continents and islands |
| <i>Felis geoffroyi</i> | 3.66 | Sunquist and Sunquist 2002 | Continents only |
| <i>Felis guigna</i> | 3.35 | Redford and Eisenberg 1992 | Continents and islands |
| <i>Felis iriomotensis</i> | 3.59 | Abe 1994 | Islands only |
| <i>Felis jacobita</i> | 3.60 | Sunquist and Sunquist 2002 | Continents only |
| <i>Felis lynx</i> | 4.38 | Kitchner 1991 | Continents and islands |
| <i>Felis manul</i> | 3.54 | Sunquist and Sunquist 2002 | Continents only |
| <i>Felis margarita</i> | 3.40 | Sunquist and Sunquist 2002 | Continents only |
| <i>Felis marmorata</i> | 3.44 | Gittleman 1985 | Continents and islands |
| <i>Felis nigripes</i> | 3.20 | Sunquist and Sunquist 2002 | Continents only |
| <i>Felis pardalis</i> | 4.03 | This study | Continents and islands |
| <i>Felis pardina</i> | 4.02 | Sunquist and Sunquist 2002 | Continents only |
| <i>Felis planiceps</i> | 3.27 | Kanchanasakha et al. 1998 | Continents and islands |
| <i>Felis rubiginosa</i> | 3.13 | Sunquist and Sunquist 2002 | Continents and islands |
| <i>Felis rufus</i> | 4.02 | This study | Continents and islands |
| <i>Felis serval</i> | 4.06 | Sunquist and Sunquist 2002 | Continents only |
| <i>Felis silvestris</i> | 3.50 | This study | Continents and islands |
| <i>Felis temminckii</i> | 4.07 | Kanchanasakha et al. 1998 | Continents and islands |
| <i>Felis tigrina</i> | 3.41 | Sunquist and Sunquist 2002 | Continents only |
| <i>Felis viverrina</i> | 3.91 | Sunquist and Sunquist 2002 | Continents and islands |
| <i>Felis wiedii</i> | 3.51 | Sunquist and Sunquist 2002 | Continents and islands |
| <i>Felis yaguaroundi</i> | 3.75 | Sunquist and Sunquist 2002 | Continents only |
| <i>Fennecus zerda</i> | 3.00 | Nowak 1999 | Continents only |
| <i>Fossa fossana</i> | 3.25 | Creel and Macdonald 1995 | Islands only |
| <i>Galerella nigrita</i> | 2.78 | Taylor and Matheson 1999 | Continents only |
| <i>Galerella ochracea</i> | 2.78 | Taylor and Matheson 1999 | Continents only |
| <i>Galerella pulverulenta</i> | 2.94 | Silva and Downing 1995 | Continents only |
| <i>Galerella sanguinea</i> | 2.81 | Silva and Downing 1995 | Continents and islands |
| <i>Galictis cuja</i> | 3.00 | Nowak 1999 | Continents and islands |
| <i>Galictis vittata</i> | 3.37 | Silva and Downing 1995 | Continents only |
| <i>Galidia elegans</i> | 2.91 | Creel and Macdonald 1995 | Islands only |
| <i>Galidictis fasciata</i> | 2.74 | Smith et al. 2003 | Islands only |
| <i>Galidictis grandidieri</i> | 3.15 | Smith et al. 2003 | Islands only |
| <i>Genetta abyssinica</i> | 3.22 | Kingdon 1997 | Continents only |
| <i>Genetta angolensis</i> | 3.22 | Kingdon 1997 | Continents only |
| <i>Genetta genetta</i> | 3.25 | Kingdon 1997 | Continents and islands |
| <i>Genetta johnstoni</i> | 3.30 | Kingdon 1997 | Continents only |
| <i>Genetta maculata</i> | 3.35 | Smith et al. 2003 | Continents and islands |
| <i>Genetta pardina</i> | 3.36 | Mass estimate ^b | Continents only |
| <i>Genetta servalina</i> | 3.18 | Kingdon 1997 | Continents and islands |
| <i>Genetta thierryi</i> | 3.15 | Kingdon 1997 | Continents only |
| <i>Genetta tigrina</i> | 3.33 | Kingdon 1997 | Continents only |
| <i>Genetta victoriae</i> | 3.48 | Kingdon 1997 | Continents only |
| <i>Gulo gulo</i> | 3.96 | This study | Continents and islands |

Table A1 (Continued)

