Carnivore Body size – aspects of geographic variation

THESIS FOR THE DEGREE "DOCTOR OF PHILOSOPHY"

BY

SHAI MEIRI

SUBMITTED TO THE SENATE OF TEL-AVIV UNIVERSITY

July 2004

This work was carried out under the supervision of:

Professor Tamar Dayan, Tel-Aviv University.

Professor Daniel Simberloff, University of Tennessee, Knoxville.

I wish to thank

Tamar Dayan and Daniel Simberloff, my advisors, for their trust, encouragement, and critical thinking. For letting me into what was their own realm, and for their guidance along its paths.

Uri Roll for inspiring ideas, critical thinking, technical and moral support, and unwillingness to accept anything but the best. More importantly, Uri, thank you for your friendship.

Guy Bar-Oz, for advice, humor, guidance, and encouragement.

The Collection managers in the museums I visited: Daphne Hills, Richard Harbord, Ray Symonds, Géraldine Véron, Jacques Cuisin, Francis Renoult, Adri G. Rol, Chris (and Nellie) Smeenk, Byrdena Shepherd, Bob Randall, Gordon Jarrell, Lesley M. Kennes, David Nagorsen, Judith Eger, Michelle Gosselin, Darlene Balkwill, Suzanne McLaren, Timothy J. McCarthy, William Stanley, Judith Chupasko, Tsila Shariv, Jan Dawson, Yang Chang Man, Mrs. H. K. Lua, Hideki Endo and Tomoko, Yutaka Kunimatsu, Richard Kraft, Georges Lenglet, Georges Coulon, Sebastian Bruaux, Angela Ross, Peter Giere and Willie, Robert Asher, Clara Stefen, Thor (and Elaine) Holmes and Eileen A. Lacey. Thanks for your support, patience, and advice, thank you for showing me how museum collections should be maintained and how museum research should be conducted, thanks for answering questions I had during my stays and in the years after. Thank you for visits to the displays (Francis, Lesley, Jan, Rob) and the zoo (Adri), thank you Lesley and Timothy for rides from and to the airport at 04:00 AM following September 11 and at other times (Chris and Nellie, Gordon, Hideki, Thor), for inviting me to dine, for arranging accommodation or even for inviting me to stay with you, and for making me feel wanted in foreign places.

I am indebted to David Nagorsen, Lawrence Heaney, Rob Freckleton, John Gittleman, Kate Jones, Chris Carbone, and Yoram Yom-Tov for interesting discussions.

Eric Meijaard, Yael Mandelik, Douglas E. Kelt, and Josh Calder provided vital data.

I thank Eli Geffen, David Wool, Uzi Motro, Kyle Ashton and my friend Oren Barnea (founder and editor of the Kfar Sirkin Journal of Biology and Stuff, an imaginary journal intended almost solely to the promotion of my scientific career) for statistical advice. Avital Gasith, Yoram Yom-Tov, the late Eitan Tchernov, and Uzi Motro directed me while acting as my PhD committee, and encouraged me along the way.

I am also indebted to the referees of this work: V. Louise Roth, Israel Hershkovitz and Brian Keith McNab, who not only read this dissertation from beginning to end (a daunting feat I'm sure few will emulate), but also made many important comments, pointed out errors and other problems, raised interesting philosophical questions and generally, as Felsenstein wrote "saved me from myself" on quite a few occasions.

I thank David Eilam and Yoram Yom-Tov (again) for helping me learn basic principles of zoology (and much, much more) while studying and later assisting in teaching their courses. I must also thank Chemda Zigman for allowing me to complain about it all.

My friends at the lab: Shirli, Yael, Roee, Annat, Dalit, Aharon, Ram, Lior, Merav, Tal, Udi, Enav, Ornit, Lidar and Ariela, and my friends in the Department of zoology (Shay, Eran, Inbal, Roi, Anat, Reut, Dana) for interesting talks and great times.

The Rami Levin, Ian Kurten, Roni Piffiano and Herbert Cohen foundations for supporting me.

Most of all though, I would like to thank Meirav.

Contents

Abstract

Islands have remained a major theme in the science of evolutionary biology ever since Darwin. Giant mice tortoises and bears, dwarf elephants, mammoths and deer and continue to excite scientists, and the general-public, to this day. Insular environments are "natural experiments" of ecological and evolutionary phenomena.

An organism's body size is probably the major factor influencing its life history, physiology, morphology, ecology, biogeography and evolution. The evolution of body size is therefore a key issue in understanding processes at these fields. The evolution of body size of insular mammals was thought to be body-mass dependent, with large mammals dwarfing and small ones growing large. This pattern, "the island rule" was believed to be one of the strongest of all ecological generalizations. The nature of the selective pressures resulting in such a pattern, however, was strongly debated. Contemporary explanations usually point to the restricted area of islands, and the resulting resource shortage and especially low species-richness as the major factors responsible to the mode of size evolution on islands. The evolution of morphological variability in species-poor environments such as islands is also believed to follow predicted routes on islands, with populations evolving to fill vacated niches.

Looking at intraspecific patterns of geographic variation in size of carnivores, I studied the effects of various selective forces on size, concentrating on islands as natural evolutionary laboratories. Carnivores are extremely diverse in their life history characteristics, diet, geographic distribution and size. I measured carnivore skulls in 28 museum collections worldwide, assembling a database unparalleled for its size and geographical scope. It contains 21,856 specimens, representing 235 carnivore species, from all eight carnivore families.

I focused on examining size patterns exhibited by insular carnivores, compared with mainland conspecifics. Comparing sizes within archipelagos, and across islands differing in area and isolation I was able to treat insular populations as controlled experiments in the evolution of size.

First, in order to understand the relationship of the measured traits within and between species I first examined patterns of variability and correlation of cranial and dental traits, in relation to phylogenetic affinity, size and diet.

I also look into patterns of intraspecific geographic variation in body size on continents, to see if they relate to latitude and longitude. The continental patterns can be thought of as null models for the insular patterns.

It appears that an inverse intraspecific relationship between trait size and its coefficient of variation is indeed ubiquitous in carnivores. However, this does not stem from the increased influence of measurement error at small sizes; CV of a given trait is not correlated with absolute size across carnivore species. We also found that both diet and phylogenetic affinities influence the

degree of correlation between carnivore carnassials. Species feeding mainly on vertebrates have higher correlations between the carnassials than those feeding mainly on invertebrates or plants, and caniform carnivores are characterized by higher correlations than feliform carnivores. It might be that the high variability of canines makes it difficult to find significant size differences between insular and mainland populations when these teeth are compared.

Reviewing the literature we found that on continents homeotherm body size is often positively correlated with latitude, as predicted by Bergmann's rule. Large mammals (>500 g) tend to follow the rule to a greater extent than do smaller ones. In the carnivores we measured Bergmann's rule is less prevalent than our results of a literature survey suggested. Significant positive associations of size and latitude greatly outnumber negative ones, but there is a large number of species that show no relationship between these two variables. I suspect this is caused by the tendency of authors finding no patterns to view such results as uninteresting, and not fit for publication ("the file drawer problem"), or even to choose species for study based on a-priory knowledge that patterns exist. That said, a considerable degree of intraspecific geographic variation in size is the rule rather than the exception in carnivores. Island/mainland comparisons must therefore be conducted solely between populations with great geographic proximity to one another.

In the Western Palearctic, where seasonality is more pronounced in easterly longitudes, differentially migrating birds tend to be sedentary in the west, and migratory in the east. Even when we control for longitude, however, there is no tendency for carnivore body size to increase from west to east, as can be expected from the fasting endurance hypothesis, raised to explain Bergmann's rule.

Perhaps the most surprising result of this study is that the island rule, thought to be one of the best supported biogeographic patterns, simply does not hold in carnivores. Carnivores are not generally dwarfed on islands, nor does their size on islands, relative to that of their near-mainland conspecifics, decrease with increasing absolute size. The "island rule", a tendency of small mammals to grow larger on islands while large mammals are dwarfed, does not apply to the Carnivora. Neither is there any pattern when different dietary categories, biogeographic regions or phylogenetic lineages are analyzed separately.

A quantitative examination of the very factors that define an island – area and isolation, did not reveale strong patterns of size evolution. Island area within an archipelago also has little influence on microevolutionary size changes. Isolation is not an influencing factor, and neither is relative carnivore richness (on the island vs. its near mainland). Interestingly, reexamining data used to support the island rule does not reveal this pattern in carnivores either.

Morphological variability was found to be lower in insular populations than in mainland populations of the same morphospecies. The degree of sexual size dimorphism is not statistically different in either setting. Area *per se* does not seem to be driving this pattern, because the same pattern holds when the islands chosen are larger than the area on the adjacent mainland from which specimens were chosen for comparison. Rapid evolution on islands when selective pressures are strong, implies that genetic bottlenecks and founder events are also unlikely causes. I suggest that it is the limited amount of gene flow on islands that drives this pattern. These results are at odds with the niche variation hypothesis, according to which lower species richness on islands will result in insular forms being more variable, or more sexually dimorphic.

I find no support for the notion that mammals have a single, optimal body size. Insular carnivores do not seem to undergo size evolution towards any one value. Species close in size to hypothesized optima do not tend to predominate the carnivore faunas on small and carnivore-poor islands. Instead carnivores occurring on islands seem to be very slightly larger (and further away from the 'optimum') than chance alone would dictate.

I conclude that the way such forces as interspecific competition, predation (or lack thereof) and resource limitation affects animal morphologies is not as straightforward as has been suggested.

"The desire for knowledge for its own sake is the one which really counts... Exploration is the physical expression of the intellectual passion. And I tell you, if you have the desire for knowledge and the power to give it physical expression, go out and explore. If you are a brave man you will do nothing: if you are fearful you may do much, for none but cowards need to prove their bravery. Some will tell you that you are mad, and nearly all will say, 'What's the use?' For we are a nation of shopkeepers, and no shopkeeper will look at research which does not promise him financial return within a year. And so you will sledge nearly alone, but those with whom you sledge will not be shopkeepers: that is worth a good deal. If you march your winter journeys you will have your reward, so long as all you want is a penguin's egg"

Apsley Cherry-Gerrard / "The worst journey in the world"

Prologue

This work sums up a project I have pursued since late 1999. In the last four and a half years I visited twenty eight museums worldwide, measuring over 16,000 carnivore skulls to understand better the evolution of mammalian body size in general and differences in the sizes of insular carnivores and their mainland counterparts in particular.

Results of this work are presented here in the form of eight manuscripts. Three of those were published in the ecological literature, four others were recently accepted for publications and another one is in review. In writing this work I have tried to present the reader with a coherent narrative in which the topic of each consecutive manuscript follows logically from the previous one. The chronological order of my work itself, however, rarely followed either the logic or the order of the manuscripts presented here. Rather I dealt with issues in the order of my personal preferences, plans and schedules. Furthermore – both the introduction and conclusions I present here were written postscript – after the major analyses and first submission of most manuscripts were all completed. Therefore the order of the works as presented here does not reflect my personal ontogeny as a student of mammalian size evolution.

This work is based on very large amounts of data. I totally agree with Connor and Simberloff (1979) who argued that data must be presented in order for results to be reproducible and refutable (Popper 1963). I therefore decided to include much data in this dissertation in the form of both tables and appendices, some of which were excluded from the published parts of this work by cost-aware journal editors. Alas this leads to works such as this, not a short one to begin with, grow too large for comfort. I apologize to the few who will receive the printed work (sorry mom), but because I intend to have this work available electronically, this will have few of the unwelcome consequences and all of the considerable advantages a large work can offer. My own experience with data-poor works (see below) makes me think this is the right way to go.

Introduction

The extraordinary morphology and size of insular organisms has captured human imagination since Odysseus dealt with the Cyclops Polyphemus, a legend that may have its basis in real dwarf elephants (*Elephas falconery* Busk). Throughout the centuries, tales of mysterious insular giants such as the Roc, a huge bird able to carry elephants in its claws (perhaps inspired by the extinct *Aepyornis maximus* St. Hilaire, of Madagascar), inspired human minds.

European voyages of discovery exposed emerging western science to extraordinary insular animals – the huge columbines of the Mascarenes (*Raphus cucullatus* L., *Pezophaps solitaria*, Gmelin), giant tortoises in the Indian (*Geochelone giganteus* Schweigger) and Pacific (*G. elephantopus* Harlan) oceans, the extinct moas (*Dinornis* Owen) of New Zealand and many more.

The most significant advance in the study of these animals, and indeed, in the history of science in general, came with the development of the theory of evolution by means of natural selection (Darwin and Wallace 1858, Darwin 1859). The co-founders of this theory, Charles Robert Darwin and Alfred Russel Wallace, developed it after inspirational first-hand impressions of insular animals (Darwin 1845, Wallace 1868, 1880). It is therefore hardly surprising that, from the very first moment the theory was introduced to the public, when it was read by Charles Lyell and Joseph Dalton Hooker at the meeting of the Linnean society on July 1, 1858 (Darwin and Wallace 1858), it involved the evolution of island forms. Darwin (Darwin and Wallace 1858, P. 49) used a hypothetical example from the morphology of insular carnivores to explain his idea: "To give an imaginary example from changes in progress on an island: Let the organization of a canine animal... become slightly plastic...those individuals with the lightest forms...would be slightly favored...these causes would... produce a marked effect, and adapt the form of the fox or dog."

Islands have remained a major theme in the science of evolutionary biology ever since Darwin, and the striking morphologies of insular animals, especially their sizes, continue to enthuse scientists, as well as the general public, to this day.

Size itself has always been a topic of interest, both general and scientific, featuring prominently in the studies of some of the greatest zoologists and evolutionists: Carl Bergmann (Bergmann 1847, in James 1970), Edward Drinker Cope (1887, 1896 in Stanley 1973), J.B.S. Haldane (1928), D'Arcy Thompson (1942), Ernst Mayr (1942, 1963), G. Evelyn Hutchinson (1959, Hutchinson and MacArthur 1959), George Gaylord Simpson (1949) and Stephen J. Gould (1966, 1974, 1988), to name but a few, all discussed patterns and consequences of size evolution.

Size is perhaps the major determinant of a variety of physiological, ecological and evolutionary characteristics of animals (Gould 1966, Peters 1983, Calder 1984, Schmidt-Nielsen 1984, Brown and West 2000). It can affect the control of resources (Hutchinson 1959) and both intra and interspecific interactions within guilds (Brown and Wilson 1956, Damuth 1993, Jones

1997, Buskirk et al. 2000, Farlow and Pianka 2003). It affects the probability of being preyed upon (Heaney 1978, Roth 1992) and the size of potential prey (Gittleman 1985, Vezina 1985, King 1991, Cohen et al. 1993, Jones 1997, Funston et al. 1998, Carbone et al. 1999, Arjo et al. 2002). Immigration ability is also thought to be size-related (Carlquist 1974, Lomolino 1985, Hoekstra and Fagan 1998), as is physiological efficiency (Maiorana 1990, Brown et al. 1993, 1996, but see Kozlowsky 1996, Perrin 1998). Finally, size may be a side effect of different life history characteristics such as developmental times and mortality rates (Melton 1982, Palkovacs 2003, Raia et al. 2003 but see Roth 1992).

Patterns of size evolution can therefore shed much light on these and other ecological phenomena, as well as on general patterns of macroevolutionary change (Stanley 1973, Brown and Maurer 1986, Gould 1988, Mckinney 1990, Jablonski 1996, 1997, Alroy 1998).

It is therefore hardly surprising that some of the oldest and best known patterns in evolution relate to body size. Prominent among such patterns is Bergmann's rule, first proposed in 1847 (Bergmann 1847 in James 1970, Rensch 1938, Mayr 1942, Thompson 1942), according to which within genera or species larger individuals will tend to inhabit cooler climes than smaller ones. Another such pattern is Cope's rule (a brief description of its origin can be found in Stanley [1973]), according to which throughout their history members of different clades will evolve towards larger sizes (Stanley 1973, Gould 1988, Jablonski 1997, Alroy 1998, Knouft and Page 2003).

Island faunas offer splendid opportunities for the study of such phenomena. Their restricted area and their isolation often make the insular environments interesting settings for "natural experiments" of ecological and evolutionary phenomena (Mayr 1967, Roth 1992). Islands have relatively depauperate faunas (MacArthur and Wilson 1967), often resulting in simpler, relatively easily studied guilds. Predators are absent from many small islands (Heaney 1984, Alcover and McMinn 1994). Therefore selection pressures related to competition and predation may be more relaxed on islands (Rothstein 1973, Heaney 1978, Dayan and Simberloff 1994, 1998), driving behavioral (MacArthur et al. 1972, Gliwicz 1980, Brown and Lomolino 1998) and morphological (Foster 1964, Lomolino 1985, Dayan and Simberloff 1994, Simberloff et al. 2000, Boback and Guyer 2003) changes in insular populations, in relation to their mainland relatives.

Many patterns of morphological evolution have been suggested for insular animals. The first nomothetic study of such pattern was by Foster (1964, See Kurten 1953, p. 108 for an idiographic description he ascribed to Rensch [1924]). Reviewing the literature, Foster (1964) found that rodents tend towards gigantism on islands, while carnivores, lagomorphs, and artiodactyls are usually characterized by insular dwarfing. Leigh Van Valen (1973) named these phenomena “the island rule” presenting it as a tendency of small mammals to grow larger on islands, while large mammals are dwarfed. He concluded that, “The regular evolution of mammalian body size on islands is an extraordinary phenomenon which seems to have fewer exceptions than any other ecotypic rule in animals" (1973, p. 32, see also Van Valen [1970]). Mark V. Lomolino (1983, 1985) expanded the scope of Foster's work. He also represented the ratio between a species' insular and mainland sizes as a function of body mass, obtaining a graded trend from gigantism in the smaller species to dwarfism in larger ones. Further work on insular proboscideans (Sondaar 1991, Roth 1992, Vartanian 1993, Lister 1996, Cavarretta et al. 2001) on the one hand, and rodents (Adler and Levins 1994, Michaux et al. 2002) on the other, seemed to confirm these results. Interestingly, it has been suggested that most mammals are dwarfed, compared with their ice-age ancestors, but this dwarfing is slower, and therefore less pronounced, in insular populations (Gordon 1986, Millien and Damuth 2004).

Scientists then naturally turned to seek explanations for the observed patterns: Climate (Foster 1965, Case 1978), resource availability (Kurten 1953, Sondaar 1977, Heaney 1978, Case 1978, Lomolino 1985, Roth 1992), intraspecific (Case 1978, Melton 1982) and interspecific competition (Heaney 1978, Lomolino 1985, Dayan and Simberloff 1998), predation (Heaney 1978, Michaux et al. 2002), social structure (Case 1978), diet (Case 1978, Lawlor 1982), physiology (Maiorana 1990, Brown et al. 1993), and founder effects (Lomolino 1985) were some of the selective forces, often contradictory, advanced as driving the course of size evolution (Angerbjörn 1986, Dayan and Simberloff 1998).

Differences in the biotic and abiotic characteristics of the islands themselves, such as area (Heaney 1978, Marquet and Taper 1998, Filin and Ziv 2004), climate (Foster 1965, Case 1978), distance from the mainland (Angerbjörn 1986), and species composition (reviewed in Dayan and Simberloff 1998) are thought to result in different selective regimes (as described above) that drive size evolution.

Another perceived difference in the morphologies of insular animals relative to their mainland counterparts is in the variance around population means. Van Valen (1965) described a situation in which niches of insular birds were broader than those of their mainland conspecifics. He then showed that variability in the trophic apparati of the insular populations was larger than that of the mainland ones. This phenomenon, named "the niche variation hypothesis", was often interpreted as meaning that morphological variability is higher on islands owing to a smaller number of competitor species there. This model (Van Valen 1965) conceives of variation as adaptive and selected for, because different individuals specialize in different resources. Alternatively, increased variability can result from relaxed stabilizing selection in environments from which competitors are absent (Rothstein 1973).

The seemingly universal success of the island rule in accounting for body size evolution of insular mammals has been taken as proof of the validity of both the pattern and processes described. Thus it has been taken as evidence that the selective pressures hypothesized to be operating in insular settings can and do influence mammalian sizes wherever similar conditions pertain (e.g. Demetrius 2000, Ginsberg 2000, Schmidt and Jensen 2003, Diniz-Filho 2004).

One of the major consequences of this consensus was the independent development of three theories claiming mammals have a single, optimal body size: Maiorana (1990) suggested that modal sized mammals have a physiological advantage that manifests itself on islands, where predation and competition pressures are weak. She did not explicitly define what this modal, optimal size, actually is. Damuth (1993) also claimed that intermediate masses are optimal and explicitly defined what this optimum mass is – one kilogram. He argued that it is at about this size that species control most energy in most dietary groups.

Brown, Marquet, and Taper (Brown et al. 1993) claimed mammals weighing about 100 grams are optimally sized, arguing that this value is close to the mammalian modal size. They suggested that mammals of this size 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 (1995) explained the island rule in terms of the higher reproductive ranges of optimal sized mammals.

Given the apparent success of the island rule (Lomolino 1985) in predicting patterns of size evolution on the one hand, but the ambiguity in regard to the selective forces driving these patterns (Angerbjörn 1986, Brown and Lomolino 1998, Dayan and Simberloff 1998), my aims in this project were to look for the patterns of size evolution on islands and to try and decipher which of the selective forces, if any, is actually acting in different settings.

Specifically, I examined the island rule (*sensu* Lomolino 1985) itself and also looked for patterns in relation to island area (Heaney 1978, Marquet and Taper 1998, Filin and Ziv 2004) and isolation (Angerbjörn 1986). I examined evidence claimed to support the theories of optimal body size (Brown et al. 1993, 1996, Damuth 1993, Marquet and Taper 1998, Kelt and Van Vuren 1999) and patterns of geographic variability related to the niche variation hypothesis.

I also analyzed geographic variation patterns in the body size of terrestrial carnivores, as a sort of null model for insular carnivore sizes. Another chapter deals with variation in the actual measurements themselves, again serving as a preliminary study, which can shed light on observed patterns of geographic variation in various taxa and traits.

The taxon chosen for this work comprised the terrestrial members of the mammalian order Carnivora. This group contains some 237 (Wozencraft 1993) to 246 (Nowak 1999) species, including two domesticated forms (*Canis familiaris* L. and *Felis catus* L.) and two or three species that can be considered marine (*Ursus maritimus* Phipps, *Enhydra lutris* [L.], and perhaps *Lontra felina* [Molina]) in eight families. Despite being only the fifth largest of mammalian orders (Nowak 1999), carnivores show an unparalleled variability in a number of ecological, behavioral, and life history traits: They are extremely diverse in social structure, habitat use, activity patterns, home range size, locomotor ability and, despite their name, in diet (Ewer 1973, Gittleman 1985, 1989, 1996, Gittleman and Van Valkenburgh 1997, Macdonald 1992, Kelt and Van Vuren 1999, 2001, Nowak 1999, Attenborough 2002, Kruuk 2002, Andersson and Werdelin 2004). This variability in turn, is reflected in carnivore morphology (Butler 1946, Ewer 1973, Radinski 1981a, 1981b, Biknevicius and Van Valkenburgh 1996, Popowics 2003, Anderson and Werdelin 2004). Carnivores are relatively well studied and are also over-represented in museum collections (Hafner et al. 1997). More importantly (in the context of this work), carnivores are the most diverse mammalian order in terms of body size, with adult masses ranging over four orders of magnitude, from 22 gram least weasels (*Mustela nivalis*) to 780000 gram brown bears (*Ursus arctos*, Nowak 1999). Thus carnivores cover nearly the entire mass range of terrestrial mammals, from small to large size. Various factors that are thought to affect body size (Simms 1979, Kiltie 1988; Dayan et al. 1989, 1990, 1992; Dayan and Simberloff 1994; 1998, Thurber et al. 1992; Van Valkenburgh and Wayne 1994, cf. McDonald 2002), such as interspecific competition (Major and Sherburne 1987, Cypher 1993, Johnson et al. 1996, Arjo et al. 2002, Loveridge and Macdonald 2002) and predation (Palomares and Caro 1999, Fedriani et al. 2000, Van Valkenburgh 2001, Arjo et al. 2002, Macdonald and Sillero-Zubiri 2004), have been widely studied in carnivores.

Actual patterns of size variation are also well known in carnivores: sexual size dimorphism (Erlinge 1979, Gliwicz 1988, Lüps and Roper 1988, Dayan and Simberloff 1994, Gittleman and Van Valkenburgh 1997, Weckerly 1998, Johnson and Macdonald 2001) and continental size patterns (Klein 1986, Dayan et al. 1991) have been intensively studied. On islands specifically, both dwarf (e.g. the island fox *Urocyon littoralis* [Baird]) and giant carnivores (e.g. the Kodiak brown bear, *Ursus arctos middendorffi*) are known. The most extreme cases of both gigantism and dwarfism in Lomolino's pioneering work on the island rule (Lomolino 1983) are carnivores, with wolves (*Canis lupus* L.) showing the greatest degree of size decrease (mere 51% of mainland size), and mink (*Mustela vison* Schreber) exhibiting the largest degree of gigantism (177% of mainland size). Carnivores are therefore an excellent group in which to examine the topics of the present work.

Materials and methods

Measurements

I studied carnivore crania and teeth as surrogates for body size. Seven measurements were chosen (see von den Driesch 1976):

1. Condylo-Basal Length.
2. Skull width at the posterior attachment point of the zygomatic arch to the skull.
3. Skull height from the foramen magnum to the attachment point between the sagittal and nuchal crests (or the median contact point between the squamosal and parietal bones).
4. Zygomatic breadth.
5. Maximum length of the upper carnassial.
6. Maximum length of the lower carnassial.
7. Maximum diameter of the upper canine.

CBL serves as a common indicator of body size (*e.g.* Miller 1912, Kurten 1973, Hall 1981, Beltran and Delibes 1993, Jones 1997, Brunner et al. 2002). Zygomatic breadth is supposed to be a good indicator to the size of the masseter and temporalis muscles (Ewer 1973, Burton 1979, Benton 1997, Jones 1997, Biknevicius and Van Valkenburgh 2001) and might therefore be relevant to the study of carnivore diets. Skull width and height were chosen to reflect skull size in dimensions other than length.

The teeth chosen serve as the chief killing apparati in carnivores (Dayan et al. 1989, 1990, 1992) and are known as indicative measurements for the detection of competition in a number of carnivore families (Dayan et al. 1990, 1992, Dayan and Simberloff 1994). These teeth are therefore suitable measures for testing the existence of resource partitioning between different species in a guild and between the sexes within a species, an indication of the existence of competition leading to character displacement or to species sorting.

Data collection

"Nothing can be more improving to a young naturalist than a journey in distant countries" (Charles Darwin, quoted in Gerald Durrell (1961): "The whispering land").

I measured specimens in 28 museum collections. Measurements from 18 other museums, taken by Tamar Dayan, Daniel Simberloff, Arieh Landsman, and Anna Demarinis, were also incorporated into the database.

For each specimen I recorded sex, age, body mass, and locality, according to label data. Latitude and longitude were obtained from specimen labels (in the small minority of specimens for which these data exists), or from maps (mainly the Rand McNally New International Atlas [1979], and the Macmillan World Atlas [1996]) and internet sources – chiefly "Canadian Geographical Names" for Canada, the "USGS National Mapping Information" for the USA, the "Worldwide Directory of Cities and Towns" for the rest of the world, and of course, the almighty Google.

