

## LETTER

## Area, isolation and body size evolution in insular carnivores

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### Abstract

Body sizes of insular mammals often differ strikingly from those of their mainland conspecifics. Small islands have reduced numbers of competitor and predator species, and more limited resources. Such reductions are believed to select for predictable changes in body sizes, with large mammals growing progressively smaller as island area decreases, while small ones grow progressively larger. Medium-sized mammals are thought to be largest on intermediate-sized islands. Increased isolation is seen as promoting insular gigantism. We searched for such patterns using a large database of insular carnivore specimens. Neither small nor large carnivores show a consistent area/body size relationship. Medium-sized carnivores are no more likely to attain large size on medium-sized islands than they are to be small there. We found no consistent patterns of body size variation in relation to isolation.

### Keywords

Carnivora, competition, island area, island rule, predation, resource limitation.

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Body size of insular mammals often differs strikingly from that of their mainland relatives. The direction and magnitude of body size evolution are believed to be predictable, with large mammals becoming smaller on islands and small mammals becoming larger (Lomolino 1985, cf. Meiri *et al.* 2004a). Remarkable patterns of size evolution on islands have long attracted attention (e.g. Darwin 1845; Wallace 1880; Hooijer 1949; Foster 1964; Sondaar 1977; Lister 1996). Body size evolution on islands has often been used as a model for the evolution of size in general, for both mammals (Heaney 1978; Lomolino 1985; Brown *et al.* 1993; Damuth 1993; Palkovacs 2003) and other vertebrates (Case 1978; Clegg & Owens 2002; Boback & Guyer 2003).

The small area of islands is theoretically the most important factor determining how size evolves, acting through faunal composition and resource abundance. It is usually assumed that both interspecific competition and predation pressures are weaker on islands because islands harbour fewer species owing to the fact that they are isolated and small. Lower numbers of predatory species on islands are perceived as indicating lower predation pressures. It is often assumed that increased predation on mainlands selects for small mammals to become still smaller and large mammals to become larger (Heaney 1978; Angerbjörn 1986; Michaux *et al.* 2002). Size changes on islands can arise

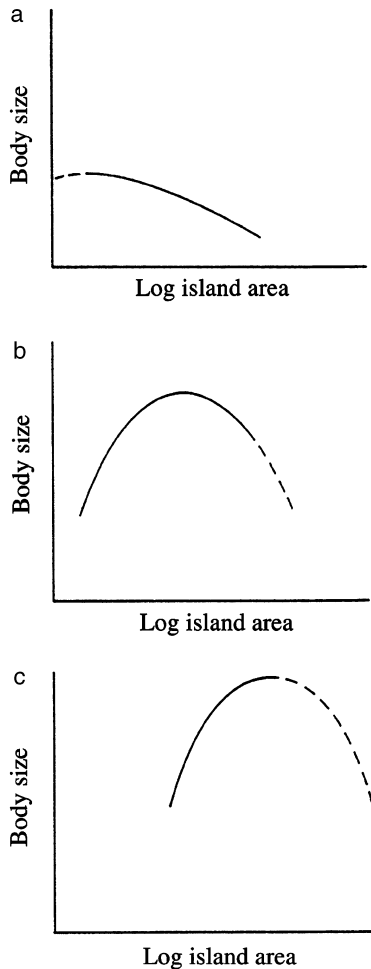
indirectly by virtue of reduced levels of predation on islands that can lead to life history shifts resulting in either gigantism (Melton 1982; Palkovacs 2003) or dwarfism (Raia *et al.* 2003, but see Roth 1992).

Interspecific competition is usually assumed to be reduced on islands [although what is actually known is that islands harbour fewer competing species (Roth 1992)]. Character release in response to reduced interspecific competition is thus believed to result in large body size (Lomolino 1985; Dayan & Simberloff 1998), at least among dietary generalists (Lawlor 1982) or territorial species (Case 1978).