| Species | Log mass (g) | Source | Occurs on |
|-------------------------------------|--------------|----------------------------|------------------------------|
| <i>Helogale hirtula</i> | 2.44 | Kingdon 1997 | Continents only |
| <i>Helogale parvula</i> | 2.45 | Kingdon 1997 | Continents only |
| <i>Hemigalus derbyanus</i> | 3.30 | Kanchanasakha et al. 1998 | Continents and islands |
| <i>Herpestes brachyurus</i> | 3.40 | Kanchanasakha et al. 1998 | Continents and islands |
| <i>Herpestes edwardsi</i> | 3.13 | Egi 2001 | Continents and islands |
| <i>Herpestes fuscus</i> | 3.13 | Silva and Downing 1995 | Continents and islands |
| <i>Herpestes ichneumon</i> | 3.36 | This study | Continents only ^c |
| <i>Herpestes javanicus</i> | 2.86 | This study | Continents and islands |
| <i>Herpestes naso</i> | 3.56 | Kingdon 1997 | Continents only |
| <i>Herpestes semitorquatus</i> | 3.50 | Mass estimate ^c | Islands only |
| <i>Herpestes smithii</i> | 3.23 | Gittleman 1985 | Continents and islands |
| <i>Herpestes urva</i> | 3.38 | Gittleman 1985 | Continents and islands |
| <i>Herpestes vitticollis</i> | 3.46 | Silva and Downing 1995 | Continents and islands |
| <i>Hyaena hyaena</i> | 4.52 | This study | Continents only |
| <i>Ichneumia albicauda</i> | 3.56 | Kingdon 1997 | Continents and islands |
| <i>Ictonyx striatus</i> | 3.02 | Kingdon 1997 | Continents only |
| <i>Liberictis kuhni</i> | 3.33 | Kingdon 1997 | Continents only |
| <i>Lontra canadensis</i> | 3.92 | This study | Continents and islands |
| <i>Lontra felina</i> | 3.60 | Johnson et al. 2000 | Continents and islands |
| <i>Lontra longicaudis</i> | 4.00 | Lariviere 1999a | Continents and islands |
| <i>Lontra provocax</i> | 3.88 | Lariviere 1999b | Continents and islands |
| <i>Lutra lutra</i> | 3.92 | This study | Continents and islands |
| <i>Lutra maculicollis</i> | 3.72 | Kingdon 1997 | Continents only |
| <i>Lutra sumatrana</i> | 3.74 | Kanchanasakha et al. 1998 | Continents and islands |
| <i>Lutrogale perspicillata</i> | 3.95 | Kanchanasakha et al. 1998 | Continents and islands |
| <i>Lycalopex vetulus</i> | 3.53 | Nowak 1999 | Continents only |
| <i>Lycaon pictus</i> | 4.43 | Kingdon 1997 | Continents only |
| <i>Lyncodon patagonicus</i> | 2.35 | Silva and Downing 1995 | Continents only |
| <i>Macrogalidia musschenbroekii</i> | 3.71 | Burness et al. 2001 | Islands only |
| <i>Martes americana</i> | 3.00 | This study | Continents and islands |
| <i>Martes flavigula</i> | 3.40 | Kanchanasakha et al. 1998 | Continents and islands |
| <i>Martes foina</i> | 3.10 | This study | Continents and islands |
| <i>Martes gwatkinsi</i> | 3.31 | Smith et al. 2003 | Continents only |
| <i>Martes martes</i> | 3.11 | Nowak 1999 | Continents and islands |
| <i>Martes melampus</i> | 3.02 | This study | Continents and islands |
| <i>Martes pennanti</i> | 3.53 | This study | Continents and islands |
| <i>Martes zibellina</i> | 3.08 | Johnson et al. 2000 | Continents and islands |
| <i>Meles meles</i> | 3.98 | This study | Continents and islands |
| <i>Mellivora capensis</i> | 3.91 | This study | Continents only |
| <i>Melogale everetti</i> | 3.30 | Johnson et al. 2000 | Islands only |
| <i>Melogale moschata</i> | 2.91 | This study | Continents and islands |
| <i>Melogale orientalis</i> | 2.93 | This study | Islands only |
| <i>Melogale personata</i> | 3.30 | Kanchanasakha et al. 1998 | Continents only |
| <i>Mephitis macroura</i> | 3.23 | Silva and Downing 1995 | Continents only |
| <i>Mephitis mephitis</i> | 3.38 | Johnson et al. 2000 | Continents and islands |
| <i>Mungos gambianus</i> | 3.18 | Kingdon 1997 | Continents only |
| <i>Mungos mungo</i> | 3.27 | Kingdon 1997 | Continents only ^c |
| <i>Mungotictis decemlineata</i> | 2.81 | Nowak 1999 | Islands only |
| <i>Mustela africana</i> | 2.73 | Smith et al. 2003 | Continents only |
| <i>Mustela altaica</i> | 2.34 | Nowak 1999 | Continents only |
| <i>Mustela erminea</i> | 2.35 | This study ^d | Continents and islands |
| <i>Mustela eversmanni</i> | 3.23 | Johnson et al. 2000 | Continents only |
| <i>Mustela felipei</i> | 2.14 | Smith et al. 2003 | Continents only |
| <i>Mustela frenata</i> | 2.38 | Eder and Pattie 2001 | Continents and islands |
| <i>Mustela kathiah</i> | 2.30 | Helin et al. 1999 | Continents and islands |
| <i>Mustela lutreola</i> | 2.77 | Gittleman 1985 | Continents only ^c |
| <i>Mustela lutreolina</i> | 2.79 | Nowak 1999 | Islands only |
| <i>Mustela macrodon</i> | 3.39 | Mass estimate ^b | Continents and islands |
| <i>Mustela nigripes</i> | 2.93 | Silva and Downing 1995 | Continents only |
| <i>Mustela nivalis</i> | 1.91 | This study ^d | Continents and islands |
| <i>Mustela nudipes</i> | 3.11 | Kanchanasakha et al. 1998 | Continents and islands |

Table A1 (Continued)

| Species | Log mass (g) | Source | Occurs on |
|-----------------------------------|--------------|----------------------------|------------------------------|
| <i>Mustela putorius</i> | 3.01 | Johnson et al. 2000 | Continents and islands |
| <i>Mustela sibirica</i> | 2.72 | This study | Continents and islands |
| <i>Mustela strididorsa</i> | 3.18 | Kanchanasakha et al. 1998 | Continents only |
| <i>Mustela vison</i> | 3.00 | This study | Continents and islands |
| <i>Mydaus javanensis</i> | 3.40 | Nowak 1999 | Islands only |
| <i>Mydaus marchei</i> | 3.40 | Nowak 1999 | Islands only |
| <i>Nandinia binotata</i> | 3.41 | Kingdon 1997 | Continents and islands |
| <i>Nasua narica</i> | 3.58 | Silva and Downing 1995 | Continents and islands |
| <i>Nasua nasua</i> | 3.52 | Silva and Downing 1995 | Continents only ^c |
| <i>Nasuella olivacea</i> | 3.13 | Smith et al. 2003 | Continents only |
| <i>Neofelis nebulosa</i> | 4.22 | Sunquist and Sunquist 2002 | Continents and islands |
| <i>Nyctereutes procyonoides</i> | 3.69 | This study | Continents and islands |
| <i>Osbornictis piscivora</i> | 3.17 | Nowak 1999 | Continents only |
| <i>Otocyon megalotis</i> | 3.62 | Nowak 1999 | Continents only |
| <i>Paguma larvata</i> | 3.44 | This study | Continents and islands |
| <i>Panthera leo</i> | 5.21 | Silva and Downing 1995 | Continents only |
| <i>Panthera onca</i> | 4.98 | Sunquist and Sunquist 2002 | Continents only |
| <i>Panthera pardus</i> | 4.54 | Kanchanasakha et al. 1998 | Continents and islands |
| <i>Panthera tigris</i> | 5.03 | Nowak 1999 | Continents and islands |
| <i>Panthera uncia</i> | 4.64 | Sunquist and Sunquist 2002 | Continents only |
| <i>Paracynictis selousi</i> | 3.24 | Silva and Downing 1995 | Continents only |
| <i>Paradoxurus hermaphroditus</i> | 3.54 | Kanchanasakha et al. 1998 | Continents and islands |
| <i>Paradoxurus jerdoni</i> | 3.55 | Silva and Downing 1995 | Continents only |
| <i>Paradoxurus lignicolor</i> | 3.54 | Kanchanasakha et al. 1998 | Islands only |
| <i>Paradoxurus zeylonensis</i> | 3.45 | Gittleman 1985 | Islands only |
| <i>Parahyaena brunnea</i> | 4.58 | Silva and Downing 1995 | Continents only |
| <i>Poecilictis libyca</i> | 2.80 | Kingdon 1997 | Continents only |
| <i>Poecilogale albinucha</i> | 2.46 | Kingdon 1997 | Continents only |
| <i>Poiana richardsonii</i> | 2.78 | Kingdon 1997 | Continents and islands |
| <i>Potos flavus</i> | 3.48 | Egi 2001 | Continents and islands |
| <i>Prionodon linsang</i> | 2.85 | Kanchanasakha et al. 1998 | Continents and islands |
| <i>Prionodon pardicolor</i> | 2.85 | Kanchanasakha et al. 1998 | Continents only |
| <i>Procyon cancrivorus</i> | 3.70 | De La Rosa and Nocke 2000 | Continents and islands |
| <i>Procyon gloveralleni</i> | 3.73 | Mass estimate ^c | Islands only |
| <i>Procyon insularis</i> | 3.82 | Mass estimate ^c | Islands only |
| <i>Procyon lotor</i> | 3.95 | Eder and Pattie 2001 | Continents and islands |
| <i>Procyon maynardi</i> | 3.69 | Mass estimate ^c | Islands only |
| <i>Procyon minor</i> | 3.56 | Mass estimate ^d | Islands only |
| <i>Procyon pygmaeus</i> | 3.54 | Zeveloff 2003 | Islands only |
| <i>Proteles cristatus</i> | 4.00 | Kingdon 1997 | Continents only |
| <i>Pseudalopex culpaeus</i> | 4.00 | Johnson et al. 1996 | Continents and islands |
| <i>Pseudalopex griseus</i> | 3.54 | Johnson et al. 1996 | Continents and islands |
| <i>Pseudalopex gymnocercus</i> | 3.64 | Moehlman and Hofer 1997 | Continents only |
| <i>Pseudalopex sechurae</i> | 3.48 | Alderton 1994 | Continents only |
| <i>Pteronura brasiliensis</i> | 4.43 | Silva and Downing 1995 | Continents only |
| <i>Rhynchogale melleri</i> | 3.38 | Kingdon 1997 | Continents only |
| <i>Salanoia concolor</i> | 2.90 | Macdonald 1984 | Islands only |
| <i>Speothos venaticus</i> | 3.78 | Reid 1997 | Continents only |
| <i>Spilogale gracilis</i> | 2.68 | Verts et al. 2001 | Continents and islands |
| <i>Spilogale putorius</i> | 2.88 | Egi 2001 | Continents and islands |
| <i>Spilogale pygmaea</i> | 2.37 | Medellin et al. 1998 | Continents only |
| <i>Suricata suricata</i> | 2.90 | Kingdon 1997 | Continents only |
| <i>Taxidea taxus</i> | 3.90 | Nowak 1999 | Continents and islands |
| <i>Tremarctos ornatus</i> | 5.13 | Van Valkenburgh 1990 | Continents only |
| <i>Urocyon cinereoargenteus</i> | 3.57 | This study | Continents and islands |
| <i>Urocyon littoralis</i> | 3.28 | Moore and Collins 1995 | Islands only |
| <i>Ursus americanus</i> | 5.19 | Eder and Pattie 2001 | Continents and islands |
| <i>Ursus arctos</i> | 5.51 | Eder and Pattie 2001 | Continents and islands |
| <i>Ursus malayanus</i> | 4.66 | Kanchanasakha et al. 1998 | Continents and islands |
| <i>Ursus thibetanus</i> | 4.98 | Abe 1994 | Continents and islands |
| <i>Ursus ursinus</i> | 4.83 | McNab 2000 | Continents and islands |