The taxonomy adhered to in this work is that of Nowak (1999), unless otherwise stated. It was chosen because it is the most recent work dealing with the entire order. This is a conservative choice, because this work recognizes more species than are recognized by other works (e.g. Wozencraft 1993 and especially Nowak 1991). Because we usually tried to compare only conspecifics, a taxonomy that tends to split rather than lump taxa will allow for fewer comparisons. Some of these taxonomic splits are probably unwarranted (e.g. in insular *Procyon*, Helgen and Wilson 2003, Zeveloff 2003). It is my personal belief, in view of the extreme variation exhibited by carnivores that have wide geographic ranges, that recognizing other insular populations as meriting specific status might also be erroneous: *Paradoxurus lignicolor*, *Urocyon littoralis* and *Melogale orientalis* can probably all be equated with their continental relatives (*P. hermaphroditus*, *U. cinereoargenteus* and *M. personata*, respectively).

Possible biases

There are several drawbacks to the use of cranial and dental components as size indices. First and foremost, the degree of intraspecific correlation between these traits and body mass is usually unknown and, when it is known, is not always very high (Meiri et al. 2003). Both random factors and selective pressures affecting body shape and tooth size (e.g. Dayan et al. 1989, 1990, 1992) can make these traits poor estimators of size (see Hirakawa et al. 1992 for a study where an insular hare population had higher body lengths and masses than the mainland ones, but shorter skulls) .

It should be noted that "body size" itself is a very vague term. Apart from skull length, the two most popular indices for total size are body mass and head-plus-body length (HBL). These variables are highly correlated interspecifically (Silva 1998). HBL does not account for width and height and in weasels has been found to be a poor estimator of other size variables (Johnson 1991). Body mass is the most obvious measure of size (Rising and Somers 1989, Dunning 1993). However mass, even of the same individual, often varies greatly on a seasonal, and even on a daily basis (with time to the last meal). It also depends on reproductive and physical condition (Ralls and Harvey 1985, Dunning 1993). In fact Gittleman and Van Valkenburgh (1997) advance the use of CBL as a measure of size because it minimizes effects of adipose tissues.

That said, cranial and dental components were chosen for this study principally on the basis of their availability and the ease with which they can be compared with results of other studies: research of this taxonomic and geographical breadth is bound to be museum-based, and museums, by nature, hold many skulls and considerably fewer skins (from which HBL can be obtained).

Mass data are also rarely recorded for museum specimens. Skulls and teeth on the other hand are readily available in large numbers. Therefore most biogeographic studies of size variation use some measurement of skull length (CBL, GTL etc.) as an index of size, while for paleontological research it is usually tooth size (generally that of the first lower molar) that serves as an index of body size (e.g. Gould 1975, Creighton 1980, Klein 1986, Koch 1986, Alroy 1998, 2003) for taphonomic reasons. Skulls and teeth are therefore the natural indices of choice for spatio-temporal studies of size variation.

Several sources of error and bias can hamper this kind of museum-based research. First the data on the specimen labels may be incorrect – taxonomy, sex, mass, and locality data may all be (and often are) in error. The recording of all these data is also prone to error – especially in the common case of handwritten, often difficult to read labels (for example, I located latitude and longitude data for a higher proportion of the specimens kept in museums with computerized databases). Even if data on the label are correct, locality may be wrongly inferred when several places have the same name (the USGS website, for instance, lists 36 places called "Round mountain" in California, making it very difficult to assign latitude and longitude correctly for the 11 specimens in my database labeled "Round mountain CA"). The locality data can also be the locality where the specimen was purchased rather than the one where it was killed (Wells 1989; Chris Smeenk, personal communication), or else it might be the locality where an animal was held captive, and the fact it spent time in captivity may not be recorded. Specimens spending any time in captivity were discarded from all analyses, because I never encountered a label designating the age at capture.

Another important source of locality error stems from the high vagility of many carnivore species (e.g. *Canis lupus*, *Panthera pardus, Ursus arctos*). This is especially relevant when one analyzes patterns of latitudinal and longitudinal size variation and when a specimen is assigned to a specific island. Many islands inhabited by carnivores are very close to other islands or to the mainland. Therefore the islands in question may not, in fact, be isolated, and some of their carnivore populations may be parts of larger metapopulations. Actual data on over water dispersal ability of mammals are extremely rare (see e.g. Sondaar 1977, Johnson 1980, Reumer and de Vos 1999). The scant data on actual carnivore inter-island dispersal are often contradictory. For example Quadra Island (BC) is advertised on the internet as being "bear free", despite being isolated from Vancouver island (inhabited by *Ursus americanus*) by a strait only ca. 2 km. wide, and from mainland British Columbia (with both *U. americanus* and *U. arctos*) by a series of small islands with even narrower straits between them. Klein (1995) recorded wolves swimming water channels between islands in calm, protected waters, but even presumably starving wolves avoided swimming the 900 meters of rough seas and heavy currents separating Coronation Island from a nearby island where food was abundant. Darimont and Paquet (2002) also report little movement of wolves between nearby islands. Friis (1985), however, claims population increase of wolves on Vancouver Island results from dispersal of mainland animals, and otters can also cover large distances by swimming (Cowan and Guiget 1956). In New Zealand, stoats (*Mustela erminea*) swim to islands a few kilometers from the mainland (Lance Shaw pers. comm.). Over-ice movements (Buskirk and Gipson 1981, Lomolino 1983, 1993) can also mean that carnivores recorded from a certain island are not, in fact, confined to it. These limitations are inherent in museum-based research and are nearly impossible to control for.

Other sources of error stem from the measurements themselves. These include the hidden assumption of perfect bilateral symmetry (usually, but not exclusively, I measured only the left lower carnassial, right upper carnassial and either canine, if teeth on both sides were present and in good condition. Worn teeth and milk teeth were not measured) and the assumption that all cranial components cease growing at the same age, so that a completely fused skull is a true sign of maximum size, an assumption that is probably incorrect (the zygomatic arch and sagittal crest probably continue growing well after other body parts reached adult size, Ansorge 1994). Another assumption that is likely to be proven untrue is that the date of collection does not affect body size. This assumption is obviously wrong in many cases: changes in faunal composition leading to character displacement or release, periods of intense trophy-hunting leading to samples being non-random, global warming and anthropogenic influences (Yom-Tov 2001, 2003, Yom-Tov et al. 2002, 2003, Schmidt and Jensen 2003) can all induce size change, or an apparent size change, well within the time frame covered by museum specimens measured (over 170 years: the oldest specimen in my database is probably # A1948 – an unsexed *Mustela nudipes* measured at the Laboratoire d'Anatomie Comparee, Musee National d'Histoire Naturelle in Paris. It is dated to 1831).

Differences in measurement techniques between me and other people whose measurements I used (see below) can also be a source of error (Yezerinac et al. 1992, Palmeirim 1998). Furthermore, some measurements seem inherently variable and not strictly related to body size – in the Mephitinae and Lutrinae, for example, bony "skirts" sometimes develop, especially in large individuals (pers. obs.), and add a factor of variability to the measurements. Sagittal crests are also not of uniform dimensions even within a morphospecies. In canines the exact position of the enamel/dentine junction is not always easy to locate. Measurements are often influenced by the particular structure of a morphological trait, the clear-cut landmarks for measurement, its proximity to other characters (such as other teeth), the ease with which calipers can be placed, etc. (Dayan et al. 2002). Other sorts of error I detected in this work are wrong identification of teeth (for example it was not until a discussion with David Nagorsen at the Royal British Columbia Museum that I discovered that the teeth I took for carnassials in ursids were not the carnassials at all), calipers going out of settings and problems related to the software ("Optoface") used to transfer data from the calipers to the computer.

While these and other sources of error (Maiorana 1990, p. 90) undoubtedly plague this research (no research is error free), I believe that none of them can be said a priori to bias the results of this work consistently in any particular direction. Of course such errors can mask real differences if such exist in the data, and therefore limit the power of the various statistical tests I apply to detect existing patterns. However I regard this problem as relatively minor, because I believe that the overwhelming majority of data are correct, and the errors that remain undetected after extensive scrutiny are small and probably unbiased in direction. The very large samples usually involved also increase the power of statistical tests.

Another issue with the evolution of body size is the question of evolutionary times and time lags. Apart from the unique fauna of Madagascar, isolated for millions of years (Yoder et al. 2003), and perhaps the enigmatic Falkland Island wolf (*Dusicyon australis* [Kerr], see Darwin 1845, Nowak 1999, Whipple 2003) and Sulawesi palm-civet (*Macrogalidia musschenbroekii* [Schlegel]), today's non-introduced insular carnivores are all confined to continental shelf islands. The implications of this distribution are clear – virtually all insular carnivores with mainland relatives (the populations this work focused upon) were isolated from their mainland counterparts by the vicariant event at the end of the last ice age, when sea levels arose by ca. 130 meters.

Other populations were introduced to many islands by humans (e.g. Simberloff et al. 2000, Long 2003, Zeveloff 2003). The short time insular carnivores thus had to evolve raises a question, often raised by reviewers of the works presented here, of evolutionary rates – did the insular populations have enough time to reach what one reviewer termed "equilibrium size"? I believe that, at least for populations naturally occurring on islands, the answer is "yes", and there is no such thing as "equilibrium size". Much has been written on body size evolution of introduced birds: within decades house sparrows (*Passer domesticus*, Johnston and Selander 1973, Murphy 1985) introduced to North America evolved to conform to a size cline according to the predictions of Bergmann's rule (Meiri and Dayan 2003). Introductions of mammals to islands also resulted in extremely rapid size evolution (e.g. Yom-Tov et al. 1986, 1999; Quin et al. 1996; Berry 1998; Simberloff et al. 2000). But body size changes today, even in places where the faunal composition remained constant for centuries: in a series of works Yoram Yom-Tov (Yom-Tov 2001, 2003, Yom-Tov et al. 2002, 2003, Yom-Tov and Yom-Tov 2004) and others (Schmidt and Jensen 2003) have shown that body size evolved rapidly over the last few decades, an effect they ascribe to the combined agency of climatic change and changes in resource availability owing to human activity. Pregill (1986) ascribed size reduction of insular lizards to the effects of predation by humans and their assorted entourage of introduced companions.

Size evolution in insular mammals is often shown to be progressing at extremely fast rates (e.g. Lister 1989, see discussion in Gould 1975, Millien 2004).

Clearly then as far as size is concerned, C. S. Elton (1930, page 17, appropriately cited in the context of mammal evolution on islands by Berry [1998, page 42]) was correct when he wrote about the assumption of ecological equilibrium that "It has the disadvantage of being untrue. The 'balance of nature' does not exist".

Insular carnivores surely have had time enough to evolve to the size that island area and faunal composition "dictate". Allopatric speciation (Mayr 1942) can cause species to emerge in a manner not different from that of Athena, bursting fully armed from Zeus's head – evolution by punctuated equilibria (Eldredge and Gould 1972, Gould and Eldredge 1977, 1993, Gould 2002) is characterized by a very quick formation of species from peripheral isolates that often form in exactly the same manner as do populations of insular carnivores. As for evolutionary rates, I believe that selective pressures resulting in morphological change are either strong (and therefore rapid), or inconsequential. The negative correlation between evolutionary rate and time is well known (Gingerich 1983, Gould 1984, Stanley 1985, Hendry and Kinnison 1999, Kinnison and Hendry 2001, Sheets and Mitchell 2001, see also Kurten 1959, pages 209-210). Actual evolutionary rates measured in extant populations are very high (e.g. Reznik et al. 1997). Williams (1992, p 129) calculated that if evolutionary rates exhibited by introduced populations of *Passer domesticus* (Johnston and Selander 1973) were to continue for one million years, sparrows could have inflated to ostrich size and shrunk back to sparrow size 54 times. Assuming mass scales with length to the 3^{rd} power, and the same 5% change in length per century, my calculation shows a 40 gram least weasel can inflate to brown bear size (450 kg.) and back 78 times during an equivalent period, a weasel taking a mere 6400 years to achieve bear size.

At the other end of the scale, Lande (1976) calculated evolutionary rates of equids, perhaps the best textbook example of an evolutionary trend of increasing size (Kurten 1953, Gould 1991) and concluded that the actual rate implies two deaths per million individuals per generation and the selective removal only of individuals four standard deviations or greater from the population mean – an extremely weak selection, if selection it is. This makes the assumption of constancy of rate implausible, especially on islands, where populations are relatively small. Thus, if natural selection affects size evolution in a novel setting it can do so extremely rapidly – as size doubling or halving can take a mere 500 years of evolution at the rates observed in actual populations. Even faster rates of size increase have been reported for insular mammals, Berry (1964) showed that mice introduced to Skokholm Island, South Wales, are ca. 16% heavier than near mainland mice. I therefore believe that for carnivores naturally inhabiting islands, and for those introduced to islands in prehistoric times, evolutionary lag can safely be discounted as a cause of carnivores not following expected patterns.

Data

The database assembled to date includes 21,856 specimens representing 235 species. Members of all carnivore families are represented. Five Pleistocene specimens (British *Crocuta crocuta* [two], one *Lutra lutra* and one *Ursus arctos*, and a French cave bear, *Ursus spelaeus*) and one Iron Age specimen (*Mustela nivalis* from Tel Balatah, Shchem) were also measured but not incorporated into any analysis. Five people measured these specimens: Anna Demarinis (22 specimens), Arieh Landsman (86), Daniel Simberloff (1268), Tamar Dayan (4091), and I (16389). Of these specimens 7912 are females, 11554 are males, and 2390 are unsexed. I designate 19472 specimens as adults (specimens with a complete closure of the dorsal sutures of the skull and complete adult dentition). Other specimens were not used for any comparison of cranial traits but were incorporated in comparisons involving teeth, if their permanent dentition was fully erupted. 8357 of the specimens come from islands and 13372 from mainland. For the other 127 specimens locality is either given as a marine feature (e.g. "Straits of Magellan") or is unknown, or the specimen was a zoo animal. Only 1277 specimens (fewer than 6%) have mass data. A list of the museums from which specimens were measured is given in Appendix 1.

A "map" showing the localities of 17999 specimens for which latitude and longitude data were obtained is shown in Appendix 2.

Papers, manuscripts, and analyses

Chapter 1

Meiri, S., Dayan, T., and Simberloff, D. 2005a. Variability and correlations in carnivore crania and dentition. *Functional Ecology* (in press).

Chapter 2

Meiri, S. and Dayan, T. 2003. On the validity of Bergmann's rule. *Journal of Biogeography* **30**: 331-351.

Meiri, S., Dayan, T., and Simberloff, D. 2004. Carnivores, biases and Bergmann's rule. *Biological Journal of the Linnean Society* **81**: 579-588.

Meiri, S., Simberloff, D. and Dayan, T. 2005b. Biogeographic patterns in the Western Palearctic: the fasting-endurance hypothesis and the status of Murphy's rule. *Journal of Biogeography* (in press).

Chapter 3

Meiri, S., Dayan, T., and Simberloff, D. 2004. Body size of insular Carnivores: Little support for the island rule. *American Naturalist* **163**: 469-479.

A new look into patterns of size evolution on islands. New Analysis.

Meiri, S., Dayan, T., and Simberloff, D. 2004a. Body size of insular carnivores: island area has little effect. *Evolution* (in review).

A general model of size evolution in island vs. mainland carnivores. New Analysis.

Reexamined again – can results of other works be duplicated? New Analysis.

Chapter 4

Meiri, S., Simberloff, D. and Dayan, T. 2005d. Variability and sexual size dimorphism in carnivores: Testing the niche variation hypothesis. *Ecology* (in press).

Chapter 5

Meiri, S., Simberloff, D. and Dayan, T. 2005c. Insular carnivore biogeography: Island area and mammalian optimal body size. *American Naturalist*. (in press).

Chapter 1

The morphological settings

1. Variability and correlations in carnivore crania and dentition
   (Manuscript, in press)

העולם בנוי מתאמים מתאמים, ואותם, לא את הסיבות, צריך לגלות. כי בניגוד למה
שחושבים, המתאמים, ולא הקשרים הסיבתיים, חשובים באמת"

מאיר שלו \ פונטנלה

Chapter 2

Null patterns: size evolution on mainlands

1. On the validity of Bergmann's rule (published)
2. Carnivores, biases and Bergmann's rule (published)
3. Biogeographic patterns in the Western Palearctic: the fasting-endurance hypothesis and the status of Murphy's rule (in press)

Chapter 3

Quo vadis island rules?

1. Body size of insular Carnivores: Little support for the island rule (published)
2. Body size of insular carnivores: island area has little effect. (Manuscript, in review)
3. A new look into patterns of size evolution on islands
4. A general model of size evolution in island vs. mainland carnivores
5. Reexamined again – can results of other works be duplicated?

New Analysis

A new look into patterns of size evolution on islands

Since the publication of Meiri et al. (2004b), I have gathered new data, which enables me to test the prevalence of the island rule in a larger database than the one we used. The database is the same as Appendix 2 in Meiri et al. 2005d. This table, minus CV, and appears here as Table 1. It contains 152 population pairs.

Table 1 – Sample sizes, locations and body masses in island and nearest-mainland population pairs

Species	sex	Island	Sample size	mainland	Sample size	log of body mass	SR
Alopex lagopus	M	Flaherty	5	Quebec N. of 55N	21	3.53	99.47%
Alopex lagopus	F	St. Lawrence	52	Alaska W. of 159W	18	3.42	101.10%
Alopex lagopus	M	St. Lawrence	57	Alaska W. of 159W	21	3.53	100.63%
Alopex lagopus	F	St. Matthew	7	Alaska W. of 159W	18	3.42	98.57%
Alopex lagopus	M	St. Matthew	9	Alaska W. of 159W	21	3.53	99.95%
Aonyx cinerea	F	Java	17	Sumatra	6	3.48[3]	100.39%
Arctogalidia trivirgata	F	Borneo	24	Indochina S. of 16N	7	3.19[5]	97.65%
Arctogalidia trivirgata	M	Borneo*	24	Malay Peninsula S. Of 7N	8	3.38[6]	99.44%
Arctogalidia trivirgata	F	Sumatra	8	Indochina S. of 16N	7	3.19[5]	98.49%
Bassariscus astutus	F	Espiritu Santo	8	Baja California S. of 27N	11	2.95[1]	102.48%
Bassariscus astutus	M	Espiritu Santo	6	Baja California S. of 27N	7	3.00[1]	101.06%
Bassariscus astutus	F	San Jose	6	Baja California S. of 27N	11	2.95[1]	101.76%
Bassariscus astutus	M	San Jose	6	Baja California S. of 27N	7	3.00[1]	99.84%
Canis aureus	M	Sri Lanka	5	India S. of 20N	14	4.05[6]	101.38%
Canis lupus	F	Prince of Wales	15	Alaska and BC, 54-60N, 127-135W	15	4.52[6]	94.71%
Canis lupus	M	Prince of Wales	11	Alaska and BC, 54-60N, 127-133W	10	4.54[6]	92.90%
Canis lupus	F	Vancouver Island	27	BC S. of 55N, W of 120W	7	4.52[6]	93.70%
Canis lupus	M	Vancouver Island	35	BC S. of 55N, W of 120W	11	4.54[6]	96.22%
Felis benegalensis	M	Bali	5	Java	18	3.52[6]	94.96%
Felis benegalensis	F	Borneo*	6	Malay Peninsula S. Of 7N	6	3.35[6]	93.61%
Felis benegalensis	M	Borneo*	12	Malay Peninsula S. Of 12N	5	3.52[6]	93.30%
Felis benegalensis	F	Java	24	Sumatra	9	3.35[6]	94.37%
Felis benegalensis	M	Java	19	Sumatra	7	3.52[6]	100.66%
Felis benegalensis	F	Sumatra*	9	Malay Peninsula S. Of 7N	6	3.35[6]	97.50%
Felis benegalensis	M	Sumatra*	7	Malay Peninsula S. Of 12N	5	3.52[6]	95.63%
Felis concolor	F	Vancouver Island	13	BC and Washington 47-55N, W of 120W	5	4.63[6]	96.58%
Felis lynx	M	Newfoundland	26	SE Canada and Maine S. of 55N, E of 67W	5	3.94	102.21%
Felis planiceps	M	Borneo*	9	Malay Peninsula S. of 6N	9	3.20[6]	99.57%
Felis silvestris	M	Britain	21	Belgium and France N. of 47N	6	3.70[1]	97.50%
Herpestes smithii	M	Sri Lanka	9	India S. of 19N	5	3.32[1]	100.10%
Herpestes urva	F	Taiwan	10	China S. of 27N, E. of 118E	5	3.30[1]	92.32%
Lontra canadensis	M	Baranof	7	Alaska and BC, 56-60N, 126-140W	7	3.93	102.76%
Lontra canadensis	M	Chichagof	6	Alaska and BC, 56-60N, 126-140W	7	3.93	102.20%
Lontra canadensis	M	Prince of Wales	5	Alaska and BC, 56-60N, 126-140W	7	3.93	101.18%
Lontra canadensis	F	Vancouver Island	8	BC and Washington 47-55N, W. of 122W	14	3.91	104.87%
Lutra lutra	F	Britain	9	Belgium and France N. of 47N	6	3.83[6]	96.58%
Lutra lutra	F	Ireland	15	Britain	9	3.83[6]	101.73%

Species	sex	Island	Sample size	mainland	Sample size	log of body mass	SR
Lutra lutra	M	Ireland	18	Britain	10	4.00[6]	101.30%
Lutra lutra	F	Sri Lanka	8	India S. of 26N	6	3.83[6]	97.15%
Martes americana	F	Chichagof	34	Alaska & BC 54-60N, 129-135W	19	2.80	101.85%
Martes americana	M	Chichagof	53	Alaska & BC 54-60N, 129-136W	20	3.14	101.69%
Martes americana	F	Louise	9	Moresby	15	2.80	100.00%
Martes americana	M	Louise	7	Moresby	33	3.14	99.56%
Martes americana	F	Mitkof	16	Alaska & BC 54-60N, 129-135W	19	2.80	99.68%
Martes americana	M	Mitkof	26	Alaska & BC 54-60N, 129-136W	20	3.14	98.77%
Martes americana	F	Moresby	15	BC 51-55N, W. of 126W	13	2.80	102.41%
Martes americana	M	Moresby	33	BC 51-55N, W. of 126W	16	3.14	101.71%
Martes americana	F	Prince of Wales	8	Alaska & BC 54-60N, 129-135W	19	2.80	99.65%
Martes americana	M	Prince of Wales	12	Alaska & BC 54-60N, 129-136W	20	3.14	101.81%
Martes americana	F	Vancouver Island	83	BC and Washington 45-54N, W. of 121W	25	2.80	100.13%
Martes americana	M	Vancouver Island	119	BC and Washington 45-54N, W. of 121W	44	3.14	103.56%
Martes flavigula	F	Borneo*	18	Malay Peninsula S. of 9N	11	3.40[3]	92.90%
Martes foina	M	Sjaelland	10	Denmark (Jutland)	5	3.13	97.61%
Martes martes	M	Sjaelland	8	Denmark (Jutland)	6	3.22[7]	100.66%
Meles meles	F	Britain*	13	Belgium and the Netherlands	9	4.00[7]	93.50%
Meles meles	M	Britain*	26	Belgium	11	4.06[7]	96.33%
Meles meles	F	Ireland	31	Britain	13	4.00[7]	101.03%
Meles meles	M	Ireland	21	Britain	26	4.06[7]	97.88%
Meles meles	F	Sjaelland	14	Denmark (Jutland)	52	4.00[7]	100.10%
Meles meles	M	Sjaelland	17	Denmark (Jutland)	55	4.06[7]	101.71%
Melogale moschata	F	Hainan	8	Vietnam and China, 21-26N, E of 102E	8	2.91	98.98%
Melogale moschata	F	Taiwan	28	China S. of 30N, E. of 113E	6	2.91	100.58%
Mustela erminea	F	Admiralty	8	Alaska & BC 54-60N, 127-140W	16	1.91	99.70%
Mustela erminea	M	Admiralty	18	Alaska & BC 54-60N, 127-140W	39	2.35	98.63%
Mustela erminea	F	Britain*	58	Belgium	47	2.32	105.18%
Mustela erminea	M	Britain*	66	Belgium	44	2.56	106.67%
Mustela erminea	M	Chichagof	5	Alaska & BC 54-60N, 127-140W	39	2.35	96.37%
Mustela erminea	F	Ireland	46	Britain	58	2.32	91.37%
Mustela erminea	M	Ireland	73	Britain	66	2.56	96.44%
Mustela erminea	M	Kodiak	11	Alaska S. of 61N, W. of 149	18	2.35	99.48%
Mustela erminea	F	Mitkof	9	Alaska & BC 54-60N, 127-140W	16	1.91	101.91%
Mustela erminea	M	Mitkof	18	Alaska & BC 54-60N, 127-140W	39	2.35	100.02%
Mustela erminea	F	Newfoundland*	8	Labrador S. 0f 54N, E of 58W	9	1.91	104.38%
Mustela erminea	M	Newfoundland*	45	Labrador S. 0f 54N, E of 58W	35	2.35	103.45%
Mustela erminea	M	Prince of Wales	17	Alaska & BC 54-60N, 127-140W	39	2.35	99.85%
Mustela erminea	F	Sjaelland	20	Denmark, Germany and Sweden, 53-60N	6	2.32	99.77%
Mustela erminea	M	Sjaelland	19	Denmark, Germany and Sweden, 53-60N	13	2.56	103.02%
Mustela erminea	F	Tukarak	12	Ontario, 50-60N, 75-90W	5	1.91	97.05%
Mustela erminea	M	Tukarak	12	Ontario and Quebec, 50-60N, 75-90W	18	2.35	95.91%
Mustela erminea	F	Vancouver Island	7	BC and Washington 49-54N, W. of 122W	15	1.91	97.37%
Mustela erminea	M	Vancouver Island	17	BC and Washington 48-54N, W. of 122W	40	2.35	90.85%
Mustela nivalis	F	Britain*	40	Belgium	82	1.77[7]	104.59%
Mustela nivalis	M	Britain*	122	Belgium	155	2.06[7]	109.69%
Mustela nivalis	F	Sardinia	8	Italy	10	1.77[7]	97.55%
Mustela nivalis	M	Sardinia	23	Italy	57	2.06[7]	98.27%
Mustela nivalis	M	Sjaelland	9	Denmark, Germany and Sweden, 53-60N	5	2.06[7]	104.57%
Mustela putorius	F	Britain*	13	Belgium	45	2.84[7]	102.00%
Mustela putorius	M	Britain*	38	Belgium	79	3.05[7]	100.18%