Another perceived consequence of smaller island area is the absolute lower abundance of resources. Especially in large mammals [and birds (McNab 1994), but less so in reptiles (Case 1978; Burness *et al.* 2001)], reduced resources are expected to select for size reduction (Lomolino 1985; Roth 1992; Palkovacs 2003), because smaller individuals have lower energetic requirements.

Isolation can also influence the size evolution of insular mammals. Lomolino (1985) argued that, especially in small species, larger individuals are more likely to survive attempts to immigrate to islands. Angerbjörn (1986) found support for this claim in British populations of *Apodemus* but not in other populations of this genus.

By studying small mammals, Melton (1982) suggested that competition and predation pressures are inversely correlated



**Figure 1** Relationship between body size and island area after Heaney (1978). Body size (not to scale) as function of island area (not to scale) of small (a), medium (b) and large (c) mammals. Dashed lines are unexpressed – this is the relationship predicted for islands too small to be inhabited by mammals (a), or too large to be called islands (b, c).

with area, resulting in increased intraspecific competition on small islands, which in turn, manifests itself in larger body sizes. Heaney (1978) presented a more complicated model accounting for the direction and magnitude of size evolution in relation to island area (Fig. 1). In his model resource limitation is most severe on small islands, whereas predation pressure and interspecific competition become more intense on progressively larger islands. He predicted that large mammals will be most affected by resource limitation and therefore grow smaller the smaller the islands are, while small mammals will be most affected by reduced levels of predation and competition, and therefore show the largest size increases on the smallest islands. Heaney (1978) suggested that for medium-sized mammals resource

limitation will be the major factor on the smallest islands, and the effects of competition and predation will manifest themselves on progressively larger islands. Accordingly, their sizes should show a complex relationship with island area; they should be small on large and small islands, and large on medium-sized ones. Empirical support for the model came from data on size in relation to area for the tricoloured squirrel, *Callosciurus prevosti* (Desmarest) (375–505 g, Medway 1969).

Filin & Ziv (2004) suggested that rates of size evolution on islands are negatively correlated with area and that the magnitude of size evolution is inversely proportional to the island area. They predict that rodents will grow larger on islands while other mammals will grow smaller.

Although many island attributes that are likely to affect body size evolution are tightly correlated with island area, little empirical research has been conducted on the relationship between body size and island area, almost all of it involving rodents (but see Burnett 1983; Kitchener *et al.* 1994; Anderson & Handley 2002; Maharadatunkamsi *et al.* 2003).

A pattern similar to that found by Heaney (1978) was found in the 16.5 g (Smith *et al.* 2003) bat *Eptesicus fuscus* (Burnett 1983) and in the even smaller tenebrionid beetle *Asida planipennis* (Palmer 2002), but not in larger animals (Lawlor 1982; Melton 1982; Angerbjörn 1986; Yom-Tov *et al.* 1999; Michaux *et al.* 2002; Boback 2003; Millien 2004). However, to our knowledge no alternative models that explicitly incorporate area have been proposed to account for patterns of intraspecific size variation in insular mammals. Most authors seem content to describe cases of dwarfism in large species and gigantism in small ones, regardless of island area. Moreover ‘small’, ‘large’ and ‘medium’ are rarely defined explicitly in relation to either body size or to area.

We examine the pattern of body size variation in relation to island area and isolation in members of the Carnivora. Carnivores are extremely diverse in body size, ranging from 50 g weasels to bears four orders of magnitude larger. Most studies of size variation in relation to area have been conducted on smaller mammals, and the middle and upper ranges of mammalian sizes remain unexplored.

## MATERIALS AND METHODS

To analyse size variation in relation to island area, we measured carnivore skulls in natural history collections (see Acknowledgements). Measurements were taken with digital calipers to 0.01-mm precision or vernier calipers to 0.02-mm precision (for measurements exceeding 300 mm). We chose condylo-basal length (CBL) as a measure of body size. A preliminary analysis revealed that nearly identical results are obtained if the size of the lower carnassial tooth is used as a size index rather than CBL, and we therefore use only the

latter. We used only wild-caught, adult specimens (those with complete closure of the dorsal sutures). All comparisons were of conspecifics. We used sexes as separate morphospecies for all comparisons. We did not use data on introduced populations.