Table A1 (Continued)

| Species | Log mass (g) | Source | Occurs on |
|----------------------------|--------------|---------------------------|------------------------|
| <i>Viverra zibetha</i> | 3.93 | Kanchanasakha et al. 1998 | Continents and islands |
| <i>Viverra tangalunga</i> | 3.74 | Kanchanasakha et al. 1998 | Continents and islands |
| <i>Viverra zibetha</i> | 3.93 | Kanchanasakha et al. 1998 | Continents and islands |
| <i>Viverricula indica</i> | 3.34 | This study | Continents and islands |
| <i>Vormela peregusna</i> | 2.41 | This study | Continents only |
| <i>Vulpes benegalensis</i> | 3.38 | Moehlman and Hofer 1997 | Continents only |
| <i>Vulpes cana</i> | 3.00 | Nowak 1999 | Continents only |
| <i>Vulpes chama</i> | 3.60 | Nowak 1999 | Continents only |
| <i>Vulpes corsac</i> | 3.40 | Helin et al. 1999 | Continents only |
| <i>Vulpes ferrilata</i> | 3.59 | Moehlman and Hofer 1997 | Continents only |
| <i>Vulpes macrotis</i> | 3.29 | Silva and Downing 1995 | Continents only |
| <i>Vulpes pallida</i> | 3.41 | Nowak 1999 | Continents only |
| <i>Vulpes rueppelli</i> | 3.28 | This study | Continents and islands |
| <i>Vulpes velox</i> | 3.38 | Silva and Downing 1995 | Continents only |
| <i>Vulpes vulpes</i> | 3.74 | This study | Continents and islands |

^a Estimate based on head and body length in Nowak 1999.

^b Estimate based on lower carnassial length measured in this study.

^c Estimate based on condylo-basal length measured in this study.

^d See text.

^e Occurs naturally on continents only but introduced to islands.

Table A2

Largest and smallest carnivores on islands of different areas

| Island | Carnivore richness | Area (km ²) | Smallest carnivore | Largest carnivore |
|--------------------------|--------------------|-------------------------|-----------------------------------|-----------------------------------|
| Admiralty | 6 | 4,310 | <i>Mustela erminea</i> | <i>Ursus arctos</i> |
| Afognak | 4 | 1,809 | <i>Mustela erminea</i> | <i>Ursus arctos</i> |
| Akimiski | 8 | 2,326 | <i>Mustela nivalis</i> | <i>Ursus americanus</i> |
| Akutan | 1 | 36 | <i>Vulpes vulpes</i> | <i>Vulpes vulpes</i> |
| Alaid | 2 | 150 | <i>Mustela erminea</i> | <i>Vulpes vulpes</i> |
| Aland | 5 | 1,505 | <i>Mustela nivalis</i> | <i>Meles meles</i> |
| Amakusa | 1 | 610 | <i>Nyctereutes procyonoides</i> | <i>Nyctereutes procyonoides</i> |
| Andros | 2 | 380 | <i>Martes foina</i> | <i>Meles meles</i> |
| Anglesey | 3 | 712 | <i>Mustela nivalis</i> | <i>Meles meles</i> |
| Anguila | 1 | 12 | <i>Mustela vison</i> | <i>Mustela vison</i> |
| Anticosti | 9 | 7,941 | <i>Mustela erminea</i> | <i>Ursus americanus</i> |
| Arran | 3 | 427 | <i>Vulpes vulpes</i> | <i>Meles meles</i> |
| Asinara | 1 | 52 | <i>Mustela nivalis</i> | <i>Mustela nivalis</i> |
| Attu | 1 | 896 | <i>Alopex lagopus</i> | <i>Alopex lagopus</i> |
| Avery | 1 | 8 | <i>Procyon lotor</i> | <i>Procyon lotor</i> |
| Baker | 2 | 135 | <i>Canis lupus</i> | <i>Ursus americanus</i> |
| Balabac | 1 | 306 | <i>Paradoxurus hermaphroditus</i> | <i>Paradoxurus hermaphroditus</i> |
| Balembangan | 1 | 150 | <i>Lutra perspicillata</i> | <i>Lutra perspicillata</i> |
| Bali | 7 | 5,620 | <i>Melogale orientalis</i> | <i>Panthera tigris</i> |
| Banggi | 4 | 441 | <i>Arctogalidia trivirgata</i> | <i>Lutra perspicillata</i> |
| Bangka | 9 | 11,330 | <i>Prionodon linsang</i> | <i>Ursus malayanus</i> |
| Banks (British Columbia) | 2 | 1,024 | <i>Lontra canadensis</i> | <i>Canis lupus</i> |
| Baranof | 4 | 4,163 | <i>Mustela erminea</i> | <i>Ursus arctos</i> |
| Barra | 1 | 90 | <i>Lutra lutra</i> | <i>Lutra lutra</i> |
| Basilan | 1 | 1,282 | <i>Paradoxurus hermaphroditus</i> | <i>Paradoxurus hermaphroditus</i> |
| Bastimentos | 1 | 52 | <i>Procyon lotor</i> | <i>Procyon lotor</i> |
| Batam | 2 | 470 | <i>Arctogalidia trivirgata</i> | <i>Arctictis binturong</i> |
| Bawean | 2 | 200 | <i>Viverricula indica</i> | <i>Paradoxurus hermaphroditus</i> |
| Belitung | 5 | 4,833 | <i>Prionodon linsang</i> | <i>Viverra tangalunga</i> |
| Biliran | 1 | 498 | <i>Paradoxurus hermaphroditus</i> | <i>Paradoxurus hermaphroditus</i> |
| Bintang | 6 | 1,140 | <i>Aonyx cinerea</i> | <i>Panthera tigris</i> |
| Bioko | 4 | 2,072 | <i>Poiana richardsoni</i> | <i>Aonyx congica</i> |
| Bjorno | 1 | 2 | <i>Mustela erminea</i> | <i>Mustela erminea</i> |
| Bohol | 2 | 3,864 | <i>Paradoxurus hermaphroditus</i> | <i>Viverra tangalunga</i> |