Species	sex	Island	Sample size	mainland	Sample size	log of body mass	SR
Mustela putorius	F	Sjaelland	8	Denmark (Jutland)	8	2.84[7]	99.19%
Mustela putorius	M	Sjaelland	16	Denmark (Jutland)	17	3.05[7]	99.64%
Mustela sibirica	F	Honshu	13	E Asia, 30-45N, E of 115E	6	2.60[2]	86.43%
Mustela sibirica	M	Honshu	90	E Asia, 30-45N, E of 115E	7	2.89	91.60%
Mustela sibirica	M	Kyushu	5	Honshu	90	2.89	103.74%
Mustela sibirica	M	Sado	9	Honshu	90	2.89	98.06%
Mustela sibirica	M	Shikoku	5	Honshu	90	2.89	95.34%
Mustela vison	M	Admiralty	5	Alaska & BC 55-59N, 127-135W	12	3.12	100.13%
Mustela vison	F	Baranof	13	Alaska & BC 55-59N, 130-135W	9	2.89	100.03%
Mustela vison	M	Baranof	29	Alaska & BC 55-59N, 127-135W	12	3.12	98.94%
Mustela vison	F	Chichagof	7	Alaska & BC 55-59N, 130-135W	9	2.89	98.72%
Mustela vison	M	Chichagof	8	Alaska & BC 55-59N, 127-135W	12	3.12	98.49%
Mustela vison	F	Nunivak	10	Alaska 60-62N, W. of 157W	7	2.89	100.12%
Mustela vison	M	Nunivak	11	Alaska 58-62N, W. of 157W	28	3.12	97.11%
Mustela vison	F	Vancouver Island	19	BC and Washington 48-54N, W. of 121W	13	2.89	100.56%
Mustela vison	M	Vancouver Island	25	BC and Washington 48-54N, W. of 122W	9	3.12	104.55%
Nyctereutes procyonoides	M	Kyushu*	5	Gifu Prefecture, Honshu	41	3.69	99.12%
Paguma larvata	F	Borneo*	9	Malay Peninsula S. of 9N	6	3.47	93.93%
Paguma larvata	M	Borneo*	6	Malay Peninsula S. of 9N	6	3.78[4]	92.00%
Paguma larvata	F	Sumatra*	9	Malay Peninsula S. of 9N	6	3.47	101.46%
Paguma larvata	M	Sumatra*	5	Malay Peninsula S. of 9N	6	3.78[4]	101.29%
Panthera tigris	M	Java	6	Sumatra	6	5.08[3]	102.23%
Panthera tigris	M	Sumatra	6	Malaya, Vietnam and Thailand S. of 17S	7	5.34[3]	96.07%
Paradoxurus hermaphroditus	M	Bali	6	Java	14	3.52[1]	92.19%
Paradoxurus hermaphroditus	F	Borneo*	11	Malay Peninsula S. of 9N	18	3.51[6]	94.94%
Paradoxurus hermaphroditus	M	Borneo*	23	Malay Peninsula S. of 9N	24	3.52[1]	93.58%
Paradoxurus hermaphroditus	F	Java	31	Sumatra	14	3.51[6]	108.59%
Paradoxurus hermaphroditus	M	Java	15	Sumatra	17	3.52[1]	105.27%
Paradoxurus hermaphroditus	M	Palawan	5	Borneo	23	3.52[1]	97.82%
Paradoxurus hermaphroditus	F	Sumatra*	14	Malay Peninsula S. of 9N	18	3.51[6]	100.49%
Paradoxurus hermaphroditus	M	Sumatra*	17	Malay Peninsula S. of 9N	24	3.52[1]	101.99%
Paradoxurus hermaphroditus	M	Terutau	7	Malay Peninsula S. of 9N	24	3.52[1]	98.58%
Procyon lotor	M	Key Largo	9	Florida	20	3.93[6]	99.00%
Procyon lotor	M	No name key	5	Florida	20	3.93[6]	93.41%
Procyon lotor	F	Vancouver Island	18	Washington N. of 46N, W. of 120W	7	3.81[6]	96.37%
Procyon lotor	M	Vancouver Island	17	Washington N. of 46N, W. of 120W	8	3.93[6]	97.29%
Urocyon littoralis	F	San Clemente	5	California, 32-34N, W. of 116W	8	3.50[6]	79.70%
Urocyon littoralis	F	San Miguel	6	California, 33-35N, W. of 117W	10	3.50[6]	85.13%
Urocyon littoralis	F	Santa Catalina	5	California, 32-34N, W. of 116W	8	3.59[6]	86.67%
Urocyon littoralis	M	Santa Catalina	6	California, 32-34N, W. of 116W	9	3.59[6]	83.72%
Urocyon littoralis	M	Santa Cruz	5	California, 33-35N, W. of 117W	23	3.59[6]	81.10%
Urocyon littoralis	M	Santa Rosa	6	California, 33-35N, W. of 117W	23	3.59[6]	81.32%
Ursus americanus	M	Kuiu	6	Kupreanof	5	5.19[6]	98.25%
Ursus americanus	M	Kupreanof	5	Alaska 55-60N, E. of 132W	10	5.19[6]	99.25%
Ursus americanus	M	Vancouver Island	6	BC S. of 55N, W of 122W	7	5.19[6]	98.33%
Ursus arctos	F	Admiralty	20	Alaska and BC, 55-60N, 127-140W	11	5.48[1]	98.32%
Ursus arctos	M	Admiralty	37	Alaska and BC, 54-61N, 127-143W	7	5.65[1]	96.24%
Ursus arctos	F	Baranof	5	Alaska and BC, 55-60N, 127-140W	11	5.48[1]	102.26%
Ursus arctos	F	Chichagof	9	Alaska and BC, 55-60N, 127-140W	11	5.48[1]	100.42%
Ursus arctos	M	Chichagof	11	Alaska and BC, 54-61N, 127-143W	7	5.65[1]	98.44%
Ursus arctos	F	Kodiak	12	Alaska S. of 60N, W. of 150W	28	5.48[1]	98.92%
Ursus arctos	M	Kodiak	8	Alaska S. of 60N, W. of 150W	21	5.65[1]	100.66%
Viverricula indica	F	Hainan	8	China, 15-26N, E of 102E	14	3.41	93.90%

Species	sex	Island	Sample size	mainland	Sample size	log of body mass	SR
Viverricula indica	M	Hainan	5	China, 15-26N, E of 102E	15	3.47[6]	94.39%
Viverricula indica	M	Sri Lanka	10	India S. of 23N	6	3.47[6]	98.69%
Viverricula indica	F	Taiwan	6	China 23-26N, E. of 113E	13	3.41	92.22%
Viverricula indica	M	Taiwan	7	China 23-26N, E. of 113E	13	3.47[6]	94.96%
Vulpes vulpes	F	Britain*	24	Belgium	18	3.74	101.00%
Vulpes vulpes	M	Britain*	29	Belgium	21	3.85	102.08%
Vulpes vulpes	F	Ireland	45	Britain	24	3.74	98.70%
Vulpes vulpes	M	Ireland	51	Britain	29	3.85	99.99%
Vulpes vulpes	F	Newfoundland	9	SE Canada and Maine S. of 55N, E of 70W	9	3.63[3]	102.58%
Vulpes vulpes	M	Newfoundland	6	SE Canada and Maine S. of 55N, E of 70W	18	3.70	101.94%
Vulpes vulpes	M	Tukarak	7	Ontario and Quebec, 50-60N, 76-85W	10	3.70	105.41%

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

I use two analyses to reveal trends in size evolution in these data: the first is a correlation between relative insular body size (S_R) and body mass (as in Meiri et al. 2004b). The second is a regression of insular CBL (S_I) on mainland CBL (S_M), as performed by Lomolino (1985). If the island rule prevails, than there should be a negative correlation between S_R and body mass. The slope of the regression line of S_I on S_M should be significantly less than one (Lomolino 1985).

There is no correlation between S_R and body mass (n = 152, Spearman r = -0.13, p = 0.11, Pearson r = -0.104, p = 0.20). The slope of the regression line of S_I on S_M is 0.997 ± 0.006 (SE), which does not differ significantly from unity. Thus a larger database leads to similar conclusions as in Meiri et al. 2004b – the island rule is invalid in carnivores.

A general model of size evolution in island vs. mainland carnivores

Selective forces suggested to account for size evolution on islands are varied (reviewed in Angerbjörn 1986, Dayan and Simberloff 1998, see above). These forces may interact and mask the effects of one another. To control for such interactions I regressed S_R on many biotic and abiotic variables of the islands and mainlands in Table 1. The independent variables were body mass (log grams), sex, relative latitude and longitude (as dummy variables, Zar 1998), absolute latitude and longitude (with populations west of Greenwich or south of the equator considered as having negative longitudes and latitudes, respectively), the logarithms of island area (in square kilometers) and isolation (in kilometers), absolute carnivore richness on both the island and the mainland, and the relative carnivore richness on the island (island richness divided by mainland richness). Data are presented in Table 2. To save space, species, sex and population data are not presented in this table, they are identical and appear in the same order as in Table 1.

Table 2 – multiple regression on relative insular body size.

SR	sex	Log area (km^2)	Log isolation (km^2)	Latitude (Decimal)	Longitude (Decimal)	North	South	West	East	Carnivore Richness On the island	Mainland carnivore richness	Relative richness	Log body mass (g)
99.47%	0	3.20	2.05	56.23	-79.28	0	1	0	1	3	10	30%	3.53
101.10%	1	3.71	2.06	63.50	-170.00	0	0	0	1	3	10	30%	3.42
100.63%	0	3.71	2.06	63.50	-170.00	0	0	0	1	3	10	30%	3.53
98.57%	1	2.55	2.55	60.50	-173.00	0	0	0	1	1	10	10%	3.42
99.95%	0	2.55	2.55	60.50	-173.00	0	0	0	1	1	10	10%	3.53
100.39%	1	5.10	1.41	-8.00	110.00	0	0	1	0	24	30	80%	3.48
97.65%	1	5.87	2.73	0.00	115.00	1	0	1	0	26	32	81%	3.20
99.44%	0	5.87	2.73	0.00	115.00	1	0	1	0	26	32	81%	3.39
98.49%	1	5.68	1.83	-0.08	102.00	0	0	0	1	30	32	94%	3.20
102.48%	1	2.00	0.85	24.50	-110.37	1	0	1	0	1	9	11%	2.95
101.06%	0	2.00	0.85	24.50	-110.37	1	0	1	0	1	9	11%	3.00
101.76%	1	2.22	0.78	25.00	-110.63	0	0	1	0	1	9	11%	2.95
99.84%	0	2.22	0.78	25.00	-110.63	0	0	1	0	1	9	11%	3.00
101.38%	0	4.81	1.73	5.00	81.00	1	0	0	0	14	21	67%	4.06
94.71%	1	3.76	0.78	55.78	-132.83	0	0	0	1	7	13	54%	4.53
92.90%	0	3.76	0.78	55.78	-132.83	0	0	0	1	7	13	54%	4.55
93.70%	1	4.50	0.30	49.75	-126.00	0	0	0	1	9	18	50%	4.53
96.22%	0	4.50	0.30	49.75	-126.00	0	0	0	1	9	18	50%	4.55
94.96%	0	3.75	0.48	-8.00	115.00	0	0	1	0	7	24	29%	3.53
93.61%	1	5.87	2.73	0.00	115.00	1	0	1	0	26	32	81%	3.36
93.30%	0	5.87	2.73	0.00	115.00	1	0	1	0	26	32	81%	3.53
94.37%	1	5.10	1.41	-8.00	110.00	0	0	1	0	24	30	80%	3.36
100.66%	0	5.10	1.41	-8.00	110.00	0	0	1	0	24	30	80%	3.53
97.50%	1	5.68	1.83	-0.08	102.00	0	0	0	1	30	32	94%	3.36
95.63%	0	5.68	1.83	-0.08	102.00	0	0	0	1	30	32	94%	3.53
96.58%	1	5.04	1.20	48.50	-56.00	0	0	1	0	10	12	83%	4.64
102.21%	0	4.50	0.30	49.75	-126.00	0	0	0	1	9	18	50%	3.94
99.57%	0	5.87	2.73	0.00	115.00	1	0	1	0	26	32	81%	3.21
97.50%	0	5.34	1.57	54.00	-2.00	0	1	0	1	11	12	92%	3.70
100.10%	0	4.81	1.73	5.00	81.00	1	0	0	0	14	21	67%	3.32
92.32%	1	4.55	2.13	23.00	121.00	1	0	1	0	14	17	82%	3.30
102.76%	0	3.62	0.78	56.75	-135.17	0	0	0	1	5	13	38%	3.93
102.20%	0	3.74	0.70	57.50	-135.50	0	0	0	1	6	13	46%	3.93
101.18%	0	3.76	0.78	55.78	-132.83	0	0	0	1	7	13	54%	3.93
104.87%	1	4.50	0.30	49.75	-126.00	0	0	0	1	9	18	50%	3.91
96.58%	1	5.34	1.57	54.00	-2.00	0	1	0	1	11	12	92%	3.84
101.73%	1	4.93	1.40	53.00	-7.00	0	0	0	1	6	11	55%	3.84
101.30%	0	4.93	1.40	53.00	-7.00	0	0	0	1	6	15	40%	4.01
97.15%	1	4.81	1.73	5.00	81.00	1	0	0	0	14	21	67%	3.84
101.85%	1	3.74	0.70	57.50	-135.50	0	0	0	1	6	13	46%	2.80
101.69%	0	3.74	0.70	57.50	-135.50	0	0	0	1	6	13	46%	3.14
100.00%	1	2.44	-0.30	52.98	-131.78	0	0	1	0	1	3	33%	2.80
99.56%	0	2.44	-0.30	52.98	-131.78	0	0	1	0	1	3	33%	3.14
99.68%	1	2.74	0.00	56.75	-132.83	0	0	0	1	7	13	54%	2.80
98.77%	0	2.74	0.00	56.75	-132.83	0	0	0	1	7	13	54%	3.14
102.41%	1	3.42	0.30	53.25	-131.82	0	0	0	1	3	18	17%	2.80
101.71%	0	3.42	0.30	53.25	-131.82	0	0	0	1	3	18	17%	3.14
99.65%	1	3.76	0.78	55.78	-132.83	0	0	0	1	7	13	54%	2.80
101.81%	0	3.76	0.78	55.78	-132.83	0	0	0	1	7	13	54%	3.14
100.13%	1	4.50	0.30	49.75	-126.00	0	0	0	1	9	18	50%	2.80
103.56%	0	4.50	0.30	49.75	-126.00	0	0	0	1	9	18	50%	3.14
92.90%	1	5.87	2.73	0.00	115.00	1	0	1	0	26	32	81%	3.40

SR	sex	Log area (km^2)	Log isolation (km^2)	Latitude (Decimal)	Longitude (Decimal)	North	South	West	East	Carnivore Richness On the island	Mainland carnivore richness	Relative richness	Log body mass (g)
97.61%	0	3.85	0.70	55.50	11.75	0	0	1	0	8	10	80%	3.13
100.66%	0	3.85	0.70	55.50	11.75	0	0	1	0	8	10	80%	3.23
93.50%	1	5.34	1.57	54.00	-2.00	0	1	0	1	11	12	92%	4.01
96.33%	0	5.34	1.57	54.00	-2.00	0	1	0	1	11	12	92%	4.07
101.03%	1	4.93	1.40	53.00	-7.00	0	0	0	1	6	12	50%	4.01
97.88%	0	4.93	1.40	53.00	-7.00	0	0	0	1	6	16	38%	4.07
100.10%	1	3.85	0.70	55.50	11.75	0	0	1	0	8	10	80%	4.01
101.71%	0	3.85	0.70	55.50	11.75	0	0	1	0	8	10	80%	4.07
98.98%	1	4.53	1.40	19.00	110.00	1	0	1	0	14	29	48%	2.91
100.58%	1	4.55	2.13	23.00	121.00	1	0	1	0	14	17	82%	2.91
99.70%	1	3.63	0.70	57.83	-134.50	0	0	0	1	6	13	46%	1.91
98.63%	0	3.63	0.70	57.83	-134.50	0	0	0	1	6	13	46%	2.35
105.18%	1	5.34	1.57	54.00	-2.00	0	1	0	1	11	12	92%	2.32
106.67%	0	5.34	1.57	54.00	-2.00	0	1	0	1	11	12	92%	2.56
96.37%	0	3.74	0.70	57.50	-135.50	0	0	0	1	6	13	46%	2.35
91.37%	1	4.93	1.40	53.00	-7.00	0	0	0	1	6	13	46%	2.32
96.44%	0	4.93	1.40	53.00	-7.00	0	0	0	1	6	17	35%	2.56
99.48%	0	3.97	1.66	57.00	-153.00	1	0	0	0	6	10	60%	2.35
101.91%	1	2.74	0.00	56.75	-132.83	0	0	0	1	7	13	54%	1.91
100.02%	0	2.74	0.00	56.75	-132.83	0	0	0	1	7	13	54%	2.35
104.38%	1	5.04	1.20	48.50	-56.00	0	0	1	0	10	12	83%	1.91
103.45%	0	5.04	1.20	48.50	-56.00	0	0	1	0	10	12	83%	2.35
99.85%	0	3.76	0.78	55.78	-132.83	0	0	0	1	7	13	54%	2.35
99.77%	1	3.85	0.70	55.50	11.75	0	0	1	0	8	10	80%	2.32
103.02%	0	3.85	0.70	55.50	11.75	0	0	1	0	8	10	80%	2.56
97.05%	1	2.54	0.30	56.45	-78.75	0	0	0	0	3	10	30%	1.91
95.91%	0	2.54	0.30	56.45	-78.75	0	0	0	0	3	10	30%	2.35
97.37%	1	4.50	0.30	49.75	-126.00	0	0	0	1	9	18	50%	1.91
90.85%	0	4.50	0.30	49.75	-126.00	0	0	0	1	9	18	50%	2.35
104.59%	1	5.34	1.57	54.00	-2.00	0	1	0	1	11	12	92%	1.78
109.69%	0	5.34	1.57	54.00	-2.00	0	1	0	1	11	12	92%	2.07
97.55%	1	4.38	2.28	40.00	9.00	0	0	0	1	4	10	40%	1.78
98.27%	0	4.38	2.28	40.00	9.00	0	0	0	1	4	10	40%	2.07
104.57%	0	3.85	0.70	55.50	11.75	0	0	1	0	8	10	80%	2.07
102.00%	1	5.34	1.57	54.00	-2.00	0	1	0	1	11	12	92%	2.85
100.18%	0	5.34	1.57	54.00	-2.00	0	1	0	1	11	12	92%	3.06
99.19%	1	3.85	0.70	55.50	11.75	0	0	1	0	8	10	80%	2.85
99.64%	0	3.85	0.70	55.50	11.75	0	0	1	0	8	10	80%	3.06
86.43%	1	5.36	2.26	37.00	137.00	0	0	1	0	10	19	53%	2.60
91.60%	0	5.36	2.26	37.00	137.00	0	0	1	0	10	19	53%	2.89
103.74%	0	4.56	0.30	33.00	131.00	1	0	0	1	8	10	80%	2.89
98.06%	0	2.93	1.51	38.00	138.42	0	0	0	1	2	10	20%	2.89
95.34%	0	4.27	0.78	34.00	134.00	1	0	0	1	9	10	90%	2.89
100.13%	0	3.63	0.70	57.83	-134.50	0	0	0	1	6	13	46%	3.12
100.03%	1	3.62	0.78	56.75	-135.17	0	0	0	1	5	13	38%	2.89
98.94%	0	3.62	0.78	56.75	-135.17	0	0	0	1	5	13	38%	3.12
98.72%	1	3.74	0.70	57.50	-135.50	0	0	0	1	6	13	46%	2.89
98.49%	0	3.74	0.70	57.50	-135.50	0	0	0	1	6	13	46%	3.12
100.12%	1	3.62	1.53	60.00	-166.50	1	0	0	1	2	13	15%	2.89
97.11%	0	3.62	1.53	60.00	-166.50	0	0	0	1	2	13	15%	3.12
100.56%	1	4.50	0.30	49.75	-126.00	0	0	0	1	9	18	50%	2.89
104.55%	0	4.50	0.30	49.75	-126.00	0	0	0	1	9	18	50%	3.12
99.12%	0	4.56	0.30	33.00	131.00	1	0	0	1	8	10	80%	3.69
93.93%	1	5.87	2.73	0.00	115.00	1	0	1	0	26	32	81%	3.47
92.00%	0	5.87	2.73	0.00	115.00	1	0	1	0	26	32	81%	3.78
101.46%	1	5.68	1.83	-0.08	102.00	0	0	0	1	30	32	94%	3.47
101.29%	0	5.68	1.83	-0.08	102.00	0	0	0	1	30	32	94%	3.78
102.23%	0	5.10	1.41	-8.00	110.00	0	0	1	0	24	30	80%	5.08
96.07%	0	5.68	1.83	-0.08	102.00	0	0	0	1	30	32	94%	5.34
92.19%	0	3.75	0.48	-8.00	115.00	0	0	1	0	7	24	29%	3.52

SR	sex	Log area (km^2)	Log isolation (km^2)	Latitude (Decimal)	Longitude (Decimal)	North	South	West	East	Carnivore Richness On the island	Mainland carnivore richness	Relative richness	Log body mass (g)
94.94%	1	5.87	2.73	0.00	115.00	1	0	1	0	26	32	81%	3.52
93.58%	0	5.87	2.73	0.00	115.00	1	0	1	0	26	32	81%	3.52
108.59%	1	5.10	1.41	-8.00	110.00	0	0	1	0	24	30	80%	3.52
105.27%	0	5.10	1.41	-8.00	110.00	0	0	1	0	24	30	80%	3.52
97.82%	0	4.09	2.26	9.50	118.00	0	1	1	0	9	26	35%	3.52
100.49%	1	5.68	1.83	-0.08	102.00	0	0	0	1	30	32	94%	3.52
101.99%	0	5.68	1.83	-0.08	102.00	0	0	0	1	30	32	94%	3.52
98.58%	0	2.18	0.85	7.25	99.67	0	0	1	0	2	32	6%	3.52
99.00%	0	1.74	-1.00	25.08	-80.45	1	0	0	1	1	11	9%	3.94
93.41%	0	0.50	-0.30	24.70	-81.33	1	0	0	1	1	11	9%	3.94
96.37%	1	4.50	0.30	49.75	-126.00	0	0	0	1	9	18	50%	3.82
97.29%	0	4.50	0.30	49.75	-126.00	0	0	0	1	9	18	50%	3.94
79.70%	1	2.18	1.51	32.90	-118.98	0	0	0	1	1	13	8%	3.51
85.13%	1	1.56	0.70	34.03	-120.37	0	0	0	1	1	13	8%	3.51
86.67%	1	2.29	1.51	33.38	-118.42	0	0	0	1	1	13	8%	3.60
83.72%	0	2.29	1.51	33.38	-118.42	0	0	0	1	1	13	8%	3.60
81.10%	0	2.40	1.48	34.02	-119.75	0	0	0	1	2	13	15%	3.60
81.32%	0	2.33	0.90	33.97	-120.10	0	0	0	1	2	13	15%	3.60
98.25%	0	3.29	0.48	56.27	-133.88	0	0	0	1	6	6	100%	5.20
99.25%	0	3.45	0.30	56.00	-133.43	0	0	0	1	6	13	46%	5.20
98.33%	0	4.50	0.30	49.75	-126.00	0	0	0	1	9	18	50%	5.20
98.32%	1	3.63	0.70	57.83	-134.50	0	0	0	1	6	13	46%	5.48
96.24%	0	3.63	0.70	57.83	-134.50	0	0	0	1	6	13	46%	5.65
102.26%	1	3.62	0.78	56.75	-135.17	0	0	0	1	5	13	38%	5.48
100.42%	1	3.74	0.70	57.50	-135.50	0	0	0	1	6	13	46%	5.48
98.44%	0	3.74	0.70	57.50	-135.50	0	0	0	1	6	13	46%	5.65
98.92%	1	3.97	1.66	57.00	-153.00	1	0	0	0	6	10	60%	5.48
100.66%	0	3.97	1.66	57.00	-153.00	1	0	0	0	6	10	60%	5.65
93.90%	1	4.53	1.40	19.00	110.00	0	0	1	0	14	29	48%	3.41
94.39%	0	4.53	1.40	19.00	110.00	0	0	1	0	14	29	48%	3.48
98.69%	0	4.81	1.73	5.00	81.00	1	0	0	0	14	21	67%	3.48
92.22%	1	4.55	2.13	23.00	121.00	1	0	1	0	14	17	82%	3.41
94.96%	0	4.55	2.13	23.00	121.00	1	0	1	0	14	17	82%	3.48
101.00%	1	5.34	1.57	54.00	-2.00	0	1	0	1	11	12	92%	3.74
102.08%	0	5.34	1.57	54.00	-2.00	0	1	0	1	11	12	92%	3.85
98.70%	1	4.93	1.40	53.00	-7.00	0	0	0	1	6	14	43%	3.74
99.99%	0	4.93	1.40	53.00	-7.00	0	0	0	1	6	18	33%	3.85
102.58%	1	5.04	1.20	48.50	-56.00	0	0	1	0	10	12	83%	3.63
101.94%	0	5.04	1.20	48.50	-56.00	0	0	1	0	10	12	83%	3.70
105.41%	0	2.54	0.30	56.45	-78.75	0	0	0	0	3	10	30%	3.70

Sex – Naturally, 1 denotes females whereas 0 denotes males.

North – Is the island polewards from mainland? (1 = yes, 0 = no)

South – Is the island more equatorial than mainland? (1 = yes, 0 = no)

West – Is the island west of mainland? (1 = yes, 0 = no)

East – Is the island east of mainland? (1 = yes, 0 = no)

Relative richness – Richness on the island divided by carnivore richness on the near mainland

I separately regressed the independent variables on S_R and on the absolute degree of change (substituting S_R for the absolute value of [1-S_R] in Table 2) – regardless of its direction (insular carnivores being either larger or smaller than the mainland ones). Results of the multiple regressions and backwards stepwise regressions are presented in Table 3.

Table 3 – results of a multiple regression analysis on the data in Table 2.

	S_R Beta	S_R p-level	S_R Stepwise Beta	S_R Stepwise p-level	amount of change Beta	amount of change p-level	change stepwise Beta	change stepwise p-level
Sex	-0.087	0.2475	ns	ns	0.055	0.492	ns	ns
Area	0.386	0.0349	ns	ns	-0.176	0.361	ns	ns
Isolation	-0.438	0.0002	ns	ns	0.348	0.006	ns	ns
Absolute latitude	0.286	0.2262	0.519	0.00001	-0.689	0.007	ns	ns
Absolute longitude	-0.113	0.5112	ns	ns	-0.125	0.496	ns	ns
Island polewards to mainland	0.011	0.9023	ns	ns	-0.151	0.130	ns	ns
Island equatorial to mainland	0.172	0.0724	ns	ns	-0.018	0.861	ns	ns
Island west of mainland	-0.105	0.5055	ns	ns	0.112	0.504	ns	ns
Island east of mainland	-0.332	0.0446	ns	ns	0.277	0.114	ns	ns
Richness on the island	0.782	0.0573	0.430	0.00026	-0.945	0.031	ns	ns
Richness on the mainland	-0.419	0.1341	ns	ns	0.289	0.330	ns	ns
Relative richness	-0.263	0.3442	ns	ns	0.401	0.177	ns	ns
Body mass	-0.113	0.1416	ns	ns	-0.024	0.770	ns	ns

Results of these four analyses are inconsistent with each other. Variables having significant effect on SR in the whole model do not have a significant effect after I introduce the stepwise procedure. When absolute change is considered there are three significant predictors, only one of them (isolation) is also significant for S_R. No independent variables have a significant effect on the degree of size change when a backwards stepwise regression is computed.