We define isolation as distance from the nearest mainland or the nearest larger island inhabited by at least an equal number of carnivore species. Area and isolation data were obtained from the literature (e.g. Lawlor 1986), from Erik Meijaard and Josh Calder (S. Meiri, personal communication), from the United Nations Environment Programme website (<http://islands.unep.ch>), and from maps. Our database consist of 2550 specimens from 15 species (and six of the eight carnivore families), originating from 148 islands worldwide.

Data on islands examined and which carnivores were measured from which island are listed in Appendix S1. Previous analyses (e.g. Heaney 1978; Lawlor 1982; Yom-Tov *et al.* 1999) used the logarithm of island area but untransformed body size indices. However, the use of linear regressions with such data may be inadequate, because the predicted relationship is curvilinear. We therefore log-transformed all data in all analyses. We calculated the mean CBL for insular populations of every morphospecies for which we had measurements from at least seven islands in an archipelago. The ermine (*Mustela erminea*) inhabits three different archipelagoes from which we had specimens (in the North Sea, Arctic Ocean and NW North America). We considered each of these separately because American ermines are generally smaller than European ones, and in North America ermines follow Bergmann's rule (Meiri *et al.* 2004b). Thus treating all specimens together would have added a large degree of variation, i.e. independent of isolation and area. All other species are represented in one archipelago only.

Because predictions for different-sized mammals are expected to show different area/size relationships, we treated small, medium and large carnivores separately. We first defined what small, medium and large carnivores actually are, using several categories for each of these size classes. We considered morphospecies either < 500 g (Heaney 1978) or < 1 kg (Damuth 1993) to be small. We also tried two classifications for medium size. In one, species weighing 0.1–2 kg were considered medium-sized, corresponding roughly to what we believe Heaney (1978) and Damuth (1993) considered as medium. In the other, we treat 1–5 kg carnivores as medium-sized, because this is the modal size class in the order (Meiri *et al.* 2005). We treated carnivores larger than 21.5 kg as large following Carbone *et al.* (1999). However, as carnivores may be more susceptible to resource limitation on small islands than are herbivorous mammals of similar sizes (Heaney 1984; Lomolino 1985; Meiri *et al.* 2004a), we perform an

additional analysis treating all morphospecies in our sample (156–207 500 g) as large.

### Statistical analysis

Small carnivores are expected to show a monotonic decrease of size with increasing area (i.e. decrease in size with increasing area throughout the area range of the islands they inhabit). To test this hypothesis we regressed CBL on area for all morphospecies of small carnivores and included isolation as an additional predictor.

Large carnivores are predicted to show the reversed pattern, and we therefore analysed the two 'large' categories in a similar fashion to the analysis of small carnivores.

Medium-sized carnivores are expected to have a maximal size at an intermediate area (Heaney 1978). We therefore ran a second-order regression of size on area and compared the frequency of negative (predicted) and positive parabolas in the two categories of medium-sized carnivores. To negate the possible effects of isolation we repeated this analysis using the residuals from a linear regression of size on isolation as the dependent variable. However, with medium-sized carnivores scale must be taken into account, because the expected pattern will be manifest only when small, medium and large islands are analysed simultaneously. Therefore, we restricted all analyses of medium-sized species to archipelagos containing islands both  $\leq 150$  and  $> 200\,000$  km<sup>2</sup>.

Finally, we calculated the slope of the linear regression of skull size on area in all morphospecies. In theory, the slope should be negative in small species (size decreasing with increasing area), zero in medium-sized mammals (parabolas have slopes of zero), and positive in large species (Heaney 1978; Filin & Ziv 2004, see Fig. 1). We used these slopes as the dependent variable in another regression – with average morphospecies body mass as the independent variable. We used our own data for morphospecies body masses supplemented by data from the literature. Morphospecies 156–5000 g were included only if they were measured in archipelagos containing islands both  $\leq 150$  and  $> 200\,000$  km<sup>2</sup>. All statistical tests were run with STATISTICA 7 software (StatSoft 2005, StatSoft Israel, Kfar Saba, Israel).