Table A2 (Continued)

| Island | Carnivore richness | Area (km ²) | Smallest carnivore | Largest carnivore |
|-------------------|--------------------|-------------------------|-------------------------------------|-------------------------------------|
| Borneo | 26 | 743,330 | <i>Prionodon linsang</i> | <i>Ursus malayanus</i> |
| Bornholm | 6 | 588 | <i>Mustela nivalis</i> | <i>Meles meles</i> |
| Britain | 11 | 229,883 | <i>Mustela nivalis</i> | <i>Ursus arctos</i> |
| Broughton | 1 | 128 | <i>Mustela vison</i> | <i>Mustela vison</i> |
| Bruit | 2 | 530 | <i>Felis bengalensis</i> | <i>Lutra sumatrana</i> |
| Bulan | 1 | 91 | <i>Arctogalidia trivirgata</i> | <i>Arctogalidia trivirgata</i> |
| Bunguran (Natuna) | 3 | 1,485 | <i>Arctogalidia trivirgata</i> | <i>Viverra tangalunga</i> |
| Busuanga | 5 | 938 | <i>Herpestes brachyurus</i> | <i>Viverra tangalunga</i> |
| Bute | 2 | 119 | <i>Mustela erminea</i> | <i>Vulpes vulpes</i> |
| Cairn | 2 | 37 | <i>Mustela erminea</i> | <i>Lontra canadensis</i> |
| Calvert | 2 | 329 | <i>Mustela vison</i> | <i>Canis lupus</i> |
| Camiguin | 2 | 255 | <i>Paradoxurus hermaphroditus</i> | <i>Viverra tangalunga</i> |
| Cape Breton | 11 | 10,280 | <i>Mustela erminea</i> | <i>Ursus americanus</i> |
| Catanduanes | 2 | 1,513 | <i>Paradoxurus hermaphroditus</i> | <i>Viverra tangalunga</i> |
| Cebu | 1 | 4,421 | <i>Felis bengalensis</i> | <i>Felis bengalensis</i> |
| Celebes | 1 | 189,070 | <i>Macrogalidia musschenbroekii</i> | <i>Macrogalidia musschenbroekii</i> |
| Charlton | 1 | 93 | <i>Mustela erminea</i> | <i>Mustela erminea</i> |
| Cheju-Do | 4 | 1,860 | <i>Mustela sibirica</i> | <i>Meles meles</i> |
| Chichagof | 5 | 5,449 | <i>Mustela erminea</i> | <i>Ursus arctos</i> |
| Chiloe | 5 | 8,394 | <i>Galictis cuja</i> | <i>Lontra provocax</i> |
| Chios | 4 | 831 | <i>Mustela nivalis</i> | <i>Lutra lutra</i> |
| Con Son | 1 | 51 | <i>Paradoxurus hermaphroditus</i> | <i>Paradoxurus hermaphroditus</i> |
| Conanicut | 1 | 24 | <i>Mustela vison</i> | <i>Mustela vison</i> |
| Corfu | 5 | 592 | <i>Mustela nivalis</i> | <i>Canis aureus</i> |
| Coronation | 2 | 91 | <i>Mustela vison</i> | <i>Lontra canadensis</i> |
| Corsica | 4 | 8,681 | <i>Mustela nivalis</i> | <i>Vulpes vulpes</i> |
| Cozumel | 3 | 490 | <i>Procyon pygmaeus</i> | <i>Nasua nelsoni</i> |
| Crete | 3 | 8,336 | <i>Mustela nivalis</i> | <i>Meles meles</i> |
| Culion | 5 | 400 | <i>Aonyx cinerea</i> | <i>Viverra tangalunga</i> |
| Cumberland | 1 | 145 | <i>Ursus americanus</i> | <i>Ursus americanus</i> |
| Cyprus | 1 | 9,250 | <i>Vulpes vulpes</i> | <i>Vulpes vulpes</i> |
| Dall | 5 | 658 | <i>Mustela erminea</i> | <i>Ursus americanus</i> |
| Deer | 9 | 72 | <i>Mustela erminea</i> | <i>Ursus americanus</i> |
| Dinagat | 1 | 670 | <i>Paradoxurus hermaphroditus</i> | <i>Paradoxurus hermaphroditus</i> |
| Domel | 2 | 250 | <i>Arctogalidia trivirgata</i> | <i>Paradoxurus hermaphroditus</i> |
| Douglas | 2 | 203 | <i>Mustela erminea</i> | <i>Ursus americanus</i> |
| Drejo | 1 | 4 | <i>Mustela erminea</i> | <i>Mustela erminea</i> |
| Duke | 1 | 155 | <i>Canis lupus</i> | <i>Canis lupus</i> |
| Dundas | 1 | 160 | <i>Canis lupus</i> | <i>Canis lupus</i> |
| Elba | 1 | 224 | <i>Martes martes</i> | <i>Martes martes</i> |
| Enggano | 1 | 397 | <i>Paradoxurus hermaphroditus</i> | <i>Paradoxurus hermaphroditus</i> |
| Espirito Santo | 1 | 100 | <i>Bassariscus astutus</i> | <i>Bassariscus astutus</i> |
| Esther | 2 | 133 | <i>Mustela vison</i> | <i>Lontra canadensis</i> |
| Etolin | 5 | 889 | <i>Mustela erminea</i> | <i>Ursus americanus</i> |
| Euboea (Evvoia) | 4 | 1,467 | <i>Mustela nivalis</i> | <i>Lutra lutra</i> |
| Falster | 4 | 514 | <i>Mustela nivalis</i> | <i>Vulpes vulpes</i> |
| Fano | 1 | 57 | <i>Mustela erminea</i> | <i>Mustela erminea</i> |
| Farasan Al kabir | 1 | 395 | <i>Ichneumia albicauda</i> | <i>Ichneumia albicauda</i> |
| Flaherty | 3 | 1,585 | <i>Mustela erminea</i> | <i>Vulpes vulpes</i> |
| Fyn | 6 | 2,985 | <i>Mustela erminea</i> | <i>Meles meles</i> |
| Galang | 2 | 74 | <i>Aonyx cinerea</i> | <i>Arctogalidia trivirgata</i> |
| Gigha | 1 | 14 | <i>Vulpes vulpes</i> | <i>Vulpes vulpes</i> |
| Gilford | 1 | 382 | <i>Martes americana</i> | <i>Martes americana</i> |
| Gotland | 1 | 3,173 | <i>Vulpes vulpes</i> | <i>Vulpes vulpes</i> |
| Graham | 4 | 6,361 | <i>Mustela erminea</i> | <i>Ursus americanus</i> |
| Grand Manan | 1 | 137 | <i>Vulpes vulpes</i> | <i>Vulpes vulpes</i> |
| Gravina | 2 | 233 | <i>Martes americana</i> | <i>Ursus americanus</i> |
| Great Wass | 1 | 11 | <i>Mustela vison</i> | <i>Mustela vison</i> |
| Gribble/Gribbell | 2 | 220 | <i>Ursus americanus</i> | <i>Ursus americanus</i> |
| Guadaloupe | 1 | 1,510 | <i>Procyon minor</i> | <i>Procyon minor</i> |