These results are highly puzzling. Theory has it that island area should influence size through the agencies of species numbers (affecting levels of competition and predation) and resource abundance (Heaney 1978, Brown et al. 1993, Marquet and Taper 1998, Burness et al. 2001). Large mammals (such as carnivores) are predicted to increase in size with increasing area (Heaney 1978). Here, however, body size increases with increasing carnivore richness, but the amount of overall size change diminishes. This might mean that species should grow smaller on depauperate islands, but not through the effects of area (non-significant effect in stepwise regressions) or relative richness (i.e. the factor actually believed to promote size changes through character release, Dayan and Simberloff 1998). Area itself is expected to have a strong effect on mammalian size through the availability of resources. This is especially true for carnivores, thought to be facing resource limitation sooner (i.e. on larger islands) than do other mammals (Heaney 1984, Lomolino 1985 see Lawlor 1982 regarding mammals specializing on foods of particulate nature – as carnivores do). I find no such patterns, either in the analyses above or when analyzing size patterns within archipelagos (Meiri et al. 2004a). Absolute island area does not affect the absolute degree of size change even when it is the sole independent variable ($\beta = -0.08$, $P = 0.33$).

Absolute latitude is not expected to affect size change, while relative latitude is (animals on islands that are more equatorial than their near mainland may grow smaller, and vice versa; Meiri and Dayan 2003), in contradiction to the actual results that show an increase of S_R at high absolute latitudes, and a negative effect of absolute latitude on size change (meaning that at equatorial latitudes insular carnivores are smaller than their mainland counterparts, but are similar to them in size at high latitudes). Sexual differences could promote different size trajectories for males (size increase) and females (size decrease) through character release, but such a pattern is not found. Isolation is expected to influence both absolute size change (if more isolated forms undergo "more evolution"), and changes in S_R, through the agency of lower levels of interspecific competition and predation. However, these mechanisms are generally believed to promote size increase, through character release and enhanced intraspecific competition (Case 1978, for territorial species [which carnivores usually are], Melton 1982, Angerbjörn 1986, but see Wassersug et al. 1979), whereas my results suggest the opposite. Lomolino argued that isolation itself should promote size change, because larger individuals are more likely to survive attempts to immigrate to islands. He noted that this is especially true for small mammals, which most carnivores are not (Lomolino 1985). Thus S_R is predicted to be larger on isolated islands (Lomolino 1983, 1985). In fact isolation either has a negative rather than positive effect on S_R (Table 3), albeit an increasing effect on size change, or no effect at all (stepwise regressions).

Finally, absolute body mass, the proposed *raison d'etre* of patterns of insular size evolution, has no effect on them, no matter what analysis is used.

The use of many independent variables is problematic (Smith 2002, p. 283), making me more inclined to regard the results of the stepwise regressions as more reliable. This leaves only absolute latitude and isolation as effecting SR – intriguingly, both associations being positive. Because the results of these analyses are inconsistent, sensitive to the exact analytical procedure and variables, and make little biological sense, I suspect these variables do not affect size evolution in any consistent way.

Reexamined again – can results of other works be duplicated?

Here I look into and try to explain the causes of the discrepancy between the results of this work and those of earlier studies of carnivore size evolution on islands.

I was unable to obtain a copy of Foster's PhD dissertation (Foster 1963, it is unavailable from UMI), but that of Lomolino (1983) does little to illuminate either his selection of data or methods of analysis. As for data, Lomolino simply gives, for each species examined, a list of references from which data were obtained. For a given island-mainland pairs these works (Foster 1964, Lomolino 1983, 1985) are silent on the issues of sample sizes, sex, age, and even the morphological traits serving as indices of size. Lomolino (1983) does not mention for each species which island and mainland population pairs were used for calculating relative size. This matter is further obscured by the fact that he does not report in which cases he used only males or mixed sex samples.

This fact makes his data extremely difficult to track down. The fact that 61 out of 91 references cited by Lomolino (1983, appendix f) are dated to 1948 or earlier (the median of all citations is 1936) makes a reexamination of these data nearly impossible for an Israel-based student. Using all of the carnivore-related sources listed by Lomolino (1983) I was able to obtain, I tried to repeat his analysis. Results are presented in Tables 4 and 5.

Table 4 - Samples of carnivores and their sizes in the sources cited by Lomolino (1983).

Species	**Source**	**Trait**	**Island**	**Island n & sex**	**Mainland n & sex**	**Mainland**	**Size On Island**	**Size On Mainland**	**S_I**	**S_I 1983**
Alopex lagopus	Miller 1912	CBL	Spitzbergen	3 M	1 M	Scandinavia	120.40	130.20	0.79	0.83
Canis lupus	Anderson 1943	CBL	Baffin	2 M	3 M	N. Quebec And Nunavut[3]	227.50	232.50	0.94	0.51
Canis lupus	Anderson 1943	CBL	Banks Island	4 M	4 M	Bathurst Inlet	232.25	228.10	1.06	0.51
Felis concolor	Cowan And Guiget 1956	Mass	Vancouver Island	6 M	8 M	S. BC	52.66	55.84	0.94[1]	0.69
Genetta genetta	Miller 1912	CBL	Majorca	1 M	4 M	Spain	90.40	91.00	0.98	1.06
Lontra canadensis	Cowan And Guiget 1956	Total Length	Graham Island	2 F	1 F	Parksville, Vancouver Island	1119	1219	0.77	1.33
Lontra canadensis	Goldman 1935	CBL	Kodiak	1 F[10]	1 F	Alaska Peninsula	111.50	105.30	1.19	1.33
Lontra canadensis	Goldman 1935	CBL	Prince of Wales	1 M	1 M	Stuart Lake, BC	127.70	113.40	1.43	1.33
Lontra canadensis	Goldman 1935	CBL	Vancouver Island	1 M	1 M	Stuart Lake, BC	120.00	113.40	1.18	1.33
Lutra lutra	Miller 1912*	CBL	Britain	1 M	1 M	France	124.00	117.40	1.18	Dwarf[2]
Martes americana	Hagmeier 1961	CBL	Vancouver Island	24 M	33 M	S. BC	79.70	80.50	0.97	1.08[4]
Martes martes	Miller 1912	CBL	Majorca	1 F	2 F	Italy	77.00	78.50	0.94	0.92
Martes martes	Miller 1912	CBL	Minorca	1 F	2 F	Italy	79.20	78.50	1.03	0.92
Martes martes	Miller 1912	CBL	Sardinia	1 M	2 M	Italy	87.00	86.50	1.02	0.92
Mustela erminea	Cowan And Guiget 1956*	Total Length	Vancouver Island	8 M	10 M	SW BC[5]	272	278	0.94	1.24
Mustela erminea	Hall 1951	Basilar Length	Admiralty	12 M[6]	8 M	Alaska Panhandle	37.80	37.50	1.02	1.24
Mustela erminea	Hall 1951	Basilar Length	Baranof	2 M	8 M	Alaska Panhandle	40.05	37.50	1.22	1.24
Mustela erminea	Hall 1951	Basilar Length	Graham Island	8 M	8 M	Alaska Panhandle	36.70	37.50	0.94	1.24
Mustela erminea	Hall 1951	Basilar Length	Prince Of Wales	5 M	8 M	Alaska Panhandle	39.50	37.50	1.17	1.24
Mustela erminea	Hall 1951	Basilar Length	Suemez	1 M	8 M	Alaska Panhandle	34.30	37.50	0.77	1.24
Mustela erminea	Hall 1951	Basilar Length	Vancouver Island	13 M	7 M	Washington[7]	34.00	33.75	1.02	1.24
Mustela erminea	Hall 1951	Basilar Length	Wrangel	1 F	3 F	Alaska Panhandle	32.20	32.78	0.95	1.24
Mustela erminea	Hall 1951	Basilar Length	Ymer	1 M	6 M	Greenland	41.60	41.27	1.02	1.24

Species	Source	Trait	Island	Island n & sex	Mainland n & sex	Mainland	Size On Island	Size On Mainland	S_I	S_I 1983
Mustela erminea	Miller 1912*	CBL	Britain	9 M	3 M	France	50.52	46.80	1.26	1.24
Mustela erminea	Miller 1912*	CBL	Fyn	1 F	2 F	Denmark	44.60	45.00	0.97	1.24
Mustela erminea	Miller 1912*	CBL	Ireland	4 M	9 M	Britain	44.90	50.52	0.70	1.24
Mustela erminea	Miller 1912*	CBL	Islay	6 M	9 M	Britain	48.67	50.52	0.89	1.24
Mustela erminea	Miller 1912*	CBL	Isle of Man	1 M	9 M	Britain	50.20	50.52	0.98	1.24
Mustela erminea	Miller 1912*	CBL	Jura	2 M	9 M	Britain	48.70	50.52	0.90	1.24
Mustela erminea	Miller 1912*	CBL	Skye	1 F	16 F	Britain	42.00	45.41	0.79	1.24
Mustela nivalis	Miller 1912	CBL	Britain	12 M	4 M	France[8]	39.48	39.70	0.98	1.13
Mustela nivalis	Miller 1912	CBL	Majorca	2 M	8 M	Spain	40.20	40.88	0.95	1.13
Mustela nivalis	Miller 1912	CBL	Malta	1m	4 M	Italy	46.00	43.35	1.19	1.13
Mustela nivalis	Miller 1912	CBL	Sardinia	2 M	4 M	Italy	42.60	43.35	0.95	1.13
Mustela nivalis	Miller 1912	CBL	Sicily	4 M	4 M	Italy	42.25	43.35	0.93	1.13
Mustela vison	Cowan And Guiget 1956	Total Length	Vancouver Island	8 M	7 M	S. BC	605	524	1.54	1.77
Procyon lotor	Cowan And Guiget 1956*	Total Length	Vancouver Island	7 U	3 U[9]	Vancouver	81.28	83.82	0.91	0.72
Dusicyon griseus	Clutton-Brock et al. 1976	CBL	Chiloe	2 M[11]	U[11]	Patagonia	115.00	120.00	0.88	0.88
Ursus americanus	Allen 1909	CBL	Gribbel	1 F	1 F	Kenai Peninsula	214	220	0.92	0.99
Ursus americanus	Hall 1928[13]	Basilar length	Kupreanof	1 M	4 M	Disenchantment and yakutat bays	275	259	1.197	0.99
Ursus americanus	Hall 1928[13]	Basilar length	Mitkof	1 M	4 M	Disenchantment and yakutat bays	272	259	1.158	0.99
Ursus americanus	Hall 1928[13]	Basilar length	Wrangell	1 M	4 M	Disenchantment and yakutat bays	258	259	0.988	0.99
Ursus americanus	Hall 1928[13]	Basilar length	Prince of Wales	1 M	4 M	Disenchantment and yakutat bays	254	259	0.943	0.99
Ursus americanus	Hall 1928[13]	Basilar length	Dall	1 M	4 M	Disenchantment and yakutat bays	282	259	1.291	0.99
Ursus arctos[11]	Merriam 1916	Basal length	Admiralty	3 M	3 M	NW BC and Alaska panhandle	313.67	340.33	0.78	0.89
Ursus arctos	Merriam 1916	Basal length	Hinchinbrook	1 M	3 M	NW BC and Alaska panhandle	360.00	340.33	1.18	0.89
Ursus arctos[12]	Allen 1903, Merriam 1902, 1916	Basal length	Kodiak	4 M	3 M	Alaska peninsula	402	340.67	1.64	0.89
Ursus arctos	Merriam 1916	Basal length	Montague Island	2 M	1 M	Kenai Peninsula	357.50	306.70	1.58	0.89
Vulpes vulpes	Miller 1912	CBL	Britain	3 M	2 M	France	150.53	139.10	1.27	0.74
Vulpes vulpes	Miller 1912	CBL	Sardinia	4 M	3 M	Italy	131.00	141.87	0.79	0.74

S_I is the cubed ratio of insular to mainland trait size. (S_I in Lomolino 1983, equivalent to S_M in Lomolino 1985). S_I 1983 is the value reported by Lomolino.

Only males were used whenever measurements existed for both insular and mainland populations. Otherwise I calculated S_I of females

*These species are used by Lomolino (1983) who cites other references. However measurements of both insular and mainland specimens exist in this study as well.

1. *Felis concolor* is the only species for which mass data were available in the original reference.

S_I in this case is therefore simply the quotient of island and mainland masses.

2. *Lutra lutra* does not appear in the database of Lomolino (1983), but data exist in a source he cites (Miller 1912). As a large (ca. 10 kg.) mammal, it is expected to dwarf on islands.
3. Mainland CBL calculated as the average of two subspecies: *Canis lupus hudsonicus* and *C. l. labradorius* (Anderson 1943).
4. S_I of populations from the Queen Charlotte Islands and the Alexander Archipelago were not calculated, because Hagmeier (1961) does not give data for separate islands. The average CBL in those archipelagoes is smaller than on the mainland, contrary to Lomolino's (1983) result for *Martes americana*.
5. Mainland sample is *Mustela erminea fallenda*.
6. Admiralty sample comprises of 12 "adult to subadult" males (Hall 1951).
7. Mainland CBL calculated as the average of two subspecies: *Mustela erminea fallenda* and *M. e. olympica*.
8. Large *Mustela nivalis boccamela* from southern France were not included in Lomolino's mainland sample, although data exist in Miller (1912).
9. Only unsexed specimens are reported; these were incorporated into the analysis because *Procyon lotor* is hardly dimorphic in size.
10. Kodiak specimen "probably female" (Goldman 1935)
11. See below.
12. Kodiak sample is not random in relation to size. These are "four of the largest old male skulls" (Allen 1903, p. 561).
13. other populations in Hall (1928) were discarded because sex was only "believed to be male" or because locality was given as "Queen Charlotte Islands" without reference to actual island.

Table 5 - Summary statistics for carnivore species in the sources cited by Lomolino (1983), reported in Table 4.

Species	Log S_M	# of races (Lomolino)	# of comparisons (This study)	All sources available?	S_I Lomolino	S_I Shai	Same sign?
Alopex lagopus	3.54	1	1	yes	0.83	0791	yes
Canis lupus	4.70	5	2	no	0.51	0.996	no
Felis concolor	4.70	1	1	yes	0.69	0.943	yes
Genetta genetta	3.18	1	1	yes	1.06	0.980	no
Lontra canadensis	3.88	6	4*	yes	1.33	1.140	yes
Lutra lutra[1]	3.92	0	1	na	not computed	1.178	no
Martes americana	3.00	2	1*	yes	1.08	0.970	no
Martes martes	3.00	3	3	yes	0.92	0.996	yes
Mustela erminea	1.88	8	8	yes	1.24	1.014	yes
Mustela erminea[2]	1.88	8	15	yes	1.24	0.974	no
Mustela nivalis	1.65	3	5	yes	1.13	1.001	yes
Mustela vison	3.30	2	1*	yes	1.77	1.539	yes
Procyon lotor[1]	3.93	10	1	no	0.72	0.912	yes
Pseudalopex griseus[3]	3.54	1	1	yes	0.88	0.880	yes
Ursus americanus	5.19	5	6	no	0.99	1.083	no
Ursus arctos[4]	5.85	6	4*	yes	0.89	1.233	no
Vulpes vulpes	3.74	1	2	yes	0.74	1.027	no

S_M is the mass of the species on the mainland as it appears in Lomolino (1983).

If these were all the sources for this species listed by Lomolino this was noted.

S_I is the mean S_I of all populations

"Same sign" denotes whether a species recognized as dwarf (S_I<1) or giant (S_I>1) by Lomolino (1983) is also recognized as such according to my calculations.

* Despite the fact that Lomolino and I used the same sources, I arrived at a different number of comparisons than he did.

1. See comment concerning this species in Table 4.
2. Data on *Mustela erminea* also appear in Miller 1912. This species therefore appears twice in this table. The first time it is only the eight races from Hall (1951), presumably the same eight listed by Lomolino [1983]); the second includes seven additional comparisons from Miller (1912).
3. See below.
4. I considered all the three "species" of grizzlies from Admiralty Island (Merriam 1916) as belonging to the same race, whereas Lomolino (1983) most probably considered them separately. If I treat each of these skulls (= each race, as n=1 in all these races) separately, S_I for *Ursus arctos* becomes 1.127.

The correlation between S_I values in Lomolino (1983) and in this work (Table 5), expected to be nearly perfect, is not very high (n = 15, R^2 = 0.49), with a slope of 0.40, where the expected slope is one. Using only ermines measured by Hall (1951) reveals 10 cases where the results of this work agree with that of Lomolino (1983) concerning whether a species is dwarfed or grows larger on islands, vs. five cases of disagreement. Adding *Lutra lutra* and ermines measured by Miller (1912) changes these figures to nine vs. seven.

A large difference between the two works is also apparent (Figure 1) when S_I is regressed on S_M: according to S_I values given by Lomolino (1983) the correlation coefficient is -0.43 (n = 15, p = 0.11, slope = -0. 116), whereas with S_I values I calculated, r equals 0.171 (p = 0.54, slope = 0.027). I used only *Mustela erminea* specimens measured by Hall [1951] and S_M values calculated by Lomolino, both cases).

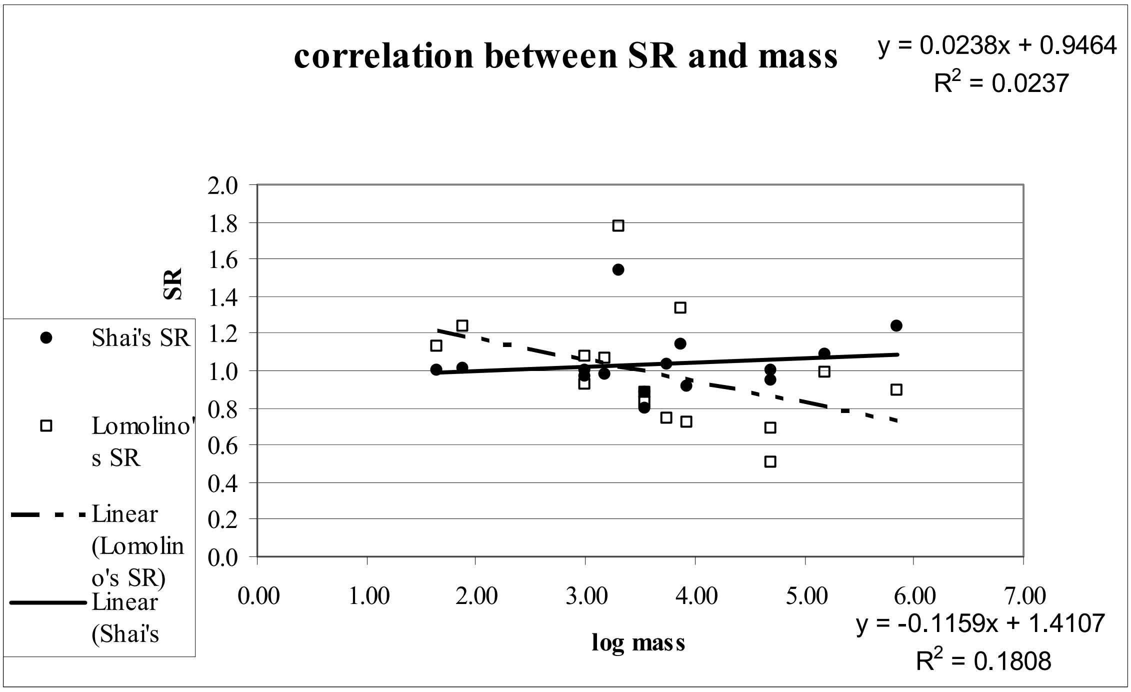


Figure 1. SR vs. body mass in Lomolino (1983, dashed line) and in table 5. The same references and same species are used in both works.

The discrepancies between Lomolino's results and mine can probably all be explained by the use of different geographical locations, sexes, and morphological traits, as well as (five) additional sources used by Lomolino (1983) that I failed to obtain. Surprisingly, even when all of Lomolino's sources were available to me I failed to duplicate his exact S_R values in all but one case – that of *Dusicyon griseus (=Pseudalopex griseus*, Wozencraft 1993, including *P. fulvipes*). Measurements of this species were published by Clutton-Brock et al. (1976), but it is uncertain what the sample sizes and geographic origin of the mainland specimens they used actually were. In addition, two insular specimens are mentioned (Clutton-Brock et al. 1976), but one is suspected to be from mainland Chile and is probably unsexed. The second specimen, the male mentioned by Darwin (1845, BMNH specimen #55.12.24.431), I also had the opportunity to measure; its CBL is 119.18 mm. The CBL of the insular *fulvipes* published by Clutton-Brock et al. (1976) is 115 mm, compared to the mainland's 120, so I believe the unsexed specimen was used as well. The resulting S_R value is 0.88, but if the first specimen is indeed a mainland animal (or a female) then S_R becomes 0.98. This strengthens my unease with Lomolino's analysis: the most common sample size in Table 4 is one; the average is 3.7 (insular samples) and 5.2 (mainland samples). For comparison, the corresponding values in Table 1 are 18.1 and 19.4, respectively, and the minimal sample size is five. This problem (See also Smith 1992) is exacerbated by the fact that the mainlands in Table 1 (and also in Meiri et al. 2004b, 2004g) are usually closer to the island in question than are those in Table 4. Lawlor (1982) likewise criticized Foster's methods arguing that it was not the closest populations that Foster (1964) compared.

Thus the small sample sizes and distant mainlands, combined with results that differ considerably from those reported by Lomolino (1983), make me suspect his expanded version of the island rule is not a robust ecological phenomenon. This conclusion is supported by the fact that the absolute magnitude of change recorded by us (absolute value of 1-SR, in the electronic tables of Meiri et al. [2004b]) is 2.9 (CBL), 3.1 (canines) and 3.8 (M_1) percent (species means). The corresponding value in the carnivores studied by Lomolino (1983 – see table 5 above), is 22.9%, with only one (*Ursus americanus* 99%) of 14 values falling beneath the averages in our study.

In sum I think that a transparent database, including locations, sexes, sample sizes, collections or references used and morphological traits measured, is essential when dealing with geographic size variation. Indeed clear and reproducible data, not only methods must be supplied together with results and analyses for the scientific method to operate (Connor and Simberloff 1979). It is also essential to detail which populations were omitted from an analysis, and why (Simberloff and Dayan 1991). In this context, for example, it would be interesting to know how come I managed, without even having all the references he used, to compare more populations of *Ursus americanus* than Lomolino (1983) did on the one hand, and why he did not use all the populations reported by Miller (1912) and Lawlor (1982).

Chapter 4

Insular patterns of variability

1. Variability and sexual size dimorphism in carnivores: Testing the niche variation hypothesis (in press)

Chapter 5

Some implications

Or: about 100 grams – the evolution of optimal body size

1. Insular carnivore biogeography: Island area and the mammalian optimal body size. (in press)

Discussion

The main theme arising from this work is that the "known" and expected patterns of size evolution are not as strong as they appeared to be.

Bergmann's rule, while emerging as a valid ecological phenomenon, is influenced by body size (in mammals), migratory habits (in birds) and a biased selection of species chosen for study. It is also influenced to a large extent by the latitudinal and sometimes longitudinal range of the study (Meiri and Dayan 2003, Meiri et al. 2004c, 2005b).

On islands, patterns described as having "fewer exceptions than any other ecotypic rule in animals" (Van Valen 1973, see also Van Valen 1970, p. 479) do not hold for carnivores. What I expected to be the main objective in this work, namely to analyze the significance of the various selective forces responsible for the patterns found by Foster (1964) and Lomolino (1985), and modeled by Case (1978), Heaney (1978), Lomolino (1985), Marquet and Taper (1998) and others, was therefore impossible. Although marked size differences and differences in the variability and sexual size dimorphism between island and mainland populations often occur, there seems to be no unifying macroecological theme from which to derive general predictions about the direction and magnitude of these differences.

Macroecology is a relatively new branch of ecology, which uses inductive, non-manipulative methods to study whole systems and emergent characteristics of large assemblages of species distributed over wide geographic scales and evolutionary time scales (Brown 1995). Looking at large scale patterns may enable emergent phenomena to be discovered (Brown 1995, Lawton 1996, 1999, Blackburn and Gaston 2002, 2003. cf. Simberloff 1997). This, indeed, was the method chosen by Foster (1964) and later Lomolino (1985) to take isolated cases of gigantism and dwarfism and create a theory that unites cases of size evolution into a coherent theory of size increase in small mammals and size decrease in large ones (Van Valen 1970, 1973).

Paradoxically, it is the same macroecological approach that makes me doubt these and other claims concerning the evolution of mammalian sizes. There are three related issues in this regard: 1. Macroecological work (and indeed, any work) must use reliable data; we should explicitly define how these data are obtained, what their nature is, and how they are analyzed. 2. To analyze macroevolutionary patterns of microevolutionary processes one must assemble as large and diverse a database as possible. 3. The failure of the macroecological approach to falsify the null hypotheses, in this case, implies that future research on the evolution of size should focus on an assembly of data from highly detailed studies of individual populations.

1. Data and analyses

Perhaps the first question to be asked, given the way our results differ from those of other studies, is – what causes these differences? This is especially relevant for the major phenomenon examined in this work, namely, the island rule. The difference is all the more striking because of the discrepancy between our results and those obtained by Lomolino (1983, 1985), even regarding the same species and populations. Although I don't know the source of this discrepancy, I suspect the data used by Foster (1964) and later incorporated and expanded by Lomolino (1983) might not be fully adequate for their purpose. This hypothesis is very difficult to test, because neither Foster's two-page paper in "Nature" (1964), nor Lomolino's "American Naturalist" publication (1985, seven pages) actually contain the data on which their analyses are based, or even the methods by which these data were obtained. This makes it impossible to examine their data in a critical, scientific way (Connor and Simberloff 1979). However an attempt to replicate their results for carnivores failed (see above). I suspect that, while the samples they used are smaller than those we use (Meiri et al. 2004b, this study), the geographical ranges over which they obtained mainland specimens were probably larger than ours, further enhancing my belief that our database, and therefore also our results, are superior.

Not to PC is not PC - a note on phylogenetic corrections.