## RESULTS

### Small carnivores

Small carnivores show no significant relationship between size and area in any of the four (< 500 g) or seven (< 1 kg) cases tested. Furthermore, the mean value of the partial regression coefficient does not differ significantly from zero (< 500 g,  $b = 0.1$ ,  $SD = 0.48$ ; < 1 kg,  $b = 0.02$ ,  $SD = 0.46$ ). Isolation has a significant effect on size in two cases:

females of NW American ermines increase in size with increasing isolation ( $n = 9$  islands,  $b = 0.89$ ,  $P = 0.019$ ), whereas female mink (*Mustela vison* Schreber) in the same archipelago decrease in size with increasing isolation ( $n = 18$  islands,  $b = -0.54$ ,  $P = 0.025$ ). The mean value of the partial regression coefficient for isolation does not differ significantly from zero in either size category of small carnivores ( $< 500$  g,  $b = 0.17$ ,  $SD = 0.49$ ;  $< 1$  kg,  $b = 0.12$ ,  $SD = 0.49$ ).

### Large carnivores

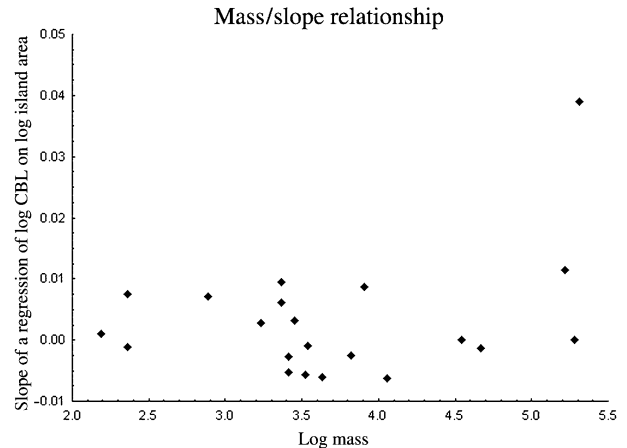
The large carnivores ( $> 21.5$  kg) in our sample are NW North American wolves (*Canis lupus* L.), and black and brown bears (*Ursus americanus* Pallas and *Ursus arctos* L. respectively). None of these show a significant relationship between size and either area or isolation, and neither do the mean values of the partial regression coefficient differ significantly from zero ( $n = 5$ , area:  $b = 0.07$ ,  $SD = 0.24$ ; isolation:  $b = 0.23$ ,  $SD = 0.28$ ).

When we treated all carnivores as large mammals in a multiple regression of CBL on area and isolation, three of 30 morphospecies showed a significant relationship between size and area: Arctic foxes [*Alopex lagopus* (L.), both sexes] decrease in size with increasing island area, whereas females of the small toothed palm civet [*Arctogalidia trivirgata* (Gray)] increase in size with increasing area. The mean partial regression coefficient for area,  $0.09 \pm 0.43$ , does not differ significantly from zero. Four of the 30 morphospecies [*M. vison*, both sexes, *Paradoxurus hermaphroditus* (Pallas) males and *Procyon lotor* (L.) males] decrease significantly in size with increasing isolation whereas one increases (NW American *M. erminea* females). The mean partial regression coefficient is  $-0.10 \pm 0.44$ , not significantly different from zero.

### Medium-sized carnivores

Five morphospecies satisfy the area-range conditions for inclusion in the 0.1–2 kg category. Entered alone, isolation does not affect CBL in any of those. Two of the five second-order regressions of size on area are convex, as expected, while three are concave. This is true regardless of whether the independent variable is CBL or the residuals from a regression of CBL on isolation. In the 1–5 kg category two of nine second-order regressions of size on area are convex and seven concave when the independent variable is the residuals from a regression of CBL on isolation. Three are convex and six concave when CBL is regressed on area. Thus the notion that mammals are largest on medium-sized islands is not supported. Isolation alone is never a significant predictor of size in this group.