Table A2 (Continued)

| Island | Carnivore richness | Area (km ²) | Smallest carnivore | Largest carnivore |
|---------------|--------------------|-------------------------|-----------------------------------|-----------------------------------|
| Guernsey | 1 | 64 | <i>Mustela erminea</i> | <i>Mustela erminea</i> |
| Hainan | 14 | 33,940 | <i>Mustela kathiah</i> | <i>Ursus thibetanus</i> |
| Halleck | 1 | 33 | <i>Lontra canadensis</i> | <i>Lontra canadensis</i> |
| Hatia | 1 | 415.7 | <i>Aonyx cinerea</i> | <i>Aonyx cinerea</i> |
| Hawkesbury | 3 | 365 | <i>Martes americana</i> | <i>Ursus americanus</i> |
| Heceta | 3 | 189 | <i>Mustela erminea</i> | <i>Ursus americanus</i> |
| Hiiumaa | 7 | 980 | <i>Mustela nivalis</i> | <i>Ursus arctos</i> |
| Hinchinbrook | 4 | 442 | <i>Mustela erminea</i> | <i>Ursus arctos</i> |
| Hokkaido | 10 | 77,978 | <i>Mustela nivalis</i> | <i>Ursus arctos</i> |
| Hong Kong | 7 | 78 | <i>Mustela kathiah</i> | <i>Vulpes vulpes</i> |
| Honshu | 11 | 227,898 | <i>Mustela nivalis</i> | <i>Ursus thibetanus</i> |
| Hoste | 2 | 4,117 | <i>Lontra provocax</i> | <i>Pseudalopex culpaeus</i> |
| Ibiza | 2 | 541 | <i>Martes foina</i> | <i>Genetta genetta</i> |
| Ikaria | 2 | 263 | <i>Martes foina</i> | <i>Canis aureus</i> |
| Iki | 1 | 135 | <i>Mustela sibirica</i> | <i>Mustela sibirica</i> |
| Ios | 1 | 108 | <i>Mustela nivalis</i> | <i>Mustela nivalis</i> |
| Ireland | 6 | 84,406 | <i>Mustela erminea</i> | <i>Canis lupus</i> |
| Iriomote | 1 | 284 | <i>Felis iriomotensis</i> | <i>Felis iriomotensis</i> |
| Islay | 2 | 622 | <i>Mustela erminea</i> | <i>Lutra lutra</i> |
| Isle au Haut | 3 | 27 | <i>Mustela vison</i> | <i>Lontra canadensis</i> |
| Ithaca | 1 | 95 | <i>Martes foina</i> | <i>Martes foina</i> |
| Iturup | 5 | 3,200 | <i>Mustela nivalis</i> | <i>Ursus arctos</i> |
| Java | 21 | 132,187 | <i>Mustela sibirica</i> | <i>Panthera tigris</i> |
| Jersey | 1 | 117 | <i>Mustela erminea</i> | <i>Mustela erminea</i> |
| Jura | 2 | 377 | <i>Mustela erminea</i> | <i>Lutra lutra</i> |
| Kangean | 3 | 430 | <i>Viverricula indica</i> | <i>Panthera pardus</i> |
| Karaginskij | 6 | 1,936 | <i>Mustela erminea</i> | <i>Ursus arctos</i> |
| Karimata | 2 | 179 | <i>Aonyx cinerea</i> | <i>Viverra zangalunga</i> |
| Karimon | 1 | 131 | <i>Aonyx cinerea</i> | <i>Aonyx cinerea</i> |
| Karimunjawa | 2 | 18.3 | <i>Aonyx cinerea</i> | <i>Felis bengalensis</i> |
| Karpathos | 1 | 280 | <i>Martes foina</i> | <i>Martes foina</i> |
| Kayak | 2 | 77 | <i>Vulpes vulpes</i> | <i>Ursus arctos</i> |
| Kefalonia | 5 | 775 | <i>Mustela nivalis</i> | <i>Meles meles</i> |
| King | 1 | 808 | <i>Mustela vison</i> | <i>Mustela vison</i> |
| Kinmen | 1 | 150 | <i>Lutra lutra</i> | <i>Lutra lutra</i> |
| Kiska | 1 | 278 | <i>Alopex lagopus</i> | <i>Alopex lagopus</i> |
| Kisseraing | 1 | 408 | <i>Paradoxurus hermaphroditus</i> | <i>Paradoxurus hermaphroditus</i> |
| Kithira | 4 | 277 | <i>Mustela nivalis</i> | <i>Meles meles</i> |
| Kodiak | 6 | 9,293 | <i>Mustela erminea</i> | <i>Ursus arctos</i> |
| Koh Samui | 1 | 233 | <i>Paradoxurus hermaphroditus</i> | <i>Paradoxurus hermaphroditus</i> |
| Koh Chang | 2 | 214.6 | <i>Herpestes javanicus</i> | <i>Viverricula indica</i> |
| Koh yao | 2 | 100 | <i>Paguma larvata</i> | <i>Paradoxurus hermaphroditus</i> |
| Korcula | 4 | 278 | <i>Mustela nivalis</i> | <i>Canis aureus</i> |
| Kos | 2 | 287 | <i>Martes foina</i> | <i>Vulpes vulpes</i> |
| Kosciusko | 2 | 482 | <i>Canis lupus</i> | <i>Ursus americanus</i> |
| Krestof | 2 | 28 | <i>Lontra canadensis</i> | <i>Ursus arctos</i> |
| Krk | 3 | 418.6 | <i>Martes foina</i> | <i>Vulpes vulpes</i> |
| Kruzof | 4 | 447 | <i>Mustela erminea</i> | <i>Ursus arctos</i> |
| Kuiu | 6 | 1,933 | <i>Martes americana</i> | <i>Ursus americanus</i> |
| Kunashir | 5 | 1,490 | <i>Mustela nivalis</i> | <i>Ursus arctos</i> |
| Kundur | 5 | 315 | <i>Arctogalidia trivirgata</i> | <i>Arctictis binturong</i> |
| Kupreanof | 7 | 2,822 | <i>Martes americana</i> | <i>Ursus americanus</i> |
| Kyushu | 8 | 36,719 | <i>Mustela sibirica</i> | <i>Ursus thibetanus</i> |
| Lamukotan | 1 | 10 | <i>Mydaus javanensis</i> | <i>Mydaus javanensis</i> |
| Langkawi | 4 | 363 | <i>Arctogalidia trivirgata</i> | <i>Lutra perspicillata</i> |
| Lantau | 4 | 142 | <i>Mustela kathiah</i> | <i>Lutra lutra</i> |
| Laut (Borneo) | 2 | 2,057 | <i>Aonyx cinerea</i> | <i>Viverra zangalunga</i> |
| Laut (Natuna) | 3 | 33 | <i>Aonyx cinerea</i> | <i>Viverra zangalunga</i> |
| Lefkada | 4 | 279 | <i>Mustela nivalis</i> | <i>Canis aureus</i> |
| Lesbos | 5 | 1,630 | <i>Mustela nivalis</i> | <i>Meles meles</i> |