Several referees of works presented herein were worried our analytic methods were unsuitable, because we failed, in their view, to account for phylogenetic effects. The problem of ignoring phylogenetic effects in data is well enough known (e.g. Felsenstein 1985, Ricklefs and Starck 1996). Any comparative method (there is more than one, McNab 2003) that does not account for phylogeny risks artificially inflating the number of degrees of freedom, and results of such a study are therefore liable to contain serious errors. Phylogenetic correction methods, however, have not rendered ordinary, OTU-based studies obsolete (Smith 1994, Ricklefs and Starck 1996, Price 1997) and often suffer serious shortcomings themselves (Westoby et al. 1995a, McNab 2003), so the question "to PC or not to PC" must be well thought of before analyzing data. Perhaps the biggest drawback of using such methods is that they are inherently extremely conservative (Westoby et al. 1995a). If, for example, a common ancestor of two groups that diverged a long time ago produced sister taxa that differ in a given trait, and that difference has persisted to this day, phylogenetic correction methods are bound to view this difference as a constraint, and to treat recent taxa, regardless of their actual numbers, as having only one degree of freedom (Garland et al. 1993). However this very difference might be maintained by natural selection, rather than actually constrain evolution in any meaningful way (Westoby et al. 1995a). Likewise, the existence of complex evolutionary trends (Gould 1988, 1997, Mckinney, 1990, Ruse 1993, Jablonski 1997), different modes of evolution (Price 1997, Smith and Cheverud 2002) and extremely labile traits, such as body size, can render the computation of phylogenetic contrasts inappropriate. Although this fact is recognized by many advocates of the use of such methods (e.g. Felsenstein 1985, Gittleman et al. 1996, Losos and Glor 2003, Rheindt et al. 2004), these problems are often ignored by many scientists who, it seems to me, often automatically assume such methods must be applied when phylogenetically diverse data are studied, regardless of the nature and lability of traits studied, the existence of evolutionary trends, and even the *biological questions asked* (Smith 1994, Westoby et al. 1995b, Meiri and Yom-Tov 2004). In this respect I wholeheartedly agree with Westoby et al. (1995a), who insisted that "No statistical procedure can substitute for serious thinking about alternative evolutionary scenarios and their credibility".

In this work I did not use orthodox phylogenetic correction methods, for several reasons: I inherently dislike the fact that, when one uses contrasts, as opposed to data, values of traits in individual cases are lost to evaluation and interpretation (Smith 1994). Furthermore, I think that the use of such methods is unwarranted with both the data we use and the questions we address. The extremely high lability of size on both mainlands and islands is discussed above. Suffice it to say that, within many species, populations follow Bergmann's rule in some parts of their geographic range but not in others (Meiri and Dayan 2003), making the application of phylogenetic correction methods in comparative studies of Bergmann's rule (Ashton et al. 2000, Freckelton et al. 2003) seem out of place. That the highest degree of difference between insular and mainland degrees of SSD - in both directions (either insular or mainland populations more dimorphic) - are found in *Mustela erminea* (see below), attests to the fact that correcting for phylogeny is unwarranted. It is not that the taxa are considered, as adherents of phylogenetic correction try to caricature the situation, as originating in a "star Phylogeny" (Harvey and Pagel 1991), but that the high lability of the traits considered makes phylogenetic signals above the species level unimportant. Another important factor is that all island-mainland comparisons we make are of conspecifics, or at least of taxa in which the mainland species are paraphyletic with respect to the insular species (*Urocyon*, *Procyon*, *Paradoxurus*, all of which have insular races derived from populations of still extant mainland ones), which should in no way be considered a problem in itself (on the contrary, it may be unavoidable, Brummit 1996) but renders ordinary species-level phylogenies (e.g. Bininda-Emmonds et al. 1999) inappropriate. Further, we often compare several mainland and insular populations within a species; again requiring intraspecific phylogenies that are simply unavailable today, so phylogenetic corrections cannot be made (Garland et al. 1999, Gittleman, pers. comm.). However, the very use of insular-mainland comparisons, in many cases, for the calculation of, for example, relative insular size (Lomolino's S_R, see below), and comparisons of these values, means that we actually deal with intraspecific contrasts (Felsenstein 1985). Because the traits we examine are so labile relative to the divergence times between species, the use of contrasts should make the use of comparative methods such as independent contrasts unwarranted. This fact was recognized by Felsenstein in the very same paper in which he introduced independent contrasts (Felsenstein 1985). It seems this point is ignored by many of his followers, who tend to view comparative studies not involving phylogenetic corrections (PC) as not Politically Correct – but for some biological questions such as those dealt with in this work, I am convinced they are scientifically correct. Biology, logic and statistics are not synonyms, and the application of one depends upon the others but cannot substitute them.

2. The macroecological perspective

"The only way for paleontologists eventually to grasp something of the true nature of this phenomenon lies in the collecting of more and more instances in which the phenomenon is shown" Hooijer 1950.

The originality of the work of Foster (1964) lies in its scale, and this is the reason this pioneering work and the works that followed (most notably that of Lomolino 1985) were raised to the status of ecological rules (Mayr 1956, 1963), even called "Foster's rule" by Quammen (1997), is their scale. Foster, and later Case (1978), Lomolino (1985), Marquet and Taper (1998), Burness et al. (2001) and others analyzed what are, by definition, macroecological (or "macrobiogeographical") patterns. One cannot have come up with such generalizations studying only mice, or only elephants (or, indeed, only carnivores). Other works (cf. Heaney 1978, Lawlor 1982, Melton 1982, Angerbjörn 1985, 1986, Roth 1992, Berry 1996, Lister 1996, Jianu and Weishampel 1999, Davis and Lister 2001, Anderson and Handley 2002, Michaux et al. 2002, Raia et al. 2003) have focused on much narrower geographic, taxonomic and size scales.

It should be borne in mind that the models suggested to account for the evolution of mammalian body size on islands try to predict patterns for animals ranging in size from shrews to mammoths. Works aiming to examine patterns and processes related to size evolution on such global scales, and in broad taxonomic groups spanning a wide range of body sizes, must be based on adequate databases. Such databases must not be restricted in size and geographic and taxonomic scope if they are to succeed in reflecting macroecological patterns. Several models aiming to describe size evolution in the Mammalia as a whole were built on very restricted datasets (e.g. Van Valen 1965, Heaney 1978). Such models risk arriving at conflicting explanations (e.g. for the effects of life history, cf. Wassersug et al. 1979, Melton 1982, Roth 1992, Palkovacs 2003, Raia et al. 2003). While these models may describe or explain patterns in a particular group or location with great precision (e.g. Heaney 1978, Angerbjörn 1986, Adler and Levins 1994, Cavarretta et al.

2001, Anderson and Handley 2002, Michaux et al. 2002, Millien and Damuth 2004), they are not automatically applicable to larger groups.

Indeed patterns of insular size evolution in mammals (Lomolino 1985) are not widespread in birds or reptiles (Case 1978, Pregil 1986, Brown and Lomolino 1998, but see Clegg and Owens 2002, Boback and Guyer 2003) and have not been described in amphibians. The models trying to account for the mammalian patterns (Foster 1964, Case 1978, Heaney 1978, Lomolino 1985, Brown et al. 1993) are based on selective forces that are, in principle, applicable to other vertebrate taxa but apparently fail to describe actual patterns in these groups. Thus it seems that the success of such models in predicting actual phenomena in nature can only be tested using a global perspective, covering a wide range of taxa.

3. Patterns and future research

The most surprising result of this study, in my view, is that using proper methods from a macroecological perspective failed to reveal patterns of size evolution in insular populations. Body size does not matter, and neither do faunal composition, biogeographic region, sex and phylogeny, whereas island area and isolation influence size on islands vs. mainlands but not in inter-island comparisons. Variability patterns run opposite to a simple, competition-based interpretation of niche structure, as variability is greater on mainlands than on islands. The one pattern most strongly supported in this work is perhaps the oldest recognized biogeographic pattern, Bergmann's rule (Bergmann 1847, Rensch 1938).

While patterns of variability may be expected (Berry 1998, Meiri et al. 2004g), and continental size variation is probably related to size and geographic range (Meiri and Dayan 2003, Meiri et al. 2004c), the absence of patterns of insular vs. continental size evolution is intriguing. Contrary to the findings of Foster (1964) and Lomolino (1985), carnivores do not, as a rule, undergo size reduction on islands. Although some populations can certainly be considered insular dwarves, this pattern is not prevalent, and absolute size seems not to influence the direction and magnitude of size change (Meiri et al. 2004b).

If these results are robust, and I have every reason to believe they are, then two possibilities exist concerning the island rule: either it is a real phenomenon that is simply not expressed in carnivores, owing to some unique characters of this group, or else the island rule may be an artifact of inadequate sampling.

What about the ROUS's?

The first possibility is that something in the biology or phylogeny of carnivores sets them apart from other mammals. Whereas I'm not sure what a 'phylogenetic tendency for not adhering to the island rule' (in the sense of some inherent constraint, unrelated to their actual way of life, McNab

1989 p. 349, 2003 p. 364) may be, carnivores do differ from other mammals examined in some important aspects. The most obvious one is diet – most carnivores feed on animal prey, usually vertebrates (Meiri et al. 2004d), whereas other taxa examined (Rodentia, Artiodactyla, Proboscidea) include animals that feed mostly, if not entirely, on vegetable matter. So while invalid for carnivores the island rule, as Monty Python said it may well "have some rat in it". Within the Carnivora there does not seem to be a relationship between familial affinity (influenced by phylogeny and influencing diet, Meiri et al. 2004d) and patterns of size evolution (Meiri et al. 2004b). Another way to examine if diet affects patterns of insular size evolution, regardless of phylogeny (McNab 2003), is to look at other carnivorous clades. It seems that insectivores do not show consistent size changes on islands (Foster 1964, Lomolino 1985, Malmquist 1985), although the largest insectivore known is *Deinogalerix koenigswaldi* from the Miocene island of Gargano (Freudenthal 1972). Very little is known about size trends in insular bats. Fruit-eating bats may tend towards insular dwarfism, at least interspecifically (McNab 1994), but to my knowledge the insectivorous species in which insular size variation was studied show a complex pattern of size evolution (Burnett 1983, Kitchener et al. 1994).

Other carnivore-specific attributes that can be argued to be affecting size evolution are competition, predation and home range sizes. A vast body of literature attests to the fact that interspecific competition in carnivores is at least as intense as it is in other mammalian taxa (reviewed in Dayan and Simberloff 1998). Other selective forces believed to influence body size may differ between carnivorous and herbivorous mammals. It is often assumed that predation pressure might affect carnivores to a lesser extent than it affects other mammals. If predation drives small mammals to grow smaller still, and large mammals to grow larger, then the absence of predation on islands may drive the island rule (Heaney 1978). If predation on carnivores is scarce, than such a pattern is not expected. This is not the case. Raptors often prey on carnivores (Powell 1973, 1982; Korpimäki and Nordahl 1989, Bosokowski and Smith 1992, Roemer et al. 2002). Predation on and interspecific killings of carnivores by other carnivores are also common (reviewed by Palomares and Caro 1999, see also Kitchen et al. 1999, Fedriani et al. 2000, Van Valkenburgh 2001, Arjo et al. 2002, Wang 2002). Predation is the predominant cause of death in some populations, and no carnivore species seem immune to it (Mulder 1990, Kitchen et al. 1999, Palomares and Caro 1999).

Another attribute of carnivores that sets them apart from other mammals derives from the nature of Eltonian food pyramids. Preying on other animals, carnivorous mammals have larger home ranges than similar-sized omnivorous mammals, which in turn have larger home ranges than do herbivores (McNab 1963, Gittleman and Harvey 1982, Kelt and Van Vuren 1999, 2001, cf. Garland et al. 1993). This should lead to stronger selection against large carnivores on small islands, especially in highly carnivorous species. Indeed Heaney (1984) found carnivores to be absent from small islands, and Lomolino (1985) predicts that large carnivorous species will show an even stronger response to insular environments than will similar-sized herbivores or omnivores. In sum, the evident lack of a consistent pattern of size change in carnivores is puzzling.

As for other mammalian taxa, it seems that artiodactyls (especially cervids and hippopotamids) and proboscideans are always or very nearly always dwarfed on islands. This is apparent in a wide variety of geographical locations and on islands differing greatly in size: the California Channel Islands (Roth 1992, Agenbroad 2001), Jersey (Lister 1996), the Lesser Sunda Islands (Hooijer 1949, Morwood et al. 1998, Van den Bergh et al. 2001), Madagascar (Dewar 1984, Burney et al. 1997), islands in the Mediterranean (Sondaar 1977, 1991, Simmons 1988, Davies and Lister 2001, Masseti 2001, Palombo 2001), and Wrangel Island north of Siberia (Vartanyan et al. 1993). Apart from Madagascar, which harbored a 17 kg fossa, *Cryptoprocta spelea*, and a large crocodile (*Crocodylus robustus*, Burness et al. 2001) and the Lesser Sunda Islands inhabited by a giant monitor lizard – the Comodo dragon (*Varanus komodensis,* Diamond 1987), and also, curiously, pygmy hominids (Brown et al. 2004, but not the sample size of one, as is common in studies of human evolution), all these islands lack large carnivores, and certainly lack large mammalian carnivores that Smith (1992) believes influence prey size to a greater degree than does reptilian ones. Interestingly however extant insular populations of *Elephas maximus* (*Loxodonta* does not inhabit islands) are *not* dwarfed (Roth 1992).

In rodents the picture is murkier. Although as a rule rodents are believed to grow larger on islands (Foster 1964, Lomolino 1985, Adler and Levins 1994, Millien and Damuth 2004), this is by no means always the case (e.g. Heaney 1978, Lawlor 1982, Melton 1982, Angerbjörn 1985, 1986, Ganem et al. 1995, Yom-Tov et al. 1999, Renaud and Michaux 2003, Millien 2004).

Another possibility is that samples are inadequate. My impression is that they certainly are, but I am not sure what the implications of this are as far as the island rule is concearned. My feeling, however, is that patterns are less prevalent than they appear to be. Dwarf elephants, and the recently discovered 1-meter tall *Homo* of Flores (Brown et al. 2004) capture the imagination, but perhaps this leads to a belief that there are patterns where none exist. *Homo floresiensis* may be no more than an abbarant *H. erectus*, or even *H. sapiens* (Israel Hershkovitz, personal communication), illustrating the dangers inherent in too small sample sizes (one in this case, and also in much of the work on the island rule, see above). But even if it is a valid dwarf descendant of H. erectus as Brown et al. (2004) claim, it is, to date, the *only* race of dwarf Homo, a species that inhabits more islands than almost any mammals. Dwarf elephants certainly existed, but current day insular elephants are probably of similar size to their mainland relatives (Roth 1992). Perhaps then the "island rule" is plagued by the same tendency to report only significant results that we showed is prevalent of studies of Bergmann's rule (the file drawer problem, Meiri et al. 2004c) – and many cases of island and mainland conspecifics similar to each other in size are left unstudied. If that is indeed the case small mammals might tend towards gigantism much more often than towards dwarfism, and vice versa for large mammals, but most insular populations may not be very different in size from their mainland relatives. The fact that our criteria for measuring specimens ("if it is insular – measure it") being very different from what others seek ("if it is different enough – publish it, if not don't bother") is what drives the large difference in the average magnitude of island-mainland size differences between our results and Lomolino's (see above, chapter 3).

Rodents and artiodactyls are at least as renowned as carnivores for displaying patterns of size evolution on islands. They are also species-rich orders, abundant both on islands and in museum collections, and, treated together, exceed the size range of carnivores. In light of the results of this study, the validity of island rule in rodents and artiodactyls, and also insectivores, needs to be reexamined.

The empirical evidence presented here does not support the pattern formerly described for the evolution of body size in carnivores. Clearly then, as Lawlor (1982) has pointed out, we must be very cautious when we generalize about body size trends in mammals (see also Dunham et al. 1978). This work casts doubt on the relevance of the various mechanisms proposed to account for size change. The roles of predation, competition, and resource limitation should be more carefully examined. Patterns of size evolution in other mammalian and non-mammal taxa should also be carefully studied. The failure of the classic macroecological approach in revealing general patterns of body size evolution means it is not absolute size per-se that drives size evolution. Thus either there really are no patterns, or there are, but we have yet to reveal them. I think it is time to go back to detailed study of the ecology of specific populations and determine actual patterns of change and the mechanisms generating them. There are'nt nearly enough of those around. Viewing many such studies covering wide geographical, phylogenetic, ecological, and size ranges, we will be able to see if a unifying pattern emerges (Hooijer 1950, Simberloff 2004), regarding the forces that direct evolutionary change.

References

Adler, G. H. and Levins, R. 1994. The island syndrome in rodent populations. Quarterly Review of Biology 69: 473-490.

Agenbroad, L. D. 2001. Channel Islands (USA) pygmy mammoths (*Mammuthus exilis*) compared and contrasted with *M. columbi*, their continental ancestral stock. Pages 473-475 in G. Cavarretta, P. Gioia, M. Mussi, M. R. Palombo (editors), The World of Elephants - Proceedings of the 1st International Congress, Rome.

Alcover, J. A. and McMinn, M. 1994. Predators of Vertebrates on Islands. Bioscience 44: 12-18.

Allen, J. A. 1903. Mammals collected in Alaska and northern British Columbia by the Andrew J. Stone expedition of 1902. Bulletin of the American Museum of Natural History 19: 521-567.

Allen, J. A. 1909. The white bear of southwestern British Columbia. Bulletin of the American Museum of Natural History 26: 233-238.

Alroy, J. 1998. Cope's rule and the dynamics of body mass evolution in North American fossil mammals. Science 280: 731-734.

Alroy, J. 2003. Taxonomic inflation and body mass distributions in North American fossil mammals. Journal of Mammalogy 84: 431-433.

Anderson, K., and Werdelin, L. 2004. The evolution of cursorial carnivores in the Tertiary: implications of elbow-joint morphology. Proceedings of the Royal Society of London B. 270 (supplement) s163-s165.

Anderson, R. M. 1943. Summary of the large wolves of Canada with description of three new arctic races. Journal of Mammalogy 24: 386-393.

Anderson, R. P. and Handley, C.O. Jr. 2002. Dwarfism in insular sloths: Biogeography, selection and evolutionary rate. Evolution 56:1045-1058.

Angerbjörn, A. 1985. The evolution of body size in mammals on islands: some comments. American Naturalist 125: 304-309.

Angerbjörn, A. 1986. Gigantism in island populations of wood mice (*Apodemus*) in Europe. Oikos 47: 47-56.

Ansorge, H. 1994. Intrapopular skull variability in the red fox, *Vulpes vulpes* (Mammalia: Carnivora: Canidae). Zoologische Abhandlungen, Staatliches Museum fur Tierkunde Dresden 6: 103-123.

Arjo, W. M., Pletscher, D. H. and Ream, R. R. 2002. Dietary overlap between wolves and coyotes in northwestern Montana. Journal of Mammalogy 83: 754-766.

Ashton, K. G., Tracy, M. C. and de Queiroz, A. 2000. Is Bergmann's rule valid for mammals? American Naturalist 156: 390-415.

Attenborough, D. 2002. The life of mammals. Princeton University Press, Princeton.

Beltran, J. F. and Delibes, M. 1993. Physical characteristics of Iberian lynxes (*Lynx pardinus*) from Donana, southwestern Spain. Journal of Mammalogy 74: 852-862.

Benton, M. J. 1997. Vertebrate paleontology. 2nd edition. Blackwell Science, Oxford.

Bergmann, C. 1847. Ueber die verha¨ ltnisse der wa¨rmeo¨ konomie der thiere zu ihrer gro¨ sse. Gottinger studien, 3: 595–708.

Berry, R. J.1964. The evolution of an island population of the house mouse. Evolution 18: 468-483.

Berry, R. J. 1996. Small mammal differentiation on islands. Philosophical Transactions of the Royal Society, London. B. 351: 753-764.

Berry, R. J. 1998. Evolution of small mammals. Pages 35-50 in P. R. Grant (editor). Evolution on islands. Oxford University Press. Oxford.

Biknevicius, A. R. and Van Valkenburgh, B. 1996. Design for killing: Craniodental adaptations of predators. Pages 393-428 in Gittleman, J. L. (editor). Carnivore Behavior, ecology, and evolution, Vol. 2. Cornell University Press, Ithaca and London.

Bininda-Emonds, O. R. P., Gittleman, J. L. and Purvis, A. 1999. Building large trees by combining phylogenetic information: a complete phylogeny of the extant Carnivora (Mammalia). Biological Reviews 74: 143-175.

Blackburn, T. M. and Gaston, K. J. 2002. Scale in macroecology. Global Ecology and Biogeography 11: 185-189.

Blackburn, T. M. and Gaston, K. J. 2003. Macroecology: concepts and consequences. Blackwell Science, Oxford.

Boback, S. M. and Guyer, C. 2003. Empirical evidence for an optimal body size in snakes. Evolution 57:345-351.

Bosokowski, T. and Smith, D. G. 1992. Comparative diets of sympatric nesting raptors in the eastern deciduous forest biome. Canadian Journal Zoology 70: 989-992.

Brown, J. H. 1995. Macroecology. The University of Chicago Press. Chicago.

Brown, J. H. and Lomolino, M. V. 1998. Biogeography. 2nd edition. Sinauser, Sunderland.

Brown, J. H., Marquet, P. A. and Taper, M. L. 1993. Evolution of body size: consequences of an energetic definition of fitness. American Naturalist 142: 573-584.

Brown, J. H. and Maurer, B. A. 1986. Body size, ecological dominance and Cope's rule. Nature 324: 248-250.

Brown, J. H., Taper, M. L. and Marquet, P.A. 1996. Darwinian fitness and reproductive power: reply to Koz³owski. American Naturalist 147: 1092-1097.

Brown, J. H. and West, G. B. 2000. (editors). Scaling in Biology. Oxford University Press, New York.

Brown, P., Sutikna, T., Morwood, M. J., Soejono, R. P., Jatmiko, Wayhu Saptomo, E. and Rokus Awe Due. 2004. A new small-bodied hominin from the late Pleistocene of Flores, Indonesia. Nature 431: 1055 – 1061.

Brown, W. L. and Wilson, E. O. 1956. Character displacement. Systematic Zoology 5: 49-64.

Brummitt, R. K. 1996. In defense of paraphyletic taxa. pp. 371-384 in: L. J. G. van der Maesen et al. (editors), The Biodiversity of African plants. Kluwer Academic Publishers, Netherlands.

Brunner, S., Shaughnessy, P. D., and Bryden, M. M. 2002. Geographic variation in skull characters of fur seals and sea lions (family Otariidae) Australian Journal of Zoology 50: 415-438.

Burness, G. P., Diamond, J. and Flannery, T. 2001. Dinosaurs, dragons, and dwarfs: The evolution of maximal body size. Proceedings of the National Academy of Sciences of the United States of America 98: 14518-14523.

Burnett, C. D. 1983. Geographic and climatic correlates of morphological variation in *Eptesicus fuscus*. Journal of Mammalogy 64: 437-444.

Burney, D. A., James, H. F., Grady, F. V., Rafamantanantosa J-G., Wright, H. T. and Cowart, J. B. 1997. Environmental change, extinction and human activity: evidence from caves in NW Madagascar. Journal of Biogeography 24: 755-767.

Burton, R. 1979. Carnivores of Europe. B. T. Batsford, London.

Buskirk, S. W. and Gipson, P. S., 1981. Zoogeography of arctic foxes (Alopex lagopus) on the Aleutian Islands. Pages 38-54 in J. A. Chapman and D. Pursley, editors, Worldwide Furbearer Conference Proceedings, Vol. 1.

Buskirk, S. W., Ruggiero, L. F. and Krebs. C. J. 2000. Fragmentation and interspecific competition: implications for lynx conservation. Pages 83-100 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires, editors. Ecology and conservation of lynx in the United States. University of Colorado Press, Boulder.

Butler, P. M. 1946. The evolution of carnassial dentitions in the Mammalia. Proceedings of the Zoological Society of London. 116: 198–220.

Calder, W. A. III. 1984. Size, function and life history. Harvard University Press, Cambridge, Mass.

Canadian Geographical Names. http://geonames.nrcan.gc.ca/search/search_e.php

Carbone, C., Mace, G. M., Roberts, C. S. and Macdonald, D. W. 1999. Energetic constraints on the diet of terrestrial carnivores. Nature 402: 286-288.

Carlquist, S. 1974. Island Biology. Columbia University Press, New York.

Case, T. J. 1978. A general explanation for insular body size trends in terrestrial vertebrates. Ecology 59: 1-18.

Cavarretta, G., Gioia, P. Mussi, M. and Palombo, M. R. 2001. (editors), The World of Elephants - Proceedings of the 1st International Congress, Rome.

Clegg, S. M. and Owens, I. P. F. 2002. The ‘island rule’ in birds: medium body size and its ecological explanation. Proceedings of the Royal Society of London B. 269: 1359-1365.

Clutton-Brock, J., Corbet, G. B., and Hills, M. 1976. A review of the family Canidae, with a classification by numerical methods. Bulletin of the British Museum (Natural History), Zoology 29: 117–199.

Cohen, J. E., Pimm, S. L., Yodzis, P. and Saldana, J. 1993. Body sizes of predators and animal prey in food webs. Journal of animal Ecology 62: 67-78.

Connor, E. F. and D. Simberloff. 1979. You can't falsify ecological hypotheses without data. Bulletin of the Ecological Society of America 60: 154-155.

Cope, E. D. 1887. The origin of the fittest. D. Appleton and co., New York.

Cope, E. D. 1896. The primary factors of organic evolution. Open Court Publication co., Chicago.

Cowan, I. M. and Guiget, C. J. 1956. The mammals of British Columbia. The British Columbia Provincial Museum Handbook 11, Victoria.

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

Creighton, G. K. 1980. Static allometry of mammalian teeth and the correlation of tooth size and body size in contemporary mammals. Journal of Zoology 191: 435-443.

Cypher, B. L. 1993. Food item use by three sympatric canids in Southern Illinois. Transactions of the Illinois State Academy of Science 86: 139-144.

Damuth, J. 1993. Cope’s rule, the island rule, and the scaling of mammalian population density. Nature 365: 748-750.

Darimont, C. T. and Paquet, P. C. 2002. The gray wolves, *Canis lupus*, of British Columbia's central and north coast: distribution and conservation assessment. Canadian Field Naturalist 116: 416-422.

Darwin, C. R. 1845. The voyage of the Beagle. John Murray, London.

Darwin, C. R. 1859. On the origin of species by means of natural selection. John Murray. London.

Darwin, C. and Wallace, A. R. 1858. On the tendency of species to form varieties; and on the perpetuation of varieties and species by natural means of selection. Journal of the Proceedings of the Linnean Society, Zoology 3: 45-62.

Davies, P., and Lister, A. M. 2001. *Palaeoloxodon cypriotes*, the dwarf elephant of Cyprus: size and scaling comparisons with *P. falconeri* (Sicily-Malta) and mainland *P. antiquus*. pages 479-480 in G. Cavarretta, P. Gioia, M. Mussi, and M. R. Palombo (editors), The World of Elephants - Proceedings of the 1st International Congress, Rome.

Dayan, T. and Simberloff, D. 1994, Character displacement, sexual size dimorphism and morphological variation among British and Irish mustelids. Ecology 75: 1063-1073.

Dayan, T. and Simberloff, D. 1998. Size patterns among competitors: ecological character displacement and character release in mammals, with special reference to island populations. Mammal review 28: 99-124.

Dayan, T., Simberloff, D., Tchernov, E. and Yom-Tov, Y. 1989. Inter- and intraspecific character displacement in mustelids. Ecology 70: 1526-1539.

Dayan, T., Simberloff, D., Tchernov, E. and Yom-Tov, Y. 1990. Feline canines: Community-wide character displacement in the small cats of Israel. American Naturalist 136: 39-60.

Dayan, T., Simberloff, D., Tchernov, E. and Yom-Tov, Y. 1991. Calibrating the paleothermometer: climate, communities, and the evolution of size. Paleobiology. 17: 189-199.

Dayan, T., Simberloff, D., Tchernov, E. and Yom-Tov, Y. 1992. Canine carnassials: Character displacement in the wolves, jackals and foxes of Israel. Biological Journal of the Linnean Society 45: 315-331.