For carnivores of all sizes, four of 22 morphospecies (0.1–5 kg morphospecies with limited range of island areas



**Figure 2** Relationship between the logarithm of body mass (g), and the slope of a linear regression of log skull length (condylo-basal length) on the logarithm of island area ( $\text{km}^2$ ).

omitted) show a significant linear relationship between CBL and area: size decreases with increasing area in both sexes of *Alopex lagopus* and in *Lontra canadensis* (Schreber) males and increases with increasing area in *Arctogalidia trivirgata* females. There is no relationship between the slopes of this regression and the average body mass of these 22 morphospecies (Spearman rank correlation,  $r = -0.037$ ,  $P = 0.87$ , Fig. 2). Thus slope does not change from negative in small species to positive in large ones the way theory predicts.

### DISCUSSION

Our data indicate that body size does not change regularly and predictably with either area or isolation. We find no tendency among carnivores to exhibit either a linear relationship between size and area (Melton 1982; Granjon & Cheylan 1990; Kitchener *et al.* 1994) or a more complex relationship (Heaney 1978), regardless of whether isolation is corrected for or not. Also there is no evidence that different sized carnivores respond differently to changes in isolation and area.

Admittedly, we often have few specimens per island and sometimes not many islands per archipelago. In addition, we are looking only at carnivores, whereas it would be advisable to search for patterns in a more diverse assemblage. However, our database is by far the most comprehensive one used to date in such an analysis. Given that the data used to generate the theories regarding size patterns in insular mammals were considerably smaller, our admittedly flawed database is a solid start.

Lomolino (1985) claimed that size increases with isolation because it is positively correlated with dispersal ability. It is perhaps not surprising that size and isolation are uncorrelated in carnivores, because virtually all insular carnivores are

not dispersers, but rather were probably isolated *in situ* when sea levels rose at the end of the last glacial (Meiri 2004).

Whereas some authors stress the importance of area, and if size evolution follows a predictable trajectory on islands it is reasonable to expect area and perhaps isolation to have an effect, most studies found area not to influence size (Lawlor 1982; Angerbjörn 1986; Yom-Tov *et al.* 1999; Anderson & Handley 2002; Boback 2003, and this study). Why is this so? We suspect some of the explanations usually advanced in support of the island rule [listed by Angerbjörn (1986) and Dayan & Simberloff (1998)] are overly simplistic. Let us consider three of the selective forces that should manifest themselves in the relationship between body size and island area: resource limitation, predation and interspecific competition.

Resource limitation is thought to induce dwarfing either as a direct selective consequence (Sondaar 1977, but see Wroe *et al.* 2004) or through selection for changes in life history characteristics (Melton 1982; Palkovacs 2003; cf. Raia *et al.* 2003). Resource limitation can exert its influence either through organismal selection or by selective extinctions of populations that 'fail' to dwarf (Wassersug *et al.* 1979; Marquet & Taper 1998). However, scale will often come into play; animals for which resources are too scant on small islands would probably never actually establish a viable population there (one that is able to evolve at a sufficient rate to endure resource limitation for long enough for selection to reduce metabolic needs). Heaney (1984) has shown that carnivores have populations only on fairly large islands. He reasoned that, because of the nature of Eltonian food pyramids, limited resources will not allow carnivores to inhabit islands suited for similar-sized herbivores (Heaney 1984; see also Burness *et al.* 2001). We strongly suspect that most islands inhabited by mammals are simply too large for resource limitation to be a real factor: Roth (1992) has shown that Sicily could have harboured a population of 3000 15-ton elephants. For smaller mammals resource limitation may come into play only on much smaller islands.