Table A2 (Continued)

| Island | Carnivore richness | Area (km ²) | Smallest carnivore | Largest carnivore |
|------------------------------|--------------------|-------------------------|-----------------------------------|-----------------------------------|
| Lewis | 1 | 2,137 | <i>Lutra lutra</i> | <i>Lutra lutra</i> |
| Leyte | 2 | 7,213 | <i>Paradoxurus hermaphroditus</i> | <i>Viverra zangalunga</i> |
| Lingga | 3 | 889 | <i>Aonyx cinerea</i> | <i>Viverra zangalunga</i> |
| Lolland | 4 | 1,243 | <i>Mustela nivalis</i> | <i>Vulpes vulpes</i> |
| Lombok | 2 | 4,725 | <i>Paradoxurus hermaphroditus</i> | <i>Felis bengalensis</i> |
| Long (Maine) | 2 | 24 | <i>Mustela vison</i> | <i>Vulpes vulpes</i> |
| Long (Alexander Archipelago) | 3 | 115 | <i>Mustela erminea</i> | <i>Lontra canadensis</i> |
| Louise | 4 | 275 | <i>Mustela erminea</i> | <i>Ursus americanus</i> |
| Luzon | 2 | 104,688 | <i>Paradoxurus hermaphroditus</i> | <i>Viverra zangalunga</i> |
| Lyo | 1 | 6 | <i>Mustela erminea</i> | <i>Mustela erminea</i> |
| Madagascar | 8 | 587,041 | <i>Galidictis fasciata</i> | <i>Cryptoprocta ferox</i> |
| Madura | 3 | 4,560 | <i>Herpestes javanicus</i> | <i>Panthera pardus</i> |
| Magdalena | 1 | 290 | <i>Canis latrans</i> | <i>Canis latrans</i> |
| Majorca | 4 | 3,640 | <i>Mustela nivalis</i> | <i>Felis silvestris</i> |
| Malta | 1 | 246 | <i>Mustela nivalis</i> | <i>Mustela nivalis</i> |
| Man | 2 | 572 | <i>Mustela erminea</i> | <i>Lutra lutra</i> |
| Marble | 1 | 23 | <i>Lontra canadensis</i> | <i>Lontra canadensis</i> |
| Margarita | 2 | 957 | <i>Conepatus semistriatus</i> | <i>Felis pardalis</i> |
| Maria Madre | 1 | 200 | <i>Procyon insularis</i> | <i>Procyon insularis</i> |
| Maria Magdalena | 1 | 150 | <i>Procyon insularis</i> | <i>Procyon insularis</i> |
| Marinduque | 1 | 958 | <i>Paradoxurus hermaphroditus</i> | <i>Paradoxurus hermaphroditus</i> |
| Maripipi | 1 | 22 | <i>Paradoxurus hermaphroditus</i> | <i>Paradoxurus hermaphroditus</i> |
| Mindanao | 2 | 94,631 | <i>Paradoxurus hermaphroditus</i> | <i>Viverra zangalunga</i> |
| Mindoro | 2 | 9,735 | <i>Paradoxurus hermaphroditus</i> | <i>Viverra zangalunga</i> |
| Minorca | 2 | 702 | <i>Mustela nivalis</i> | <i>Martes martes</i> |
| Mitkof | 7 | 547 | <i>Mustela erminea</i> | <i>Ursus americanus</i> |
| Mljet | 1 | 104 | <i>Martes foina</i> | <i>Martes foina</i> |
| Montague | 2 | 850 | <i>Lontra canadensis</i> | <i>Ursus arctos</i> |
| Moresby | 3 | 2,636 | <i>Mustela erminea</i> | <i>Lontra canadensis</i> |
| Mount Desert | 11 | 275 | <i>Mustela erminea</i> | <i>Ursus americanus</i> |
| Mull | 4 | 909 | <i>Mustela erminea</i> | <i>Lutra lutra</i> |
| Nagai | 1 | 310 | <i>Lontra canadensis</i> | <i>Lontra canadensis</i> |
| Naxos | 2 | 436 | <i>Mustela nivalis</i> | <i>Martes foina</i> |
| Negros | 3 | 13,670 | <i>Paradoxurus hermaphroditus</i> | <i>Viverra zangalunga</i> |
| Newfoundland | 10 | 108,860 | <i>Mustela erminea</i> | <i>Ursus americanus</i> |
| Nias | 2 | 4,600 | <i>Felis bengalensis</i> | <i>Arctictis binturong</i> |
| Nootka | 4 | 529 | <i>Mustela vison</i> | <i>Ursus americanus</i> |
| North Pagai | 1 | 530 | <i>Paradoxurus hermaphroditus</i> | <i>Paradoxurus hermaphroditus</i> |
| North Twin | 1 | 157 | <i>Alopex lagopus</i> | <i>Alopex lagopus</i> |
| North Uist | 1 | 294 | <i>Lutra lutra</i> | <i>Lutra lutra</i> |
| Nunivak | 2 | 4,209 | <i>Mustela vison</i> | <i>Alopex lagopus</i> |
| Nusa Barung | 1 | 1 | <i>Viverricula indica</i> | <i>Viverricula indica</i> |
| Oki | 1 | 262.8 | <i>Nyctereutes procyonoides</i> | <i>Nyctereutes procyonoides</i> |
| Oland | 6 | 1,351 | <i>Mustela nivalis</i> | <i>Meles meles</i> |
| Orcas | 1 | 143 | <i>Lontra canadensis</i> | <i>Lontra canadensis</i> |
| Orkney | 2 | 490 | <i>Mustela erminea</i> | <i>Lutra lutra</i> |
| Padang | 2 | 1,109 | <i>Paradoxurus hermaphroditus</i> | <i>Ursus malayanus</i> |
| Padre | 5 | 119 | <i>Procyon lotor</i> | <i>Canis rufus</i> |
| Palawan | 9 | 11,785 | <i>Felis planiceps</i> | <i>Arctictis binturong</i> |
| Panaitan | 5 | 118 | <i>Herpestes javanicus</i> | <i>Panthera pardus</i> |
| Panay | 3 | 12,300 | <i>Paradoxurus hermaphroditus</i> | <i>Viverra zangalunga</i> |
| Panembangan | 1 | 26 | <i>Viverra zangalunga</i> | <i>Viverra zangalunga</i> |
| Paramushir | 4 | 2,053 | <i>Mustela nivalis</i> | <i>Ursus arctos</i> |
| Parida | 1 | 15 | <i>Potos flavus</i> | <i>Potos flavus</i> |
| Pemba | 1 | 984 | <i>Atilax paludinosus</i> | <i>Atilax paludinosus</i> |
| Pender | 1 | 26 | <i>Procyon lotor</i> | <i>Procyon lotor</i> |
| Pinang | 5 | 293 | <i>Viverricula indica</i> | <i>Viverra megaspila</i> |
| Pini | 1 | 313 | <i>Arctogalidia trivirgata</i> | <i>Arctogalidia trivirgata</i> |
| Pitt | 4 | 1,349 | <i>Martes americana</i> | <i>Ursus americanus</i> |