Dayan, T., Wool, D. and Simberloff, D. 2002. Variation and covariation of skulls and teeth: modern carnivores and the interpretation of fossil mammals. Paleobiology 28: 508-526.

Demetrius, L. 2000. Directionality theory and the evolution of body size. Proceedings of the Royal Society of London B 267: 2385-2391.

Dewar, R. E. 1984. Extinctions in Madagascar: the loss of the subfossil fauna. pages 574-593. In P. S. Martin and R. G. Klein, editors. Quaternary extinctions, a prehistoric revolution. The University of Arizona Press. Tucson.

Diamond, J. M. 1987. Did Komodo dragons evolve to eat pygmy elephants? Nature 326: 832.

Diniz-Filho, J. A. F. 2004. Macroecology and the hierarchical expansion of evolutionary theory. Global Ecology and Biogeography 13: 1-5.

Dunham, A. E., Tinkle, D. W., and Gibbons, J. W. 1978. Body Size in Island Lizards: A Cautionary Tale. Ecology 59: 1230–1238.

Dunning, J. B. Jr. 1993. CRC handbook of Avian body masses. CRC, Press London.

Durrell, G. 1961. The Whispering land. Collins, London.

Eldredge, N. and Gould. S. J. 1972. Punctuated equalibria: An alternative to phyletic gradualism. pages 82-115 In T. J. M. Schopf. Models in paleobiology. Freeman, Cooper & Co. San Francisco.

Elton, C. S. 1930. Animal ecology and evolution. Oxford University Press, New York.

Erlinge, S. 1979. Adaptive significance of sexual dimorphism in weasels. Oikos 33: 233-245.

Ewer, R. F. 1973. The carnivores. Cornell University Press. New York.

Farlow, J. O. and Pianka, E. R. 2003. Body Size Overlap, Habitat Partitioning and Living Space Requirements of terrestrial vertebrate Predators: Implications for the Paleoecology of Large Theropod Dinosaurs. Historical Biology 16: 21-40.

Fedriani, J. M., Fuller, T. K., Sauvajot, R. M. and York, E. C. 2000. Competition and intraguild predation among three sympatric carnivores. Oecologia 125: 258-270.

Felsenstein, J. 1985. Phylogenies and the comparative method. American Naturalist 70:1-15.

Filin, I. and Ziv, Y. 2004. New theory of insular evolution: unifying the loss of dispersability and body-mass change. Evolutionary Ecology Research 6: 1-10.

Foster, J. B. 1963. The evolution of the native land mammals of the Queen Charlotte Islands and the problem of insularity. PhD Dissertation, University of British Columbia, Vancouver.

Foster, B. J. 1964. Evolution of mammals on islands. Nature 202: 234-235.

Foster, J. B. 1965. The evolution of the mammals of the Queen Charlotte Islands, British Columbia. British Columbia Provincial Museum, Victoria, Occasional Paper no. 14. 130 pp.

Freckleton, R. P., Harvey, P. H. and Pagel, M. 2003. Bergmann's rule and body size in mammals. American Naturalist 161: 821-825.

Freudenthal, M. 1972. *Deinogalerix koenigswaldi* nov. gen., nov. spec., a giant insectivore from the Neogen of Italy. Scripta Geol. 14: 1-10.

Friis, L. K. 1985. An investigation of subspecific relationships of the grey wolf, Canis lupus, in British Columbia. MSc. Thesis, Department of Biology, University of Victoria, Canada.

Funston, P. J. Mills, M. Biggs, H. and Richardson, P. 1998. Hunting by male lions: ecological influences and socioecological implications. Animal Behaviour 56: 1333-1345.

Ganem, G., Granjon, L., Ba, K. and Duplantier, J. -M. 1995. Body size variability and water balance: A comparison between mainland and island populations of *Mastomys huberti* (Rodentia: Muridae) in Senegal. Experientia 51: 402-410.

Garland, T., Jr., Dickerman, A. W. Janis, C. M. and Jones, J. A. 1993. Phylogenetic analysis of covariance by computer simulation. Systematic Biology 42:265-292.

Garland, T., Jr, P. E. Midford, and A. R. Ives. 1999. An introduction to phylogenetically based statistical methods, with a new method for confidence intervals on ancestral values. American Zoologist 39:374-388.

Gingerich, P. D. 1983. Rates of evolution: Effects of time and temporal scaling. Science 222: 159-161.

Ginsberg, J. R. 2000. Mammals, biodiversity of. Pages 777-810 in S. A. Levin, Editor. Encyclopedia of Biodiversity. Volume 3. Academic Press, San Diego.

Gittleman, J. L. 1985. Carnivore body size: Ecological and taxonomic correlates. Oecologia 67: 540-554.

Gittleman, J. L. 1989. editor. Carnivore Behavior, Ecology, and Evolution. Chapman and Hall, London.

Gittleman, J. L. 1996. Carnivore behavior, Ecology, and evolution. vol. 2. Cornell University Press. Ithaca.

Gittleman, J. L. Anderson, C. G., Kot, M. and Luh, H. K. 1996. Phylogenetic lability and rates of evolution: A comparison of behavioral, morphological and life history traits. Pages 166-205 in E. P. Martins (editor) Phylogenies and the comparative method in animal behavior. Oxford University Press, Oxford.

Gittleman J. L. and Harvey, P. H. 1982. Carnivore home-range size, metabolic needs and ecology. Behavioral Ecology and Sociobiology 10: 57-63.

Gittleman, J. L. and Van Valkenburgh, B. 1997. Sexual dimorphism in the canines and skulls of Carnivores: effects of size, Phylogeny and behavioural ecology. Journal of Zoology 242: 97-117.

Gliwicz, J. 1988. Sexual dimorphism in small mustelids: body diameter limitation. Oikos 53: 411-414.

Goldman, E. A. 1935. New American Mustelids of the genera *Martes*, *Gulo*, and *Lutra*. Proceedings of the biological Society of Washington 48: 175-186.

Gordon, K. R. 1986. Insular evolutionary body size trends in Ursus. Journal of Mammalogy 67: 395-399.

Gould, S. J. 1966. Allometry in size in ontogeny and phylogeny. Biological reviews 41: 587-640.

Gould, S. J. 1974. On size and shape. Natural History 83: 20-26.

Gould, S. J. 1975. On the scaling of tooth size in mammals. American Zoologist 15: 351-362.

Gould, S. J. 1984. Smooth curve of evolutionary rate: A psychological and mathematical artifact. Science 226: 994-995.

Gould, S. J. 1988. Trends as change in variance: a new slant on progress and directionality in evolution. Journal of Paleontology 62: 319-329.

Gould, S. J. 1991. Bully for the Brontosaurus. WW. Norton, New York.

Gould, S. J. 1997. The paradox of the visibly irrelevant. Natural History 106: 12-18.

Gould, S. J. 2002. The structure of evolutionary theory. Harvard University Press, Cambridge.

Gould, S. J. and Eldredge, N. 1977. Punctuated equalibria: the tempo and mode of evolution reconsidered. Paleobiology 3: 115-151.

Gould, S. J. and Eldredge, N. 1993. Punctuated equilibrium comes of age. Nature 366: 223-227.

Hafner, M. S., W. L. Gannon, J. Salazar-Bravo, S. T. Alvarez-Castañeda. 1997. Mammal collections in the Western Hemisphere: A survey and directory of existing collections. American Society of Mammalogists, Allen Press, Lawrence, Kansas, 93 p.

Hagmeier, E. M. 1961. Variation and relationships in North American marten. Canadian Field Naturalist 75: 122-138.

Haldane, J. B. S. 1928. On being the right size. pages 20-28 in Possible Worlds. Harper, New York.

Hall, R. E. 1928. A new race of black bears from Vancouver Island, British Columbia, with remarks on other Northwest Coast forms of Euarctos. University of California Publications in Zoology 30: 231-242.

Hall, R. E. 1951. American Weasels. University of Kansas Publications Museum of Natural History 4: 1-466.

Hall, R. E. 1981. The mammals of North America.2nd edition. John Wiley & Sons. New York.

Harvey, P. H. and Pagel, M. D. 1991. The Comparative Method in Evolutionary Biology. Oxford University Press, Oxford.

Heaney, L. R. 1978. Island area and body size of insular mammals: Evidence from the tri-colored squirrel (*Callosciurus prevosti*) of Southeast Asia. Evolution 32: 29-44.

Heaney, L. R. 1984. Mammalian species richness on islands on the Sunda Shelf, Southeast Asia. Oecologia 61: 11-17.

Helgen, K. M. and Wilson, D. E. 2003. Taxonomic status and conservation relevance of the raccoons (*Procyon* spp.) of the West Indies. Journal of Zoology 259: 69-76.

Hendry, A. P. and Kinnison, M. T. 1999. The pace of modern life: Measuring rates of contemporary microevolution. Evolution 53: 1637-1653.

Hirakawa, H., kuwahata T., Shibata Y. and Yamada, E. 1992. Insular variation of the Japanese hare (*Lepus-brachyurus*) on the Oki islands, Japan. Journal of Mammalogy, 73: 672-679.

Hoekstra, H. and Fagan, W. 1998. Body size, dispersal ability and compositional disharmony: the carnivore-dominated fauna of the Kuril Islands. Diversity & Distributions 4: 135-149.

Hooijer, D. A. 1949. Mammalian evolution in the Quaternary of Southern and Eastern Asia. Evolution 3: 125-128.

Hooijer, D. A. 1950. The study of subspecific advances in the Quaternary. Evolution 4: 360-361.

Hutchinson, G. E. and MacArthur, R. H. 1959. A theoretical ecological model of size distributions among species of animals. American Naturalist 93: 117-125.

Hutchinson, G. E. 1959. Homage to Santa Rosalia, or why are there so many kinds of animals? American Naturalist 93: 145-159.

Jablonski, D. 1996. Body size and macroevolution. Pp. 256-288 in D. Jablonski and J. H. Lipps, editors. Evolutionary paleobiology. The University of Chicago Press, Chicago.

Jablonski, D. 1997, Body-size evolution in Cretaceous molluscs and the status of Cope's rule. Nature 385: 250-252.

James, F. C. 1970. Geographic size variation in birds and its relationship to climate. Ecology 51: 365-390.

Jianu, C. M., and Weishampel, D. B. 1999. The smallest of the largest: a new look at possible dwarfing in sauropod dinosaurs. Geologie en Mijnbouw 78: 335-343.

Johnson, D. D. P. and Macdonald, D. W. 2001. Why are group-living badgers (*Meles meles*) sexually dimorphic? Journal of Zoology 255: 199-204.

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

Johnson, D. L. 1980. Problems in the land vertebrates zoogeography of certain islands and the swimming powers of elephants. Journal of Biogeography 7: 383-389.

Johnson, D. R. 1991. Measurement of weasel body size. Canadian Journal of Zoology 69: 2277-2279.

Johnson, W. E., Fuller, T. K. and Franklin, W. L. 1996. Sympatry in Canids: A review and assessment. pages 189-218 in J. L. Gittleman. editor. Carnivore behavior, Ecology, and evolution. vol. 2. Cornell University Press, Ithaca.

Johnston, R. F. and Selander, R. K. 1973. Evolution in the house sparrow. III. Variation in size and sexual dimorphism in Europe and North and South America. American Naturalist 107: 373-390.

Jones, M. 1997. Character displacement in Australian dasyurid carnivores: size relationships and prey size patterns. Ecology 78: 2569-2587.

Kelt, D. E. and Van Vuren, D. 1999. Energetic constraints and the relationship between body size and home range area in mammals. Ecology 80: 337-340.

Kelt, D. E. and Van Vuren, D. 2001. The ecology and macroecology of mammalian home range area. American Naturalist 157: 637-645.

Kiltie, R. A. 1988. Interspecific size regularities in tropical felid assemblages. Oecologia 76: 97-105.

King, C. M. 1991. Body size-prey size relationships in European stoats Mustela erminea: a test case. Holarctic Ecology 14: 173-185.

Kinnison, M. T. and Hendry, A. P. 2001. The pace of modern life II: From rates of contemporary microevolution to pattern and process. Genetica 112-113: 145-164.

Kitchen, A. M., Gese, E. M., and Schauster, E. R. 1999. Resource partitioning between coyotes and swift foxes: space, time, and diet. Canadian Journal of Zoology 77: 1645-1656.

Kitchener, D. J., Schmitt, L. H. and Maharadatunkamsi. 1994. Morphological variation in *Suncus murinus* (Soricidae: Crocidurinae) from Java, Lesser Sunda islands, Maluku and Sulawesi, Indonesia. Mammalia 58: 433-451.

Klein, R. G. 1986. Carnivore size and Quaternary climatic change in Southern Africa. Quaternary Research 26: 153-170.

Klein, D. R. 1995. The introduction, increase, and demise of wolves on Coronation Island, Alaska. Pages 275-280 in L. N. Carbyn, S. H. Fritts and D. R. Seip. Editors. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, University of Alberta, Edmonton.

Knouft, J. H. and Page, L. M. 2003. The evolution of body size in extant groups of North American freshwater fishes: speciation, size distributions and Cope's rule. American Naturalist 161: 413-421.

Koch, P. L. 1986. Clinal geographic variation in mammals: implications for the study of chronoclines. Paleobiology 12: 269-281.

Korpimäki, E. and Nordahl, K. 1989. Avian predation on mustelids in Europe 1: occurrence and effects on body size variation and life traits. Oikos 55: 205-215.

Kozlowski, J. 1996. Energetic definition of fitness? Yes, but not that one. American Naturalist 147: 1087-1091.

Kruuk, H. 2002. Hunter and Hunted. Relationships between carnivores and people. Cambridge University Press, Cambridge.

Kurten, B. 1953. On the variation and population dynamics of fossil and recent mammal populations. Acta Zoologica Fennica 76: 1-122.

Kurtén, B. 1959. Rates of evolution in fossil mammals. Cold Springs Harbor Symposium on Quantitative Biology 24: 205–215.

Kurten, B. 1973. Geographic variation in size in the Puma (*Felis concolor*). Commentationes Biologicae 63: 1-8.

Lande, R. 1976. Natural selection and random genetic drift in phenotypic evolution. Evolution 30: 314-334.

Lawlor, T. E. 1982. The evolution of body size in mammals: evidence from insular populations in Mexico. American Naturalist 119: 54-72.

Lawton, J. H. 1996. Patterns in ecology. Oikos. 75: 145-147.

Lawton, J. H. 1999.Are there general laws in ecology? Oikos 84: 177-192.

Lister, A. M. 1989. Rapid dwarfing of red deer on Jersey in the last interglacial. Nature 342: 539-542.

Lister, A. M. 1996. Dwarfing in island elephants and deer: processes in relation to time and isolation. Symposium of the Zoological Society of London 69: 277-292.

Lomolino, M. V. 1983. Island biogeography, immigrant selection and body size of mammals on islands. PhD Dissertation. University of New York.

Lomolino, M. V. 1985. Body size of mammals on islands: The island rule reexamined. American Naturalist 125: 310-316.

Lomolino, M. V. 1993.Winter filtering, immigrant selection and species composition of insular mammals of Lake Huron. Ecography 16: 24-30.

Long, J. L. 2003. Introduced mammals of the world. CSIRO Publishing, Melbourne, Australia.

Losos, J. B. and Glor, R. E. 2003. Phylogenetic comparative methods and the geography of speciation. Trends in Ecology and Evolution 18: 220-227.

Loveridge, A. J. and Macdonald, D. W. 2002. Habitat ecology of two sympatric species of jackals in Zimbabwe. Journal of Mammalogy 83: 599-607.

Lüps, P. and Roper, T. J. 1988. Tooth size in the European badger (*Meles meles*) with special reference to sexual dimorphism, diet and intraspecific aggression. Acta Theriologica 33: 21-33.

MacArthur, R. H., Diamond, J. M. and Karr, J. R. 1972. Density compensation in island faunas. Ecology 53: 330-342.

MacArthur, R. H. and Wilson, E. O. 1967. The theory of Island Biogeography. Princeton University Press, New Jersey.

Macdonald, D. W. 1992. The velvet claw. A Natural History of the Carnivores. BBC Books, London.

Macdonald, D. W. and Sillero-Zubiri, C. 2004. Dramatis personae. Pages 3-36 in Macdonald & Sillero-Zubiri (editors). The biology and conservation of wild canids. Oxford University Press, Oxford.

Macmillan world atlas 1996. John Wiley & Sons. Macmillan, New York.

Maiorana, V. C. 1990. Evolutionary strategies and body size in a guild of mammals. Pages 69-102 In J. Damuth and B. J. MacFadden. Editors. Body size in mammalian paleobiology. Cambridge University Press, Cambridge.

Major, J. T. and Sherburne, J. A. 1987. Interspecific relationships of coyotes, bobcats, and red foxes in western Maine. Journal of Wildlife Management 51: 606-616.

Malmquist, M. G. 1985. Character displacement and biogeography of the pygmy shrew in northern Europe. Ecology 66: 372–377.

Marquet, P. A. and Taper, M. L. 1998. On size and area: Patterns of mammalian body size extremes across landmasses. Evolutionary Ecology 12: 127-139.

Masseti, M. 2001. Did endemic dwarf elephants survive on Mediterranean islands up to protohistorical times? Pages 402-406 in G. Cavarretta, P. Gioia, M. Mussi and M. R. Palombo. Editors. The World of Elephants - Proceedings of the 1st International Congress, Rome.

Mayr, E. 1942. Systematics and the origin of species. Columbia University Press, New York.

Mayr, E. 1956. Geographical character gradients and climatic adaptation. Evolution 10: 105-108.

Mayr, E. 1963. Animal species and evolution. Belknap Press, Cambridge. Mass.

Mayr, E. 1967. The challenge of island faunas. Australian Natural History 15: 369-374.

McDonald, R. A. 2002. Resource partitioning among British and Irish mustelids. Journal of Animal Ecology 71: 185-200.

Mckinney, M. L. 1990. Trends in body size Evolution. pages 75-118 In K. J. McNamara, editor. Evolutionary Trends. University of Arizona Press, Tucson.

McNab, B. K. 1963. Bioenergetics and the determination of home range size. American Naturalist 97: 133–140.

McNab, B. K. 1994. Resource use and the survival of land and freshwater vertebrates on islands. American Naturalist 144: 643-660.

McNab, B. K. 2003. Standard energetics of phyllostomid bats: the inadequacies of phylogenetic-contrast analyses. Comparative Biochemistry and Physiology 135: 357-368.

Meiri, S. and Dayan, T. 2003. On the validity of Bergmann's rule. Journal of Biogeography 30: 331-351.

Meiri, S., Dayan, T., and Simberloff, D. 2003. Relationships among indices of body size. Israel Journal of Zoology 49: 84.

Meiri, S., Dayan, T., and Simberloff, D. 2004a. Body size of insular carnivores: island area has little effect. *Evolution* (in review).

Meiri, S., Dayan, T., and Simberloff, D. 2004b. Body size of insular carnivores: Little support for the island rule. American Naturalist 163: 469-479.

Meiri, S., Dayan, T., and Simberloff, D. 2004c. Carnivores, biases and Bergmann's rule. Biological Journal of the Linnean Society 81: 579-588.

Meiri, S., Dayan, T., and Simberloff, D. 2005a. Variability and correlations in carnivore crania and dentition. *Functional Ecology* (in press).

Meiri, S., Simberloff, D. and Dayan, T. 2005b. Biogeographic patterns in the Western Palearctic: the fasting-endurance hypothesis and the status of Murphy's law. *Journal of Biogeography* (in press).

Meiri, S., Simberloff, D. and Dayan, T. 2005c. Insular carnivore biogeography: Island area and mammalian optimal body size. *American Naturalist*. (in press).

Meiri, S., Simberloff, D. and Dayan, T. 2005d. Variability and sexual size dimorphism in carnivores: Testing the niche variation hypothesis. *Ecology* (in press).

Meiri, S. and Yom-Tov, Y. 2004. Ontogeny of large birds: Migrants do it faster. *Condor* 106: 540-548.

Melton, R. H. 1982. Body size and island *Peromyscus*: A pattern and a hypothesis. Evolutionary Theory 6: 113-126.

Merriam, C. H. 1902. Two new bears from the Alaska Peninsula. Proceedings of the Biological Society of Washington 15: 77-79.

Merriam, C. H. 1910. *Ursus sheldoni*. A new bear from Montague Island. Proceedings of the Biological Society of Washington 23: 127-130.

Merriam, C. H. 1916. Nineteen apparently new grizzly and brown bears from Western America. Proceedings of the biological Society of Washington 29: 133-154.

Michaux, J. R., De Belloco, J. G., Sara, M. and Morand, S. 2002. Body size in insular rodent populations: a role for predators? Global Ecology and Biogeography 11: 427-436.

Miller, G. S. 1912. Catalogue of the mammals of Western Europe (Europe exclusive of Russia) in the collection of the British Museum. British Museum, London.

Millien, V. 2004. Relative effects of climate change, isolation and competition on body-size evolution in the Japanese field mouse, Apodemus argenteus. Journal of Biogeography 31: 1267-1276.

Millien, V. and Damuth, J. 2004. Climate change and size evolution in an island rodent species: new perspectives on the island rule. Evolution 58: 1353-1360.

Morwood, M. J., O'Sullivan, P. B., Aziz, F. and Raza, A. 1998. Fission-track ages of stone tools and fossils on the east Indonesian island of Flores. Nature 392: 173-176.

Mulder, J. L. 1990. The stoat *Mustela erminea* in the Dutch Dune Region, its local extinction, and a possible cause: the arrival of the fox *Vulpes vulpes*. Lutra 33: 1–21.

Murphy, E. L. 1985. Bergmann's rule, seasonality and geographic variation in body size of house sparrows. Evolution 39: 1327- 1334.

Nowak, R. M. 1991. Walker's "Mammals of the world" 5th edition. Johns Hopkins University Press, Baltimore.

Nowak, R. M. 1999. Walker's "Mammals of the world" 6th edition. Johns Hopkins University Press, Baltimore.

Palkovacs, E. P. 2003. Explaining adaptive shifts in body size on islands: a life history approach. Oikos 103: 37-44.

Palmeirim, J. M. 1998. Analysis of skull measurements and measurers: can we use data obtained by different observers? Journal of Mammalogy 79: 1021-1028.

Palomares, F. and Caro, T. M. 1999. Interspecific killing among mammalian carnivores. American Naturalist 153: 492-508.

Palombo, M. R. 2001. Endemic elephants of the Mediterranean Islands: knowledge, problems and perspectives. Pages 486-491 in G. Cavarretta, P. Gioia, M. Mussi and M. R. Palombo, editors. The World of Elephants - Proceedings of the 1st International Congress, Rome.

Perrin, N. 1998. On body size, energy and fitness. Functional Ecology 12: 500-502.

Peters, H. R. 1983. The ecological implications of body size. Cambridge University Press, New York.

Poper, K. 1963. Conjectures and Refutations: The Growth of Scientific Knowledge. Routledge & Kegan, London.

Popowics, T. E. 2003. Postcanine dental form in the mustelidae and viverridae (Carnivora: Mammalia). Journal of Morphology 256: 322-341.

Powell, R. A. 1973. A model for raptor predation on weasels. Journal of Mammalogy 54: 259-263.

Powell, R. A. 1982. Evolution of black-tipped tails in weasels: predator confusion. American Naturalist 119: 126-131.

Pregill, G. 1986. Body size of insular lizards: a pattern of Holocene Dwarfism. Evolution 40: 997-1008.

Price, T. 1997. Correlated evolution and independent contrasts. Philosophical transactions of the Royal Society of London B. 352: 519-529.

Quammen, D. 1997. The Song of the Dodo: Island Biogeography in an Age of Extinctions. Touchstone Books, New-York.

Quin, D.G., Smith, A.P. and Norton, T.W. 1996. Eco-geographic variation in size and sexual dimorphism in sugar gliders and squirrel gliders (Marsupialia: Petauridae). Australian Journal of Zoology 44: 19-45.

Radinsky, L. B. 1981a. Evolution of skull shape in carnivores 1. Representative modern carnivores. Biological Journal of the Linnean Society 15: 369-388.

Radinsky, L. B. 1981b. Evolution of skull shape in carnivores 2. Additional modern carnivores. Biological Journal of the Linnean Society 16: 337-355.

Raia, P., Barbera, C. and Conte, M. 2003. The fast life of a dwarfed giant. Evolutionary Ecology 17: 293-312.

Ralls, K. and Harvey, P. H. 1985. Geographic variation in size and sexual dimorphism of North American weasels. Biological Journal of the Linnean Society 25: 119-167.

Renaud, S., and Michaux, J. R. 2003. Adaptive latitudinal trends in the mandible shape of Apodemus wood mice. Journal of Biogeography 30: 1617-1628.

Rensch, B. 1924. Das Deperetsche gesetz und die regel von der kleinheit der insel formen als spezialfall des Bergmannsche gesetzes und ein erklarungsversuch derselben: eine hypothese. Z. Ind. Abst.-Vererb.-Lehre, 35.

Rensch, B. 1938. Some problems of geographical variation and species formation. Proceedings of the Linnean Society of London 150:275-285.

Reumer, J. W. F. and de Vos, J. 1999. Elephants have a snorkel! : papers in honor of Paul Y. Sondaar. Deinsea, Rotterdam.

Reznik, D. N., Shaw, F. H., Rodd, H., and Shaw, R. G. 1997. Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). Science 275: 1934-1937.

Rheindt, F. E., Grafe, T. U. and Abouheif, E. 2004. Rapidly evolving traits and the comparative method: how important is testing for phylogenetic signal? Evolutionary Ecology Research 6: 377-396.

Ricklefs, R. E. and Starck, J. M. 1996. Applications of phylogenetically independent contrasts: a mixed progress report. Oikos 77: 167-172.

Rising, J. D. and Somers, K. M. 1989. The measurement of overall body size in birds. Auk 106: 666-674.

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

Roemer, G. W., C. J. Donlan, and F. Courchamp. 2002. Golden eagles, feral pigs, and insular carnivores: How exotic species turn native predators into prey. Proceedings of the National Academy of Sciences of the United States of America 99: 791-796.

Roth, V. L. 1992. Inferences from allometry and fossils: dwarfing of elephants on islands. Pages 259-288 in D. Futuyma and J. Antonovics, editors. Oxford Surveys in Evolutionary Biology, vol. 8. Oxford University Press, Oxford.

Rothstein, S. I. 1973. Niche-variation model - Is it valid? American Naturalist 107: 598-620.

Ruse, M. 1993. Evolution and progress. Trends in Ecology and Evolution 8: 55-59.

Schmidt, N. M. and Jensen, P. M. 2003. Changes in Mammalian Body Length over 175 Years—Adaptations to a Fragmented Landscape? Conservation Ecology 7: 6.

Schmidt-Nielsen, K. 1984. Scaling. Why is animal size so important? Cambridge University Press, Cambridge.

Sheets, H. D. and Mitchell, C. E. 2001. Uncorrelated change produces the apparent dependence of evolutionary rate on interval. Paleobiology 27: 429-445.

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

Silva, M. 1998. Allometric scaling of body length: elastic or geometric similarity in mammalian design. Journal of Mammalogy 79: 20-32.

Silva, M. and Downing, J. A. 1995. CRC handbook of Mammalian body masses. CRC Press. New York.