Predation may be among the main causes of mortality in mammals, and carnivores are no exception (Palomares & Caro 1999). There is evidence that the absence of carnivores from islands can lead to increase in size of small rodents (Angerbjörn 1986; Smith 1992; Michaux *et al.* 2002). However, we do question two rarely tested assumptions: that predation pressures are inherently weaker on islands, and that predation really does cause large mammals to grow larger and its absence causes them to grow smaller. We raise two unaddressed questions in this respect: (i) does predation pressure depend on the number of predator species rather than on their density? (ii) does any direct evidence support the notion that small and large mammals really encounter lowered predation levels relative to medium-sized ones? It is

not unlikely that mammals large enough to fend off predators are at least equal in size to their enemies, i.e. they are *c.* 21 kg or larger (Carbone *et al.* 1999) – much larger than the perceived size at which absence of predation should lead to the decrease in size (Lomolino 1985; Brown *et al.* 1993; but see Meiri *et al.* 2004a). Intraspecific size change of insular mammals is measured in tens of per cents at most (Lomolino 1985, cf. Meiri 2004). Whether such moderate change really confer an advantage in predator avoidance has never been tested.

Reduced levels of interspecific competition on islands are thought to lead to size changes through character release (Dayan & Simberloff 1998) or by enabling evolution towards an optimum size (Brown *et al.* 1993; Damuth 1993; but see Meiri *et al.* 2004a, 2005). However, competition may not be lower on smaller islands, not only because of deviations from a perfect species–area relationship, but also because the number of species within an assemblage does not necessarily correspond to the intensity of interspecific competition 'felt' by any particular species. The presence or absence of wolverines (*Gulo gulo*) from most islands in the Alexander Archipelago, for example, might be more likely to affect stoat (*M. erminea*) size through predation rather than through interspecific competition. Is the level of competition among carnivores lower in Java than on Sumatra because it has 'only' 22 carnivore species compared with Sumatra's 30? We know of no empirical evidence that suggests this is so. Rather than just species richness, it is faunal composition, population density, and the nature of the resource spectrum itself (composition, availability and abundance) that matters.

Lawlor ([1982]), cf. Smith [1992]) suggested that mammals specializing on diets of a particulate nature should decrease in size on islands, whereas those feeding on non-particulate foods should increase in size. We find no tendency for strict carnivores (which can be considered particulate feeders) such as felids or weasels to show different patterns than omnivores such as ursids and procyonids.

Finally, interactions between different selective forces may obscure overall patterns. Brown and black bears, for example, are never found on the same island today (although the US National Museum of Natural History holds black bear specimens originating in the 'grizzly only' islands of Admiralty and Chichago). Should insular black bears evolve to be small to deal better with limited resources – or should they evolve to be large to fill the niche of their absent larger congener? Heaney (1978) based his model on the pattern exhibited by one species, urging others to try and verify or reject it based on more empirical data. Our large and diverse assemblage, the first large scale effort of the kind, does not support the model.

We found no consistent patterns of size change on islands of different areas and degrees of isolation. It may be

that 'large', 'small', 'far' and 'near' islands are different for different-sized carnivores. Nonetheless, the scarcity of even intraspecific patterns suggests that an insular environment does not in itself entail universal selective forces and evolutionary trajectories. Clearly, as Lawlor (1982) has pointed out, a great deal of caution is in order when one generalizes about body size trends in mammals. An understanding of the actual relationship between size and area should probably be species- and archipelago-specific and take into consideration guild composition and resource-based parameters.

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## SUPPLEMENTARY MATERIAL

The following supplementary material is available online for this article from <http://www.Blackwell-Synergy.com>:

### Appendix S1 Island areas and isolation.

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## Appendix S1 Island areas and isolation.