Table A2 (Continued)

| Island | Carnivore richness | Area (km ²) | Smallest carnivore | Largest carnivore |
|------------------------------------|--------------------|-------------------------|-----------------------------------|-----------------------------------|
| Polillo | 1 | 769 | <i>Viverra zibetha</i> | <i>Viverra zibetha</i> |
| Popa | 2 | 53 | <i>Potos flavus</i> | <i>Procyon lotor</i> |
| Porcher | 4 | 521 | <i>Mustela erminea</i> | <i>Canis lupus</i> |
| Price | 1 | 171 | <i>Mustela vison</i> | <i>Mustela vison</i> |
| Prince Edward | 11 | 5,657 | <i>Mustela erminea</i> | <i>Ursus americanus</i> |
| Prince of Wales | 6 | 6,675 | <i>Mustela erminea</i> | <i>Ursus americanus</i> |
| Princess Royal | 2 | 2,355 | <i>Canis lupus</i> | <i>Ursus americanus</i> |
| Qeshm | 4 | 1,488 | <i>Herpestes javanicus</i> | <i>Felis silvestris</i> |
| Quadra | 2 | 270 | <i>Canis lupus</i> | <i>Felis concolor</i> |
| Raasey | 2 | 60 | <i>Vulpes vulpes</i> | <i>Lutra lutra</i> |
| Rab | 2 | 90.8 | <i>Mustela nivalis</i> | <i>Martes foina</i> |
| Read | 5 | 407.7 | <i>Mustela erminea</i> | <i>Ursus americanus</i> |
| Revillagigedo | 6 | 3,024 | <i>Mustela erminea</i> | <i>Ursus americanus</i> |
| Rhodes | 4 | 1,398 | <i>Mustela nivalis</i> | <i>Meles meles</i> |
| Rhum | 1 | 110 | <i>Lutra lutra</i> | <i>Lutra lutra</i> |
| Rishiri | 2 | 192 | <i>Mustela sibirica</i> | <i>Vulpes vulpes</i> |
| Rugen | 1 | 926 | <i>Vulpes vulpes</i> | <i>Vulpes vulpes</i> |
| Rupat | 3 | 1,490 | <i>Paradoxurus hermaphroditus</i> | <i>Ursus malayanus</i> |
| Saaremaa | 10 | 2,673 | <i>Mustela nivalis</i> | <i>Ursus arctos</i> |
| Sado Shima | 2 | 937 | <i>Mustela sibirica</i> | <i>Nyctereutes procyonoides</i> |
| Saint Lawrence | 4 | 5,135 | <i>Alopex lagopus</i> | <i>Ursus arctos</i> |
| Saint Matthew (Mergui Archipelago) | 1 | 176 | <i>Paradoxurus hermaphroditus</i> | <i>Paradoxurus hermaphroditus</i> |
| Saint Matthew (Alaska) | 1 | 354 | <i>Alopex lagopus</i> | <i>Alopex lagopus</i> |
| Saint Paul (Pribilof) | 1 | 91 | <i>Vulpes vulpes</i> | <i>Vulpes vulpes</i> |
| Sakhalin | 11 | 76,400 | <i>Mustela nivalis</i> | <i>Ursus arctos</i> |
| Saltspring | 3 | 187 | <i>Mustela erminea</i> | <i>Felis concolor</i> |
| Samar | 1 | 13,429 | <i>Viverra zibetha</i> | <i>Viverra zibetha</i> |
| Samos | 3 | 159 | <i>Mustela nivalis</i> | <i>Canis aureus</i> |
| Alonisos | 1 | 64.0 | <i>Martes foina</i> | <i>Martes foina</i> |
| Samothraki (Samothrace) | 1 | 183.8 | <i>Martes foina</i> | <i>Martes foina</i> |
| San Clemente | 1 | 152 | <i>Urocyon littoralis</i> | <i>Urocyon littoralis</i> |
| San Cristobal | 2 | 37 | <i>Potos flavus</i> | <i>Procyon lotor</i> |
| San Jose | 1 | 165 | <i>Bassariscus astutus</i> | <i>Bassariscus astutus</i> |
| San Miguel | 2 | 36 | <i>Spilogale gracilis</i> | <i>Urocyon littoralis</i> |
| San Nicholas | 1 | 57 | <i>Urocyon littoralis</i> | <i>Urocyon littoralis</i> |
| Sanga-Sanga | 1 | 67.1 | <i>Paradoxurus hermaphroditus</i> | <i>Paradoxurus hermaphroditus</i> |
| Sanibel | 1 | 45 | <i>Procyon lotor</i> | <i>Procyon lotor</i> |
| Santa Catalina | 1 | 193 | <i>Urocyon littoralis</i> | <i>Urocyon littoralis</i> |
| Santa Cruz | 2 | 249 | <i>Spilogale gracilis</i> | <i>Urocyon littoralis</i> |
| Santa Rosa | 2 | 215 | <i>Spilogale gracilis</i> | <i>Urocyon littoralis</i> |
| Sardinia | 4 | 23,813 | <i>Mustela nivalis</i> | <i>Vulpes vulpes</i> |
| Sebangka | 1 | 120 | <i>Aonyx cinerea</i> | <i>Aonyx cinerea</i> |
| Seguam | 1 | 215 | <i>Alopex lagopus</i> | <i>Alopex lagopus</i> |
| Setoko | 2 | 17 | <i>Aonyx cinerea</i> | <i>Panthera tigris</i> |
| Shantar | 4 | 1,766 | <i>Mustela erminea</i> | <i>Ursus arctos</i> |
| Sheppey | 3 | 91 | <i>Mustela nivalis</i> | <i>Meles meles</i> |
| Shetland | 1 | 899 | <i>Lutra lutra</i> | <i>Lutra lutra</i> |
| Shikoku | 9 | 18,292 | <i>Mustela sibirica</i> | <i>Ursus thibetanus</i> |
| Shrubby | 2 | 15 | <i>Mustela vison</i> | <i>Lontra canadensis</i> |
| Shumshu | 4 | 388 | <i>Mustela nivalis</i> | <i>Ursus arctos</i> |
| Shuyak | 2 | 168 | <i>Lontra canadensis</i> | <i>Ursus arctos</i> |
| Siberut | 2 | 3,829 | <i>Hemigalus derbyanus</i> | <i>Paradoxurus lignicolor</i> |
| Sibuyan | 2 | 465 | <i>Paradoxurus hermaphroditus</i> | <i>Viverra zibetha</i> |
| Sicily | 7 | 25,460 | <i>Mustela nivalis</i> | <i>Canis lupus</i> |
| Sidney | 1 | 9 | <i>Mustela vison</i> | <i>Mustela vison</i> |
| Siguijor | 1 | 334 | <i>Viverra zibetha</i> | <i>Viverra zibetha</i> |
| Simeulue | 1 | 1,754 | <i>Paradoxurus hermaphroditus</i> | <i>Paradoxurus hermaphroditus</i> |
| Singapore | 19 | 536 | <i>Viverricula indica</i> | <i>Panthera tigris</i> |
| Singkep | 1 | 175 | <i>Arctogalidia trivirgata</i> | <i>Arctogalidia trivirgata</i> |