Simberloff, D. 1997. Review of 'Macroecology'. Journal of Wildlife Management 61: 570-571.

Simberloff, D. 2004. Community ecology: is it time to move on? American Naturalist 163: 787-799.

Simberloff, D. and Dayan, T. 1991. The guild concept and the structure of ecological communities. Annual Review of Ecology and Systematics 22: 115-143.

Simberloff, D., Dayan, T., Jones, C. and Ogura, G. 2000. Character displacement and release in the small Indian mongoose, *Herpestes javanicus*. Ecology 81: 2086-2099.

Simmons, A. H. 1988. Extinct pygmy hippopotamus and early man in Cyprus. Nature 333: 554-557.

Simms, D. A. 1979. North American weasels: resource utilization and distribution. Canadian Journal of Zoology 57: 504-520.

Simpson, G. G. 1949. Tempo and mode in evolution. Columbia University Press, New York.

Smith, R. J. 1994. Degrees of freedom in interspecific allometry: an adjustment for the effects of phylogenetic constraint. American Journal of Physical Anthropology 93: 95-107.

Smith, R. J. 2002. Estimation of body mass in paleontology. Journal of Human Evolution 43: 271-287.

Smith, R. J. and J. M. Cheverud. 2002. Scaling of sexual dimorphism in body mass: a phylogenetic analysis of Rensch's Rule in primates. International Journal of Primatology 23:1095-1135.

Sondaar, P. Y. 1977. Insularity and its effects on mammal evolution. pages 671-707 in M. K. Hecht, P. C. Goody and B. M. Hecht, editors. Major patterns of vertebrate evolution. Plenum Press, New York.

Sondaar, P. Y. 1991. Island mammals of the past. Science Progress 75: 249-264.

Stanley, S. M. 1973. An explanation for Cope's rule. Evolution 27: 1-26.

Stanley, S. M. 1985. Rates of evolution. Paleobiology 11: 13-26.

Thompson, D. W. 1942. On growth and form. Cambridge University Press, Cambridge.

Thurber, J. M., Peterson, R. O., Woolington, J. D. and Vucetich, J. A. 1992. Coyote coexistence with wolves on the Kenai Peninsula, Alaska. Canadian Journal of Zoology 70: 2494-2498.

USGS National Mapping Information. http://geonames.usgs.gov/pls/gnis/web_query.gnis_web_query_form

Van den Bergh, G. D., de Vos, J., Aziz, F., and Morwood, M. J. 2001. Elephantoidea in the Indonesian region: new *Stegodon* findings from Flores. pages 623-627 in G. Cavarretta, P. Gioia, M. Mussi and M. R. Palombo, editors. The World of Elephants - Proceedings of the 1st International Congress, Rome.

Van Valen, L. M. 1965. Morphological variation and the width of the ecological niche. American Naturalist 99: 377-390.

Van Valen, L. 1970. Late Pleistocene extinctions. Pages 469-485 in the Proceedings of the North American Paleontological Convention, Allen Press, Lawrence.

Van Valen, L. M. 1973. Pattern and the balance of nature. Evolutionary theory 1: 31-49.

Van Valkenburgh, B. 2001. The dog-eat-dog world of carnivores. A review of past and present carnivore community dynamics. pages 101-121 in C. B. Stanford and H. T. Bunn, editors. Meat eating and human evolution. Oxford University Press, Oxford.

Van Valkenburgh, B. and Wayne, R. K. 1994. Shape divergence associated with size convergence in sympatric East African jackals. Ecology 75: 1567-1581.

Vartanyan, S. L., Garutt, V. E. and Sher, A. V. 1993. Holocene Dwarf mammoths from Wrangel-Island in the Siberian arctic. Nature 362: 337-340.

Vezina, A. F. 1985. Empirical relationships between predator and prey size among terrestrial vertebrate predators. Oecologia 67: 555-565.

Von den Driesch, A. 1976. A guide to the measurement of animal bones from archaeological sites. Peabody Museum Bulletin I. Cambridge.

Wallace, A. R. 1868. The Malay archipelago. Macmillan & Co., London.

Wallace, A. R. 1880. Island life. Macmillan & Co., London.

Wassersug, R. J., Yang, H., Sepkosky J. J. Jr. and Raup, D. M. 1979. The evolution of body size on islands: A computer simulation. American Naturalist 114: 287-295.

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

Wells, D. R. 1989. Notes on the distribution and taxonomy of peninsular Malaysian mongooses (*Herpestes*). Natural History Bulletin of the Siam Society 37: 87-97.

Westoby, M. Leishman, M. and Lord, J. 1995a. On misinterpreting 'phylogenetic correction. Journal of Ecology 83: 531-534.

Westoby, M. Leishman, M. and Lord, J. 1995b. Further remarks on phylogenetic correction. Journal of Ecology 83: 727-734.

Whipple, D. 2003. Alas, poor warrah…New Scientist 180 (2426-8): 80-81.

Williams, G. C. 1992. Natural selection: domains, levels, and challenges. Oxford University Press, New York.

Worldwide Directory of Cities and Towns. http://www.fallingrain.com/world/

Wozencraft, C. W. 1993. Order Carnivora. Pages 279-348 in D. E. Wilson and D. M. Reeder, editors. Mammal species of the world. 2nd edition. Smithsonian institution Press, Washington.

Yezerinac, S. M., Lougheed, S. C. and Handford, P. 1992. Measurement error and morphometric studies - statistical power and observer experience. Systematic Biology 41: 471-482.

Yoder, A. D., Burns, M. M., Zehr, S., Delefosse, T., Veron, G., Goodman, S. M. and Flynn, J. J. 2003. Single origin of Malagasy Carnivora from an African ancestor. Nature 421: 734-737.

Yom-Tov, Y. 2001. Global warming and body mass decline in Israeli passerine birds. Proceedings of the Royal Society of London B. Biological Sciences 268: 947-952.

Yom-Tov, Y. 2003. Body sizes of carnivores commensal with humans have increased over the past 50 years. Functional Ecology 17: 323-327.

Yom-Tov, Y., Benjamini, Y. and Kark, S. 2002. Global warming, Bergmann's rule and body mass – are they related? The chukar partridge (*Alectoris chukar*) case. Journal of Zoology 257: 449-455.

Yom-Tov, Y., Green, W. O. and Coleman, J. D. 1986. Morphological trends in the common brushtail possum, *Trichosurus vulpecula* in New Zealand. Journal of Zoology 208: 583-593.

Yom-Tov, Y. and Yom-Tov, S. 2004. Climatic change and body size in two species of Japanese rodents. Biological Journal of the Linnean Society 82: 263–267.

Yom-Tov, Y., Yom-Tov, S. and Baagøe, H. 2003. Increase of skull size in the red fox (*Vulpes vulpes*) and Eurasian badger (*Meles meles*) in Denmark during the twentieth century: an effect of improved diet? Evolutionary Ecology Research 5: 1037-1048.

Yom-Tov, Y., Yom-Tov, S. Moller, H. 1999. Competition, coexistence and adaptation amongst rodent invaders to Pacific and New Zealand islands. Journal of Biogeography 26: 947-958.

Zar, J. H. 1998. Biostatistical analysis. 4th edition. Prentice hall, New Jersey.

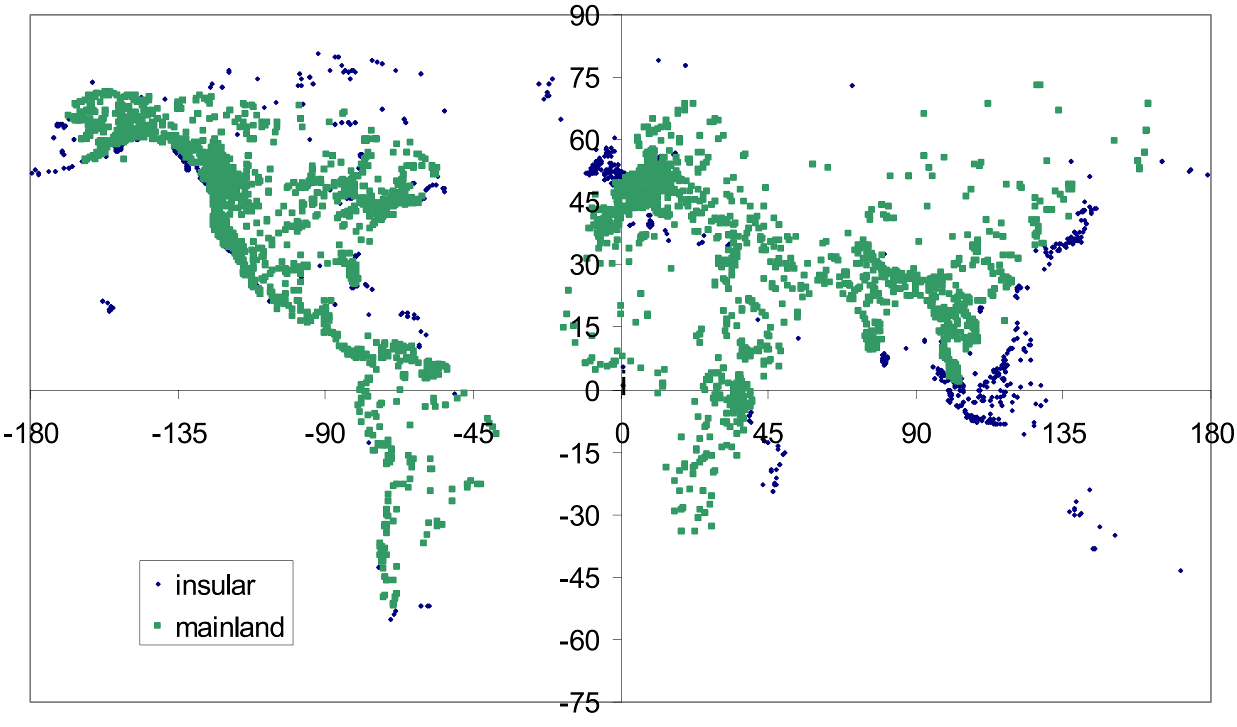
Zeveloff, S. I. 2003. A review of the taxonomic and conservation statuses of the island raccoons. Small Carnivore Conservation 29: 10-12.

Appendix 1 – Museums in which specimens were measured and number of specimens measured by each researcher.

Museum	Arieh Landsman	Anna Demarinis	Tamar Dayan	Shai Meiri	Daniel Simberloff
American Museum of Natural History			219	1375	175
Ann Arbor Museum of Zoology			375		
Archeozoological Museum London			31		
Bell Museum of Natural History			184		
British Museum (Natural History)			1270	1350	138
Canadian Museum of Nature				456	
Carnegie Museum of Natural History				460	
Department of Zoology, University College, Cork					13
Field Museum, Chicago				744	
Harrison Zoological Museum			46		
Institut Royal des Sciences Naturelles de Belgique				792	
Laboratoire d'Anatomie Comparee				21	
Musee National d'Histoire Naturelle, Paris				218	7
Museo Civico di Storia Naturale "Giacomo Doria," Genoa					116
Museo Nacional de Ciencias Naturales, Madrid	75				
Museu de Zoologia, Barcelona	11				
Muséum d'Histoire Naturelle de la Ville de Genève					41
Museum für Naturkunde, Humboldt Universität zu Berlin				962	
Museum of Comparative Zoology, Harvard University			322	523	
Museum of Vertebrate Zoology, University of California Berkeley			504	908	
National Museum of Natural History "Naturalis", Leiden				573	
National Museum of Natural History at Tel-Aviv University				329	
National Museum of Natural History, Smithsonian Institution			721	2909	41
National Science Museum, Tokyo				315	
National Wildlife Institute, Bologna		22			28
Natural History Collections, the Hebrew University, Jerusalem				39	
Natural History Museum of Los Angeles County			74		
New-Walk museum, Leicester				132	
Primate Research Institute, Kyoto University				229	
Royal British Columbia Museum				874	
Royal Museum, Edinburgh			101		
Royal Ontario Museum				423	
San Diego Natural History Museum			87		
Sebastian Payne Collection			48		
Staatliche Naturhistorische Sammlungen, Dresden				366	
Swedish Museum of Natural History					7
The National Museum of Ireland					155
Ulster Museum				308	5
University College, Dublin					42
University of Alaska, Fairbanks, Museum of Natural History			109	999	
University of Amsterdam, Zoological museum				202	
University of Kansas Museum of Natural History				514	
Zoological Museum, University of Copenhagen					500
Raffles Museum of Biodiversity Research				244	
Zoologische Staatsamlung, München				101	
Zoology Museum of Cambridge University				23	

Appendix 2

Localities of 17799 specimens measured, for which I found latitude and longitude data.



Appendix 3

Main food types, and correlation coefficients between the upper and lower carnassials in carnivore species analyzed in manuscript 1 – Variability and correlations in carnivore crania and dentition.

Family	Species	Main Food	r	n
Mustelidae	*Aonyx cinerea*[54]	Crabs	0.7	99
Mustelidae	*Lontra felina*[31]	Crabs	0.878	12
Viverridae	*Cynogale bennettii*[42]	Crabs	0.731	16
Mustelidae	*Lontra canadensis*[33]	Fish	0.866	223
Mustelidae	*Lontra longicaudis*[45]	Fish	0.895	27
Mustelidae	*Lutra lutra*[10]	Fish	0.662	217
Mustelidae	*Lutra perspicillata*[54]	Fish	0.676	31
Mustelidae	*Lutra sumatrana*[54]	Fish	0.847	16
Canidae	*Urocyon littoralis*[40]	Fruit	0.532	70
Procyonidae	*Bassaricyon gabbii*[28]	Fruit	0.92	12
Procyonidae	*Potos flavus*[38]	Fruit	0.58	41
Procyonidae	*Procyon cancrivorus*[11]	Fruit	0.552	30
Procyonidae	*Procyon lotor*[36]	Fruit	0.775	282
Procyonidae	*Procyon maynardi**	Fruit	0.525	13
Ursidae	*Ursus americanus*[47]	Fruit	0.637	32
Ursidae	*Ursus arctos*[18]	Fruit	0.722	70
Ursidae	*Ursus thibetanus*[17]	Fruit	0.84	14
Viverridae	*Arctictis binturong*[42]	Fruit	0.801	15
Viverridae	*Arctogalidia trivirgata*[38]	Fruit	0.592	86
Viverridae	*Paguma larvata*[26]	Fruit	0.843	66
Viverridae	*Paradoxurus hermaphroditus*[25]	Fruit	0.811	318
Canidae	*Fennecus zerda*[32]	Invertebrates	0.756	10
Herpestidae	*Herpestes urva*[9]	Invertebrates	0.771	40
Herpestidae	*Ichneumia albicauda*[42]	Invertebrates	0.613	18
Mustelidae	*Arctonyx collaris*[42]	Invertebrates	0.918	30
Mustelidae	*Martes melampus*[50]	Invertebrates	0.88	144
Mustelidae	*Meles meles*[15]	Invertebrates	0.763	466
Mustelidae	*Melogale everetti*[19]	Invertebrates	0.604	21
Mustelidae	*Melogale moschata*[63]	Invertebrates	0.712	95
Mustelidae	*Mephitis mephitis*[60]	Invertebrates	0.613	48
Mustelidae	*Mydaus javanensis*[21]	Invertebrates	0.297	30
Mustelidae	*Spilogale gracilis*[58]	Invertebrates	0.62	120
Mustelidae	*Spilogale putorius*[29]	Invertebrates	0.678	49
Procyonidae	*Nasua narica*[38]	Invertebrates	0.439	40
Viverridae	*Civettictis civetta*[46]	Invertebrates	0.754	18
Viverridae	*Fossa fossana*[42]	Invertebrates	0.843	16
Viverridae	*Genetta maculata*[1]	Invertebrates	0.748	30
Viverridae	*Hemigalus derbyanus*[42]	Invertebrates	0.592	54
Viverridae	*Viverra tangalunga*[26]	Invertebrates	0.743	130
Viverridae	*Viverricula indica*[9]	Invertebrates	0.661	255
Canidae	*Alopex lagopus*[49]	Vertebrates	0.807	607
Canidae	*Canis aureus*[39]	Vertebrates	0.898	149
Canidae	*Canis latrans*[2]	Vertebrates	0.835	220
Canidae	*Canis lupus*[2]	Vertebrates	0.894	467

Family	Species	Main Food	r	n
Canidae	*Cuon alpinus*[65]	Vertebrates	0.824	59
Canidae	*Nyctereutes procyonoides*[27]	Vertebrates	0.663	157
Canidae	*Pseudalopex culpaeus*[51]	Vertebrates	0.864	37
Canidae	*Pseudalopex griseus*[24]	Vertebrates	0.892	70
Canidae	*Urocyon cinereoargenteus*[13]	Vertebrates	0.838	166
Canidae	*Vulpes macrotis*[62]	Vertebrates	0.806	18
Canidae	*Vulpes ruppelli*[39]	Vertebrates	0.906	35
Canidae	*Vulpes velox*[30]	Vertebrates	0.882	25
Canidae	*Vulpes vulpes*[42]	Vertebrates	0.877	987
Felidae	*Acinonyx jubatus*[42]	Vertebrates	0.902	11
Felidae	*Felis bengalensis*[16]	Vertebrates	0.803	208
Felidae	*Felis canadensis*[7]	Vertebrates	0.722	265
Felidae	*Felis caracal*[42]	Vertebrates	0.725	39
Felidae	*Felis chaus*[39]	Vertebrates	0.856	133
Felidae	*Felis concolor*[22]	Vertebrates	0.814	134
Felidae	*Felis lynx*[23]	Vertebrates	0.218	12
Felidae	*Felis marmorata*[42]	Vertebrates	0.766	17
Felidae	*Felis pardalis*[61]	Vertebrates	0.78	69
Felidae	*Felis pardina*[42]	Vertebrates	0.771	11
Felidae	*Felis planiceps*[56]	Vertebrates	0.507	38
Felidae	*Felis rufus*[7]	Vertebrates	0.822	101
Felidae	*Felis silvestris*[39]	Vertebrates	0.741	181
Felidae	*Felis temminckii*[42]	Vertebrates	0.841	18
Felidae	*Felis viverrina*[42]	Vertebrates	0.894	31
Felidae	*Felis wiedii*[61]	Vertebrates	0.855	30
Felidae	*Felis yagouaroundi*[12]	Vertebrates	0.779	17
Felidae	*Neofelis nebulosa*[12]	Vertebrates	0.907	24
Felidae	*Panthera leo*[14]	Vertebrates	0.896	27
Felidae	*Panthera onca*[43]	Vertebrates	0.859	11
Felidae	*Panthera pardus*[46]	Vertebrates	0.898	141
Felidae	*Panthera tigris*[42]	Vertebrates	0.895	100
Herpestidae	*Atilax paludinosus*[55]	Vertebrates	0.664	22
Herpestidae	*Cryptoprocta ferox*[42]	Vertebrates	0.64	10
Herpestidae	*Galerella sanguinea*[8]	Vertebrates	0.813	66
Herpestidae	*Galidia elegans*[42]	Vertebrates	0.748	25
Herpestidae	*Herpestes brachyurus*[26]	Vertebrates	0.784	42
Herpestidae	*Herpestes edwardsii*[52]	Vertebrates	0.684	132
Herpestidae	*Herpestes ichneumon*[39]	Vertebrates	0.757	77
Herpestidae	*Herpestes javanicus*[52]	Vertebrates	0.851	539
Herpestidae	*Herpestes smithii*[52]	Vertebrates	0.677	24
Herpestidae	*Herpestes vitticollis*[20]	Vertebrates	0.69	16
Hyaenidae	*Hyaena hyaena*[42]	Vertebrates	0.59	32
Mustelidae	*Eira barbara*[38]	Vertebrates	0.674	68
Mustelidae	*Gulo gulo*[3]	Vertebrates	0.899	169
Mustelidae	*Martes americana*[41]	Vertebrates	0.916	854
Mustelidae	*Martes flavigula*[26]	Vertebrates	0.9	111
Mustelidae	*Martes foina*[44]	Vertebrates	0.798	300
Mustelidae	*Martes martes*[37]	Vertebrates	0.829	214
Mustelidae	*Martes pennanti*[64]	Vertebrates	0.914	94
Mustelidae	*Martes Zibellina*[6]	Vertebrates	0.909	19

Family	Species	Main Food	r	n
Mustelidae	*Mellivora capensis*[4]	Vertebrates	0.89	36
Mustelidae	*Melogale personata*[35]	Vertebrates	0.767	38
Mustelidae	*Mustela erminea*[37]	Vertebrates	0.949	2696
Mustelidae	*Mustela frenata*[53]	Vertebrates	0.903	960
Mustelidae	*Mustela kathiah*[42]	Vertebrates	0.939	19
Mustelidae	*Mustela nigripes*[42]	Vertebrates	0.81	29
Mustelidae	*Mustela nivalis*[37]	Vertebrates	0.903	1203
Mustelidae	*Mustela nudipes*[26]	Vertebrates	0.766	37
Mustelidae	*Mustela putorius*[34]	Vertebrates	0.829	456
Mustelidae	*Mustela sibirica*[63]	Vertebrates	0.93	272
Mustelidae	*Mustela vison*[42]	Vertebrates	0.933	831
Mustelidae	*Vormela peregusna*[5]	Vertebrates	0.748	26
Procyonidae	*Bassariscus astutus*[48]	Vertebrates	0.864	65
Viverridae	*Genetta genetta*[59]	Vertebrates	0.654	50
Viverridae	*Genetta servalina*[46]	Vertebrates	0.949	12
Viverridae	*Prionodon linsang*[57]	Vertebrates	0.793	21
Viverridae	*Viverra zibetha*[26]	Vertebrates	0.845	58

r values are the correlation coefficients. n is the number of individuals measured. Sources for dietary data are: 1 - Angelici 2000; 2 - Arjo et al. 2002; 3 - Banci 1994; 4 - Begg et al. 2003; 5 - Ben David 1988; 6 - Buskirk et al. 1996; 7 - Buskirk et al. 2000; 8 - Cavallini and Nel 1995; 9 - Chuang and Lee 1997; 10 - Clavero et al. 2003; 11 - De Fatima et al. 1999; 12 - de Oliveira 1998; 13 - Fritzel and Haroldson 1982; 14 - Funston et al. 1998; 15 - Goszczynski et al. 2000; 16 - Grassman 2000; 17 - Hashimoto et al. 2003; 18 - Hilderbrand et al. 1999; 19 - http://www.badgers.org.uk/; 20 - Hussain 1999; 21 - Hwang and Lariviere 2003; 22 - Iriarte et al. 1990; 23 - Jobin et al. 2000; 24 - Johnson and Franklin 1994; 25 - Joshi et al. 1995; 26 - Kanchanasakha et al. 1998; 27 - Kauhala and Auniola 2001; 28 - Kays 2000; 29 - Kinlaw 1995; 30 - Kitchen et al. 1999; 31 - Laviviere 1998; 32 - Laviviere 2002; 33 - Laviviere and Walton 1998; 34 - Lode 2003; 35 - Long and Killingley 1983; 36 - Lotze and Anderson 1979; 37 - McDonald 2002; 38 - McNab 1995; 39 - Mendelssohn and Yom-Tov 1999; 40 - Moore and Collins 1995; 41 - Nagorsen et al. 1991; 42 - Nowak 1999; 43 - Nunez et al. 2000; 44 - Padial et al. 2002; 45 - Quadros and Monteiro-Filho 2001; 46 - Ray and Sunquist 2001; 47 - Rode and Robbins 2000; 48 - Rodriguez-Estrella et al. 2000; 49 - Roth 2002; 50 - Shusei et al. 2003; 51 - Silva et al. 2004; 52 - Simberloff et al. 2000; 53 - Simms 1979; 54 - Sivasothi and Nor 1994; 55 - Somers and Purves 1996; 56 - Sunquist and Sunquist 2002; 57 - Van Rompaey 1993; 58 - Verts et al. 2001; 59 - Virgos et al. 1999; 60 - Wade-Smith and Verts 1982; 61 - Wang 2002; 62 - White et al. 1996; 63 - Wu 1999; 64 - Zielinski et al. 1999; 65 - Karanth and Sunquist 2000.
* - dietary preferences of *Procyon maynardi* are based on those of *P. lotor*.

References

Angelici, F.M. 2000. Food habits and resource partitioning of carnivores (Herpestidae, Viverridae) in the rainforests of southeastern Nigeria: Preliminary results. Revue D Eologie la Terre et la Vie 55: 67-76.

Arjo, W.M., Pletscher, D.H. and Ream, R.R. 2002. Dietary overlap between wolves and coyotes in northwestern Montana. Journal of Mammalogy 83: 754-766.

Banci, V. 1994. Wolverine. Pages 99-127. in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, L.J. Lyon, and W.J. Zielinski, editors. The Scientific Basis for Conserving Forest Carnivores American Marten, Fisher, Lynx, and Wolverine in the Western United States. USDA Forest Service General Technical Report RM-254.