<b>Island</b>	<b>Area (km<sup>2</sup>)</b>	<b>Isolation (km)</b>
1. Admiralty	4310	4.1
2. Afognak	1809	6.8
3. Attu	896	785.0
4. Baffiin	507451	10.0
5. Balabac	281	55.0
6. Bali	5560	3.0
7. Banggi	441	13.0
8. Bangka	11413	13.0
9. Banks	70028	10.0
10. Baranof	4163	1.1
11. Barter	38	1.0
12. Batam	399	17.0
13. Bathurst	16042	25.0
14. Bawal	48	7.0
15. Bawean	200	112.0
16. Big Pine key	17	53.0
17. Billiton	4788	84.0
18. Bintang	1173	6.0
19. Borneo	743244	533.6
20. Britain	229850	30.0
21. Broughton	135	2.0
22. Bunguran	1485	94.0
23. Busuanga	980	9.0
24. Cairn	37	1.0
25. Calvert	260	6.0
26. Charlton	308	25.0
27. Cheju Do	1829	82.0
28. Chichagof	5449	8.7
29. Con Son	58	86.0
30. Cornwallis	6995	36.0
31. Coronation	91	7.8
32. Culion	400	6.0
33. Dall	658	2.3
34. Denny	132	2.3
35. Devon	55247	12.0
36. Douglas	203	1.2
37. Ellesmere	196236	10.0
38. Esther	133	2.0
39. Etolin	889	3.8
40. Falster	486	1.0
41. Flaherty	1585	113.0
42. Fyn	3012	1.0
43. Galang	74	0.2
44. Gambier	70	27.0
45. Gilford	384	2.0
46. Graham	6436	77.0
47. Greenland	2175600	830.0
48. Hainan	33210	20.0
49. Halleck	33	0.3
50. Heceta	189	2.3

<b>Island</b>	<b>Area (km<sup>2</sup>)</b>	<b>Isolation (km)</b>
51. Herschel	112	5.0
52. Hinchinbrook	442	22.0
53. Honshu	230510	184.0
54. Iki	137	49.0
55. Ireland	85114	34.0
56. Iriomoto	289	187.0
57. Isla Bastimentos	52	1.4
58. Isla Popa	53	1.8
59. Isla San Cristobal	37	0.3
60. Islay	603	1.0
61. Java	125628	25.0
62. Jersey	116	21.0
63. Kadan Kyun	450	10.0
64. Kangean	430	15.0
65. Kariamata	179	14.0
66. Karimon	131	1.0
67. Key West	12	4.1
68. King	839	1.0
69. Kiska	278	81.0
70. Kodiak	9293	46.0
71. Kosciusko	482	1.4
72. Krestof	28	3.5
73. Kruzof	447	1.5
74. Kuiu	1933	1.0
75. Kupreanof	2822	8.3
76. Kyushu	36555	1.0
77. Langkawi	363	7.0
78. Laut	2057	2.0
79. Leyte	7213	50.0
80. Lignum Vitae	1	1.4
81. Lingga	889	11.0
82. Lolland	1264	1.0
83. Louise	250	0.5
84. Lowther	145	58.5
85. Luzon	108171	375.0
86. Marble	23	3.0
87. Mindanao	99078	334.0
88. Mindoro	9735	18.0
89. Mitkof	547	2.0
90. Montague	850	32.6
91. Moresby	2745	0.5
92. Negros	13670	1450.0
93. New Providence	228	30.0
94. No Name key	3	0.5
95. North twin	157	57.0
96. Nunivak	4209	30.0
97. Oland	1344	6.0
98. Palau Pagai Utara	530	0.2
99. Palawan	12189	147.0
100. Panebangan	26	18.0
101. Pinang	295	5.0
102. Price	166	2.0

<b>Island</b>	<b>Area (km<sup>2</sup>)</b>	<b>Isolation (km)</b>
103. Prince of Wales (BC)	6675	6.9
104. Prince of Wales (Nunavut)	33339	533.3
105. Prince Patrick	15848	12.0
106. Pulo kundur	315	12.0
107. Quadra	270	2.0
108. Read	408	1.5
109. Revillagigedo	3024	1.4
110. Rishiri	183	21.0
111. Rupert	1490	5.0
112. Sado	857	32.0
113. Saint George	90	70.0
114. Saint Lawrence	5135	75.0
115. Saint Matthew	354	350.0
116. Saint Matthews	176	2.0
117. Saint Paul	113	361.0
118. Saltspring	181	1.0
119. Samar	13429	138.0
120. Sanibel	44	3.2
121. Setoko	17	0.5
122. Shikoku	18765	10.0
123. Sidney	9	5.4
124. Simeulue	1754	131.0
125. Singapore	536	2.0
126. Singkep	757	10.0
127. Sipura	601	46.0
128. Sjaelland	7180	5.0
129. Somerset	24786	5.0
130. South Pagi	987	0.2
131. South Twin	150	11.4
132. Southampton	41214	25.0
133. Sri Lanka	67655	29.0
134. Suemez	153	1.9
135. Sumatra	473607	60.0
136. Svalbard	62700	773.0
137. Taiwan	34507	130.0
138. Telebon	33	3.0
139. Terutau	150	7.0
140. Tioman	228	39.0
141. Tsushima	689	48.0
142. Tukarak	349	2.0
143. Unimak	4119	5.0
144. Vancouver	33800	2.5
145. Whidby	445	1.0
146. Wrangell	569	1.0
147. Yakushima	539	58.0
148. Ymer	2437	2.8