Table A2 (Continued)

| Island | Carnivore richness | Area (km ²) | Smallest carnivore | Largest carnivore |
|-------------------|--------------------|-------------------------|-----------------------------------|-----------------------------------|
| Sipora | 2 | 840 | <i>Hemigalus derbyanus</i> | <i>Paradoxurus hermaphroditus</i> |
| Sjaelland | 7 | 7,031 | <i>Mustela nivalis</i> | <i>Lutra lutra</i> |
| Skaro | 1 | 2 | <i>Mustela erminea</i> | <i>Mustela erminea</i> |
| Skye | 5 | 1,735 | <i>Mustela nivalis</i> | <i>Lutra lutra</i> |
| South Pagai | 2 | 1,410 | <i>Hemigalus derbyanus</i> | <i>Paradoxurus hermaphroditus</i> |
| South Twin | 1 | 150 | <i>Alopex lagopus</i> | <i>Alopex lagopus</i> |
| South Uist | 1 | 365 | <i>Lutra lutra</i> | <i>Lutra lutra</i> |
| Sri Lanka | 14 | 65,000 | <i>Felis rubiginosus</i> | <i>Ursus ursinus</i> |
| Suemez | 3 | 153 | <i>Mustela erminea</i> | <i>Canis lupus</i> |
| Sugi | 1 | 89.9 | <i>Arctogalidia trivirgata</i> | <i>Arctogalidia trivirgata</i> |
| Sullivan | 1 | 188 | <i>Paradoxurus hermaphroditus</i> | <i>Paradoxurus hermaphroditus</i> |
| Sumatra | 30 | 473,607 | <i>Mustela lutreolina</i> | <i>Panthera tigris</i> |
| Swans | 1 | 28 | <i>Mustela vison</i> | <i>Mustela vison</i> |
| Taiwan | 14 | 35,989 | <i>Mustela sibirica</i> | <i>Ursus thibetanus</i> |
| Tanegashima | 1 | 456 | <i>Mustela sibirica</i> | <i>Mustela sibirica</i> |
| Tebing Tinggi | 3 | 1,598 | <i>Arctogalidia trivirgata</i> | <i>Arctictis binturong</i> |
| Telebon | 1 | 33 | <i>Paradoxurus hermaphroditus</i> | <i>Paradoxurus hermaphroditus</i> |
| Terutao | 2 | 152 | <i>Arctogalidia trivirgata</i> | <i>Paradoxurus hermaphroditus</i> |
| Thasos | 2 | 300 | <i>Martes foina</i> | <i>Canis aureus</i> |
| Tiburon | 3 | 1,212 | <i>Bassariscus astutus</i> | <i>Canis latrans</i> |
| Tierra del Fuego | 6 | 73,746 | <i>Conepatus humboldti</i> | <i>Felis concolor</i> |
| Tioman | 3 | 140 | <i>Arctogalidia trivirgata</i> | <i>Arctictis binturong</i> |
| Tobago | 1 | 300 | <i>Procyon cancrivorus</i> | <i>Procyon cancrivorus</i> |
| Trinidad | 4 | 4,828 | <i>Eira barbara</i> | <i>Felis pardalis</i> |
| Tukarak | 3 | 349 | <i>Mustela erminea</i> | <i>Vulpes vulpes</i> |
| Tuxekan | 1 | 85 | <i>Ursus americanus</i> | <i>Ursus americanus</i> |
| Umnak | 1 | 1,793 | <i>Vulpes vulpes</i> | <i>Vulpes vulpes</i> |
| Unalaska | 2 | 2,722 | <i>Mustela erminea</i> | <i>Vulpes vulpes</i> |
| Unimak | 8 | 4,119 | <i>Mustela nivalis</i> | <i>Ursus arctos</i> |
| Urup | 1 | 1,450 | <i>Vulpes vulpes</i> | <i>Vulpes vulpes</i> |
| Vancouver | 9 | 31,285 | <i>Mustela erminea</i> | <i>Ursus americanus</i> |
| Vargas | 1 | 28 | <i>Mustela vison</i> | <i>Mustela vison</i> |
| Vinal Haven | 3 | 52 | <i>Mustela vison</i> | <i>Lontra canadensis</i> |
| Warren | 2 | 50 | <i>Lontra canadensis</i> | <i>Canis lupus</i> |
| Wetar | 1 | 445 | <i>Paradoxurus hermaphroditus</i> | <i>Paradoxurus hermaphroditus</i> |
| Whidby | 1 | 445 | <i>Mustela erminea</i> | <i>Mustela erminea</i> |
| Wight | 5 | 392 | <i>Mustela nivalis</i> | <i>Meles meles</i> |
| Woewodski | 2 | 41 | <i>Martes americana</i> | <i>Canis lupus</i> |
| Wolin | 3 | 246 | <i>Martes martes</i> | <i>Meles meles</i> |
| Woronkofski | 1 | 60 | <i>Lontra canadensis</i> | <i>Lontra canadensis</i> |
| Wrangel | 8 | 569 | <i>Mustela erminea</i> | <i>Ursus americanus</i> |
| Serifos | 1 | 73 | <i>Martes foina</i> | <i>Martes foina</i> |
| Kythnos | 1 | 102 | <i>Martes foina</i> | <i>Martes foina</i> |
| Skopelos | 2 | 90 | <i>Mustela nivalis</i> | <i>Martes foina</i> |
| Tinos | 1 | 193 | <i>Meles meles</i> | <i>Meles meles</i> |
| Thera (Santoríni) | 2 | 76 | <i>Mustela nivalis</i> | <i>Martes foina</i> |
| Yakushima | 1 | 524 | <i>Mustela sibirica</i> | <i>Mustela sibirica</i> |
| Zakynthos | 2 | 419 | <i>Mustela nivalis</i> | <i>Martes foina</i> |
| Zanzibar | 5 | 1,651 | <i>Galerella sanguinea</i> | <i>Panthera pardus</i> |
| Zarembó | 4 | 472 | <i>Mustela erminea</i> | <i>Ursus americanus</i> |