Islands from which carnivores were measured (numbers refer to the above table).

*Alopex lagopus* females, 3, 4, 9, 13, 30, 37, 41, 47, 69, 84, 105, 113, 114, 115, 117, 129, 131, 132, 136; males 3, 4, 9, 13, 30, 35, 37, 41, 47, 51, 69, 95, 96, 104, 113, 114, 115, 117, 132, 142, 148. *Aonyx cinerea* females, 19, 43, 61, 78, 99, 121, 135; males, 8, 18, 19, 61, 66, 99, 135. *Arctogalidia trivirgata*, females, 7, 8, 12, 19, 22, 61, 125, 126, 135, 142; males, 12, 19, 22, 61, 63, 81, 106, 125, 135, 142. *Canis lupus*, females, 71, 74, 75, 103, 107, 108, 109, 144, 146; males, 44, 50, 74, 75, 103, 108, 109, 144, 146. *Felis bengalensis*, females, 6, 19, 48, 61, 92, 99, 101, 125, 135; males, 6, 19, 48, 61, 92, 99, 135, 137. *Lontra canadensis*, females, 10, 28, 46, 86, 90, 91, 103, 144, 146; males, 1, 10, 28, 34, 46, 49, 72, 73, 74, 91, 103, 144. *Martes americana*, females, 1, 46, 83, 89, 91, 109, 144; males, 1, 45, 46, 75, 83, 89, 91, 109, 144. *Mustela erminea*, females, 1, 20, 36, 40, 42, 46, 50, 55, 60, 62, 70, 89, 91, 97, 103, 128, 144; males, 1, 2, 4, 10, 11, 20, 24, 26, 28, 39, 40, 41, 42, 46, 47, 51, 55, 60, 62, 70, 82, 89, 91, 103, 109, 118, 128, 132, 134, 139, 143, 144, 145, 146, 148. *Mustela sibirica*, males, 27, 53, 54, 56, 76, 110, 112, 122, 137, 141, 147. *Mustela vison*, females, 1, 10, 21, 28, 31, 38, 39, 52, 70, 74, 75, 89, 102, 103, 109, 123, 144, 146; males, 1, 10, 25, 28, 31, 39, 52, 68, 74, 75, 89, 103, 109, 123, 134, 144, 146. *Paradoxurus hermaphroditus*, females, 5, 6, 8, 17, 19, 48, 61, 64, 85, 87, 98, 99, 101, 106, 124, 127, 130, 135, 138, 139, 140; males, 6, 7, 15, 19, 23, 29, 48, 61, 64, 77, 79, 85, 87, 92, 99, 101, 116, 125, 127, 133, 135, 139, 140. *Procyon lotor*, males, 16, 57, 58, 59, 67, 80, 93, 94, 120. *Ursus americanus*, males, 1, 28, 33, 46, 74, 75, 89, 103, 144. *Ursus arctos*, females, 1, 2, 10, 28, 52, 70, 72, 90; males, 1, 2, 10, 28, 70, 73, 114. *Viverra zibetha*, females, 14, 17, 18, 19, 22, 23, 32, 65, 78, 79, 81, 85, 88, 100, 111, 119, 135; males, 8, 17, 19, 22, 23, 32, 61, 85, 87, 101, 135.