Begg, C.M., Begg. K.S., Du Toit, J.T. and Mills, M.G.L. 2003. Sexual and seasonal variation in

the diet and foraging behaviour of a sexually dimorphic carnivore, the honey badger (*Mellivora capensis*). Journal of Zoology 260: 301-316.
Ben David, M. 1988. The biology and ecology of the marbled polecat (*Vormela peregusna syriaca*) in Israel. MSc Thesis, Department of Zoology, Tel Aviv University (In Hebrew).
Buskirk, S. W., L. F. Ruggiero, and C. J. Krebs. 2000. Fragmentation and interspecific competition: implications for lynx conservation. Pages 83-100 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires, editors. Ecology and conservation of lynx in the United States. University Press of Colorado, Boulder, CO.
Buskirk, S.W., Ma, Y., Xu, L., and Lang, Z. 1996. Diets of, and prey selection by, sables (*Martes zibellina*) in northern China. Journal of Mammalogy 77: 725-730.
Butler, P. M. 1946. The evolution of carnassial dentitions in the Mammalia. Proceedings of the Zoological Society of London. 116: 198–220.
Cavallini, P. and Nel, J.A.J. 1995, Comparative behavior and ecology of 2 sympatric mongoose species (*Cynictis penicillata* and *Galerella pulverulenta*). South African Journal of Zoology 30: 46-49.
Chuang, S.H. and Lee, L.L. 1997. Food habits of three carnivore species (*Viverricula indica*, *Herpestes urva*, and *Melogale moschata*) in Fushan Forest, northern Taiwan 243: 71-79.
Clavero, M., J. Prenda and M. Delibes. (2003). Trophic diversity of the otter (*Lutra lutra* L.) in temperate and Mediterranean habitats. Journal of Biogeography 30: 761-769.
de Fatima, M., Dos Santos, M., and Hartz, S.M. 1999. The food habits of *Procyon cancrivorus* (Carnivora, Procyonidae) in the Lami biological reserve, Porto Alegre, southern Brazil. Mammalia 63: 525-530.
de Oliveira, T.G. 1998. *Herpailurus yagouaroundi*. Mammalian Species 578: 1-6.
Fritzel, E.K. and Haroldson, K.J. 1982. *Urocyon cinereoargenteus*. Mammalian Species 189: 1-8.
Funston, P.J. Mills, M. Biggs, H. Richardson, P.1998. Hunting by male lions: ecological influences and socioecological implications. Animal Behaviour 56: 1333-1345.
Gingerich, P.D. and Schoeninger, M.J. 1979. Patterns of tooth variability in the dentition of primates. American Journal of Physical Anthropology 51: 457-466.
Goszczynski, J., Jedrzejewska, B. and Jedrzejewski, W. 2000. Diet composition of badgers (*Meles meles*) in a pristine forest and rural habitats of Poland compared to other European populations. Journal of Zoology 250: 495-505.
Grassman, L.I. 2000. Movements and diet of the leopard cat *Prionailurus bengalensis* in a seasonal evergreen forest in south-central Thailand. Acta Theriologica 45: 421-426.
Hashimoto, Y., Kaji, M., Sawada, H., Takatsuki, S. 2003. Five-year study on the autumn food habits of the Asiatic black bear in relation to nut production. Ecological Research 18: 485-492.
Hilderbrand, G.V., Schwartz, C.C., Robbins, C.T., Jacoby, M.E., Hanley, T.A., Arthur, S.M. and Servheen, C. 1999. The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. Canadian Journal of Zoology 77: 132-138.
Hussain, S.A. (editor) 1999. Mustelids, Viverrids and Herpestids of India: Species Profile and Conservation Status. ENVIS Bulletin: Wildlife and Protected Areas Volume 2.
Hwang, Y.T. and Lariviere, S. 2003. *Mydaus javanensis*. Mammalian Species 723: 1-3.
Iriarte, J.A., Franklin, W.L., Johnson, W.E. & Redford, K.H. 1990. Biogeographic variation of food habits and body size of the American puma. Oecologia 85: 185-190.
Jobin, A., Molinari, P., and Breitenmoser, U. 2000.Prey spectrum, prey preference and consumption rates of Eurasian lynx in the Swiss Jura Mountains. Acta Theriologica 45: 243-252 .
Johnson, W. E., and W. L. Franklin. 1994, Role of body size in the diets of sympatric gray and culpeo foxes: Journal of Mammalogy. 75 163–174.
Joshi, A.R., Smith, J.L.D., and Cuthbert, F.J. 1995. Influence of food distribution and predation

pressure on spacing behavior in palm civets. Journal of Mammalogy 76: 1205-1212.
Kanchanasakha, B., Simcharoen, and Tin-Than, U. 1998. Carnivores of mainland South East Asia. WWF, Bangkok
Karanth, U.K. and Sunquist, M.E. 2000. Behavioural correlates of predation by tiger (*Panthera tigris*), leopard (*Panthera pardus*) and dhole (*Cuon alpinus*) in Nagarahole, India. Journal Zoology 250: 255-265.
Kauhala, K. and Auniola, M. 2001. Diet of raccoon dogs in summer in the Finnish archipelago. Ecography 24: 151–156.
Kays, R.W. 2000. The behavior and ecology of olingos (Bassaricyon gabbii) and their competition with kinkajous (*Potos flavus*) in central Panama. Mammalia 64: 1-10.
Kinlaw, A. 1995. *Spilogale putorius*. Mammalian Species 511: 1-7.
Kitchen, A.M., Gese, E.M., and Schauster, E.R. 1999. Resource partitioning between coyotes and swift foxes: space, time, and diet. Canadian Journal of Zoology 77: 1645-1656.
Lariviere, S. 1998. *Lontra felina*. Mammalian Species 575: 1-5.
Lariviere, S. 2002. *Vulpes zerda*. Mammalian Species 714: 1-5.
Lariviere, S. and Walton, R. 1998. *Lontra canadensis*. Mammalian Species 587: 1-8.
Lode, T. 2003. Sexual dimorphism and trophic constraints: Prey selection in the European polecat (*Mustela putorius*). Ecoscience 10: 17-23.
Long, C., and C. Killingley. 1983. The Badgers Of The World. Springfield, Illinois: Charles C Thomas.
Lotze, J.H. and Anderson, S. 1979. *Procyon Lotor*. Mammalian Species 119: 1-8.
McDonald, R.A. 2002. Resource partitioning among British and Irish mustelids. Journal of Animal Ecology 71: 185-200.
McNab, B.K. 1995, Energy expenditure and conservation in frugivorous and mixed-diet carnivorans: Journal of Mammalogy 76: 206–222.
Mendelssohn, H. and Yom-Tov, Y. 1999. Mammalia of Israel. The Israel academy of sciences and humanities. Jerusalem.
Moore, C.M. and Collins, P.W. 1995. *Urocyon littoralis*. Mammalian Species 489: 1-7.
Nagorsen, D.W., Campbell, R.W. and Giannico, G.R. 1991. Winter food habits of marten, *Martes americana*, on the Queen Charlotte islands. Canadian Field Naturalist 105: 55-59.
Nowak, R.M. 1999. Walker's "Mammals of the world" 6th edition. Johns Hopkins University Press. Baltimore.
Nunez, R., Miller, B. and Lindzey, F. 2000. Food habits of jaguars and pumas in Jalisco, Mexico. Journal of Zoology: 252: 373-379.
Padial, J.M., Avila, E. and Gil-Sanchez, J.M. 2002. Feeding habits and overlap among red fox (*Vulpes vulpes*) and stone marten (*Martes foina*) in two Mediterranean mountain habitats. Mammalian Biology 67: 137-146.
Quadros, J. and Monteiro-Filho, E.L.A. 2001. Diet of the neotropical otter, *Lontra longicaudis*, in an Atlantic Forest Area, Santa Catarina State, southern Brazil. Studies on Neotropical Fauna & Environment: 36: 15-21.
Ray, J.C. and Sunquist, M.E. 2001. Trophic relations in a community of African rainforest carnivores. Oecologia 127: 395-408 .
Rode, K. D., and Robbins, C. T. 2000. Why bears consume mixed diets during fruit abundance. Canadian Journal of Zoology 78: 1640-1645.
Rodriguez-Estrella, R., Moreno, A.R., and Tam , K.G. 2000. Spring diet of the endemic ring-tailed cat (*Bassariscus astutus insulicola*) population on an island in the Gulf of California, Mexico. Journal of Arid Environments 44: 241-246.
Roth, J.D. 2002. Temporal variability in arctic fox diet as reflected in stable-carbon isotopes; the importance of sea ice. Oecologia 133: 70-77.
Shusei, A., Takayuki, A., Yoshiko, K.., and Yoshida K. 2003. Food habit of the Japanese marten (*Martes melampus*) at Kuju Highland in Kyushu, Japan. Honyurui Kagaku 43: 19-28.
Silva, S.I., Jaksic, F.M., and Bozinovic, F. 2004. Interplay between metabolic rate and diet quality

in the South American fox, *Pseudalopex culpaeus*. Comparative Biochemistry and Physiology Part A 137: 33–38.
Simberloff, D., Dayan, T., Jones, C. & Ogura, G. 2000. Character displacement and release in the small Indian mongoose, *Herpestes javanicus*. Ecology 81: 2086-2099.
Simms, D.A. 1979. North American weasels: resource utilization and distribution. Canadian Journal of Zoology 57: 504-520.
Sivasothi, N. and B. Nor. 1994. A review of otters (Carnivora: Mustelidae: Lutrinae) in Malaysia and Singapore. Hydrobiologia 285: 151-170.
Somers, M.J. and M. G. Purves. 1996. Trophic overlap between three syntopic semi-aquatic carnivores: Cape clawless otter, spotted-necked otter and water mongoose. African Journal of Ecology 34: 158–166.
Sunquist, M. and Sunquist, F. 2002. Wild cats of the world. University of Chicago Press, Chicago.
Van Rompaey, H. 1993. The Banded linsang, *Prionodon linsang*. Small Carnivore Conservation 9: 11-15.
Verts, B.J., Carraway, L.N., and Kinlaw, A. 2001. *Spilogale gracilis*. Mammalian Species 674: 1-10.
Virgos, E., Llorente, M. and Cortes, Y. 1999. Geographical variation in genet (*Genetta genetta* L.) diet: a literature review. Mammal Review 29: 119-128.
Wade-Smith, J. and Verts, B.J. 1982. *Mephitis mephitis*. Mammalian Species 173: 1-7.
Wang, E. 2002. Diets of Ocelots (*Leopardus pardalis*), Margays (*L. wiedii*), and Oncillas (*L. tigrinus*) in the Atlantic Rainforest in Southeast Brazil. Studies on Neotropical Fauna & Environment 37: 207-213.
White, P.J., White, C.A.V., and Ralls K. 1996. Functional and numerical responses of kit foxes to a short-term decline in mammalian prey. Journal of Mammalogy 77: 370-376.
Wu, H-Y. 1999. Is there current competition between sympatric Siberian weasels (*Mustela sibirica*) and Ferret Badgers (*Melogale moschata*) in a subtropical forest ecosystem of Taiwan. Zoological Studies 38: 443-451.
Zielinski, W.J. Duncan, N.P., Farmer, E.C., Truex, R.L., Clevenger, A.P., and Barrett, R.H. 1999. Diet of fishers (*Martes pennanti*) at the southernmost extent of their range. Journal of Mammalogy 80: 961-971.

Appendix 4.
Indigenous carnivores of 366 islands for which I obtained area data.

Island	Species	Specimen / Reference
Admirality	*Lontra canadensis*	Carnegie Museum
	Martes americana	UAF Museum
	Mustela erminea	MVZ
	Mustela vison	Smithsonian, MVZ
	Ursus americanus	Smithsonian
	Ursus arctos	Carnegie, MCZ, UAF
Aero	*Mustela putorius*	Copenhagen
Afognak	*Lontra canadensis*	Hall 1981, Goldman 1935
	Mustela erminea	Kansas
	Ursus arctos	UAF Museum
	Vulpes vulpes	WorldWideWeb
Akimiski	*Alopex lagopus*	Banfield 1974
	Gulo gulo	Banfield 1974
	Lontra canadensis	Banfield 1974
	Martes americana	Banfield 1974
	Mephitis mephitis	Banfield 1974
	Mustela nivalis	Banfield 1974
	Ursus americanus	Banfield 1974
	Vulpes vulpes	Banfield 1974
Akutan	*Vulpes vulpes*	Peterson 1967
Alaid (Kurils)	*Mustela erminea*	Hoekstra and Fagan 1998
	Vulpes vulpes	Hoekstra and Fagan 1998
Aland	*Martes martes*	Mitchell-Jones et al. 1999
	Meles meles	Mitchell-Jones et al. 1999
	Mustela erminea	Mitchell-Jones et al. 1999
	Mustela nivalis	Mitchell-Jones et al. 1999
	Vulpes vulpes	Mitchell-Jones et al. 1999
Alonisos	*Martes foina*	Masseti 1995
Amakusa	*Nyctereutes procyonoides*	Tokyo
Andros	*Martes foina*	Mitchell-Jones et al. 1999
	Meles meles	Mitchell-Jones et al. 1999
Anglesey	*Lutra lutra*	Corbet and Southern 1977
	Meles meles	Corbet & Harris 1991
	Mustela erminea	Corbet & Harris 1991
	Mustela nivalis	Corbet & Harris 1991
Anguila	*Mustela vison*	UAF Museum
Anticosti	*Alopex lagopus*	Hall 1981
	Felis lynx (Canadensis)	Forsyth 1985
	Lontra canadensis	Newsom 1937, Forsyth 1985
	Martes americana	Newsom 1937, Hall 1981
	Martes pennanti	Hall 1981
	Mustela erminea	Hall 1981
	Mustela vison	Banfield 1974

Island	**Species**	**Specimen / Reference**
	Ursus americanus	Paris, AMNH
	Vulpes vulpes	Newsom 1937, Hall 1981
Aquidneck	*Canis lupus*	Hall 1981
Arran	*Lutra lutra*	Corbet & Harris 1991
	Meles meles	Corbet & Harris 1991
	Vulpes vulpes	WorldWideWeb
Asinara	*Mustela nivalis*	De Marinis and Masseti 2003
Attu	*Alopex lagopus*	UAF Museum
Axel Heiberg	*Alopex lagopus*	Hall 1981
	Mustela erminea	Hall 1981
Bacan (=Batchian)	*Viverra zibetha*	Wallace 1868
Baffin	*Alopex lagopus*	Hall 1981
	Felis lynx (Canadensis)	Hall 1981
	Gulo gulo	Hall 1981
	Mustela erminea	British Museum
	Vulpes vulpes	Hall 1981, Long 2003
Baker	*Canis lupus*	Conroy et al. 1999
	Ursus americanus	Conroy et al. 1999
Balabac	*Paradoxurus hermaphroditus*	Smithsonian
Balembangan	*Lutra perspicillata*	Shukor 1996
Bali	*Felis bengalensis*	British Museum
	Felis viverrina	Honacki et al. 1982, Meijaard 2003
	Melogale orientalis	Corbet & Hill 1992, Riffel 1991
	Panthera pardus	Meijaard 2003
	Panthera tigris	British, Leiden
	Paradoxurus hermaphroditus	Leiden, AMNH
	Viverricula indica	AMNH, Brussels
Banggi	*Arctogalidia trivirgata*	Field Museum
	Lutra perspicillata	Shukor 1996
	Paradoxurus hermaphroditus	Field Museum
	Viverra tangalunga	Shukor 1996
Bangka	*Aonyx cinerea*	Meijaard 2003
	Arctictis binturong	Leiden
	Arctogalidia trivirgata	Leiden
	Lutra sumatrana	Corbet & Hill 1992, Meijaard 2003
	Martes flavigula	Nowak 1991
	Paradoxurus hermaphroditus	Leiden, Smithsonian
	Prionodon linsang	Leiden
	Ursus malayanus	Meijaard 2003
	Viverra tangalunga	Leiden
Banks	*Alopex lagopus*	Canadian Museum of Nature
	Canis lupus	Canadian Museum of Nature
Banks (BC)	*Canis lupus*	Darimont and Paquet 2002

Island	Species	Specimen / Reference
	Lontra canadensis	WorldWideWeb
Baranof	*Lontra canadensis*	UAF Museum
	Mustela erminea	MVZ
	Mustela vison	MVZ, UAF
	Ursus arctos	Field, Smithsonian, UAF
Barbados	*Procyon gloveralleni*	Helgen and Wilson 2003
Barra	*Lutra lutra*	Corbet and Southern 1977
Basilan	*Paradoxurus hermaphroditus*	Heaney 1986
Batam	*Arctictis binturong*	Meijaard 2003
	Arctogalidia trivirgata	British Museum, Singapore
Bathurst	*Alopex lagopus*	Canadian Museum of Nature
Bawal	*Viverra tangalunga*	Smithsonian
Bawean	*Paradoxurus hermaphroditus*	Naturalis
	Viverricula indica	Naturalis
Bear island (Bjornoja)	*Alopex lagopus*	Mitchell-Jones et al. 1999
Belitung	*Aonyx cinerea*	Meijaard 2003
	Arctogalidia trivirgata	Corbet & Hill 1992, Meijaard 2003
	Paradoxurus hermaphroditus	Smithsonian
	Prionodon linsang	Leiden
	Viverra tangalunga	Smithsonian
Belyi	*Alopex lagopus*	Smithsonian
Bengkalis	*Ursus malayanus*	Meijaard 2003
Bering	*Alopex lagopus*	British Museum, Smithsonian
Biliran	*Paradoxurus hermaphroditus*	Rickart et al., 1993
Bintan	*Aonyx cinerea*	British Museum
	Arctictis binturong	Meijaard 2003
	Arctogalidia trivirgata	Meijaard 2003
	Panthera tigris	Meijaard 2003
	Viverra tangalunga	Smithsonian
	Viverricula indica	Meijaard 2003
Bioko	*Aonyx congica*	http://www.bioko.org/
	Genetta maculata	Schreiber et al. 1989
	Nandinia binotata	http://www.bioko.org/
	Poiana richardsoni	Nowak 1991
Bjorno	*Mustela erminea*	Angerbjorn 1986
Bohol	*Paradoxurus hermaphroditus*	Heaney 1986
	Viverra tangalunga	Heaney 1986
Borneo	*Aonyx cinerea*	British Museum
	Arctictis binturong	British Museum
	Arctogalidia trivirgata	Nowak 1991
	Cuon alpinus	Corbet 1978
	Cynogale bennettii	British Museum

Island	Species	Specimen / Reference
	Diplogale hosei	British Museum
	Felis badia	Wilson & Reeder 1993
	Felis bengalensis	British Museum
	Felis marmorata	British Museum
	Felis planiceps	British Museum
	Hemigalus derbyanus	British Museum
	Herpestes brachyurus	Kansas
	Herpestes semitorquatus	British Museum
	Lutra perspicillata	Berlin
	Lutra sumatrana	British Museum
	Martes flavigula	British Museum
	Melogale everetti	British Museum
	Mustela nudipes	British Museum
	Mydaus javanensis	Wilson & Reeder 1993
	Neofelis nebulosa	British Museum
	Paguma larvata	British Museum
	Paradoxurus hermaphroditus	British Museum
	Prionodon linsang	British Museum
	Ursus malayanus	Wilson & Reeder 1993
	Viverra tangalunga	British Museum
	Viverricula indica	Brussels
Bornholm	*Martes martes*	Mitchell-Jones et al. 1999
	Meles meles	Mitchell-Jones et al. 1999
	Mustela erminea	Mitchell-Jones et al. 1999
	Mustela nivalis	Mitchell-Jones et al. 1999
	Mustela putorius	Mitchell-Jones et al. 1999
	Vulpes vulpes	Yom-Tov et al. 2003
Britain	*Canis lupus*	Nowak 1991
	Felis lynx (lynx)	Yalden 1999
	Felis silvestris	British Museum
	Lutra lutra	British Museum
	Martes martes	Dayan & Simberloff 1994
	Meles meles	Dayan & Simberloff 1994
	Mustela erminea	Dayan & Simberloff 1994
	Mustela nivalis	Dayan & Simberloff 1994
	Mustela putorius	Dayan & Simberloff 1994
	Ursus arctos	Yalden 1999
	Vulpes vulpes	British Museum
Broughton	*Mustela vison*	Royal BC Museum
Bruit	*Felis bengalensis*	Meijaard 2003
	Lutra sumatrana	Meijaard 2003
Bulan	*Arctogalidia trivirgata*	Meijaard 2003
Bunguran (Natuna)	*Arctogalidia trivirgata*	Singapore, Smithsonian
	Mydaus javanensis	Singapore
	Viverra tangalunga	Smithsonian

Island	Species	Specimen / Reference
Busuanga	*Felis bengalensis*	Heaney 1986
	Herpestes brachyurus	Heaney 1986
	Mydaus marchei	Field Museum
	Paradoxurus hermaphroditus	Field Museum
	Viverra tangalunga	Field Museum
Bute	*Vulpes vulpes*	WorldWideWeb
Cabo San Juan	*Lontra provocax*	Redford & Eisenberg 1992
Cairn Is	*Lontra canadensis*	Carnegie Museum
	Mustela erminea	Carnegie Museum
Calvert	*Canis lupus*	Friis 1985, Cowan and Guiget 1956
	Mustela vison	MVZ
Camiguin	*Paradoxurus hermaphroditus*	Field Museum website
	Viverra tangalunga	Field Museum website
Campobello	*Mustela macrodon*	Hall 1981
Cape Breton	*Canis lupus*	Hall 1981
	Felis concolor	Cameron 1958
	Felis lynx (Canadensis)	Forsyth 1985
	Felis rufus	Parker & Smith 1983
	Lontra canadensis	Canadian Museum of Nature
	Martes americana	Hall 1981
	Martes pennanti	Hall 1981
	Mustela erminea	Canadian Museum of Nature
	Mustela vison	Canadian Museum of Nature
	Ursus americanus	Hall 1981
	Vulpes vulpes	Hall 1981
Catanduanes	*Paradoxurus hermaphroditus*	Heaney et al., 1991
	Viverra tangalunga	Heaney et al., 1991
Cayo Nancy	*Procyon lotor*	Smithsonian
Cebu	*Felis bengalensis*	Heaney 1986
Charlton	*Mustela erminea*	Carnegie Museum
Cheju Do	*Felis bengalensis*	Nowak 1991
	Meles meles	Abe et al. 1994
	Mustela sibirica	British Museum
Chichagof	*Lontra canadensis*	UAF Museum
	Mustela erminea	UAF Museum
	Mustela vison	UAF Museum
	Ursus americanus	Smithsonian
	Ursus arctos	Carnegie, MCZ, Smithsonian
Chiloe	*Felis guigna*	Field Museum
	Galictis cuja	Field Museum
	Lontra felina	Field Museum
	Lontra provocax	Field Museum
	Pseudalopex griseus	British, Field, Leiden
Chios	*Lutra lutra*	Mitchell-Jones et al. 1999

Island	Species	Specimen / Reference
	Martes foina	Masseti 1995
	Mustela nivalis	Mitchell-Jones et al. 1999
	Vulpes vulpes	Mitchell-Jones et al. 1999
Colonsay	*Lutra lutra*	Harris et al. 1995
Con Son	*Paradoxurus hermaphroditus*	Smithsonian
Conanicut	*Mustela vison*	Field Museum
Corfu	*Canis aureus*	Giannatos 2004
	Lutra lutra	Harris 1968
	Martes foina	Wilson & Reeder 1993
	Mustela nivalis	De Marinis and Masseti 2003
	Vulpes vulpes	Mitchell Jones et al. 1999
Cornwallis	*Alopex lagopus*	Smithsonian
	Mustela erminea	Smithsonian
	Vulpes vulpes	Long 2003
Coronation	*Lontra canadensis*	Klein 1995
	Mustela vison	MVZ
Corsica	*Felis silvestris*	Munchen
	Martes martes	Mitchell-Jones et al. 1999, Schreiber et al. 1989
	Mustela nivalis	Berlin
	Vulpes vulpes	Munchen
Cozumel	*Nasua narica*	MCZ
	Procyon pygmaeus	MCZ, Kansas
	Urocyon cinereoargenteus	Cuaron et al. 2004
Crete	*Felis silvestris*	Mitchell-Jones et al. 1999
	Martes foina	British Museum
	Meles meles	Amsterdam
Culion	*Aonyx cinerea*	Meijaard 2003
	Herpestes brachyurus	Meijaard 2003
	Mydaus marchei	Naturalis
	Paradoxurus hermaphroditus	Heaney 1986
	Viverra tangalunga	Field Museum
Cyprus	*Vulpes vulpes*	British Museum
Dall	*Canis lupus*	Conroy et al. 1999
	Lontra canadensis	Macdonald and Cook 1996
	Mustela erminea	Cook et al. 2001
	Mustela vison	MVZ
	Ursus americanus	Smithsonian
Deer	*Felis rufus*	Crowell 1986
	Lontra canadensis	Crowell 1986
	Martes pennanti	Crowell 1986
	Mephitis mephitis	Crowell 1986
	Mustela erminea	Crowell 1986
	Mustela vison	Crowell 1986
	Procyon lotor	Crowell 1986

Island	Species	Specimen / Reference
	Ursus americanus	Crowell 1986
	Vulpes vulpes	Crowell 1986
Devon	*Alopex lagopus*	Smithsonian
Dinagat	*Paradoxurus hermaphroditus*	Heaney 1986
Domel	*Arctogalidia trivirgata*	Schreiber et al. 1989
	Paradoxurus hermaphroditus	Schreiber et al. 1989
Douglas	*Mustela erminea*	UAF Museum
	Ursus americanus	Conroy et al. 1999
Drejo	*Mustela erminea*	Angerbjorn 1986
Duke	*Canis lupus*	Conroy et al. 1999
Dundas	*Canis lupus*	Darimont and Paquet 2002
Eigg	*Lutra lutra*	Corbet and Southern 1977
Elba	*Martes martes*	Michaux et al. 2002
Enggano	*Paradoxurus hermaphroditus*	Corbet & Hill 1992
Erimomilos	*Martes foina*	Masseti 1995
Espirito Santo	*Bassariscus astutus*	Smithsonian, MVZ
Esther	*Lontra canadensis*	Testa et al. 1994
	Mustela vison	UAF Museum
Etolin	*Canis lupus*	Kansas
	Martes americana	Conroy et al. 1999
	Mustela erminea	UAF Museum
	Mustela vison	Smithsonian
	Ursus americanus	Conroy et al. 1999
Euboea (Evvoia)	*Canis aureus*	Krystufek et al. 1997
	Lutra lutra	Mitchell-Jones et al. 1999
	Martes foina	Mitchell-Jones et al. 1999
	Mustela nivalis	De Marinis and Masseti 2003
	Vulpes vulpes	Mitchell-Jones et al. 1999
Falster	*Martes foina*	Copenhagen
	Mustela erminea	Copenhagen
	Mustela nivalis	Copenhagen
	Vulpes vulpes	Mitchell-Jones et al. 1999
Fano	*Mustela erminea*	Angerbjorn 1986
Farasan Al kabir	*Ichneumia albicauda*	British Museum
Flaherty	*Alopex lagopus*	Carnegie Museum
	Mustela erminea	Carnegie Museum
	Vulpes vulpes	Carnegie Museum
Franz-Josef Land	*Canis lupus*	Stroganov 1969
Fyn	*Lutra lutra*	Pertoldi et al. 2003
	Martes foina	Copenhagen
	Meles meles	Copenhagen
	Mustela erminea	Copenhagen
	Mustela putorius	Copenhagen
	Vulpes vulpes	Mitchell-Jones et al. 1999

Island	Species	Specimen / Reference
Galang	*Aonyx cinerea*	Singapore
	Arctogalidia trivirgata	Meijaard 2003
Gigha	*Vulpes vulpes*	WorldWideWeb
Gilford	*Martes americana*	Royal BC Museum
Gotland	*Vulpes vulpes*	Mitchell-Jones et al. 1999
Graham	*Lontra canadensis*	Smithsonian
	Martes americana	Smithsonian
	Mustela erminea	AMNH, Smithsonian
	Ursus americanus	Royal BC Museum, Smithsonian
Grand Manan	*Vulpes vulpes*	MCZ
Gravina	*Martes americana*	Conroy et al. 1999
	Ursus americanus	Conroy et al. 1999
Great Wass	*Mustela vison*	Crowell 1986
Greenland	*Alopex lagopus*	British Museum
	Canis lupus	Nowak 1991
	Gulo gulo	Boitani & Bartoly 1983
	Mustela erminea	British Museum
Gribble/Gribbell	*Ursus americanus*	Royal BC Museum
Guaitecas	*Felis guigna*	Sunquist and Sunquist 2002
Guernsey	*Mustela erminea*	British Museum
Hainan	*Aonyx cinerea*	Wilson & Reeder 1993
	Felis bengalensis	British Museum
	Herpestes javanicus	MVZ
	Herpestes urva	AMNH
	Lutra lutra	MCZ
	Martes flavigula	Nowak 1991
	Melogale moschata	AMNH
	Mustela kathiah	Corbet & Hill 1992, Kanchanasakha et al. 1998
	Neofelis nebulosa	Nowak 1991
	Paguma larvata	AMNH
	Paradoxurus hermaphroditus	AMNH
	Ursus thibetanus	Berlin
	Viverra zibetha	AMNH
	Viverricula indica	AMNH
Halleck	*Lontra canadensis*	UAF Museum
Hatia	*Aonyx cinerea*	WorldWideWeb
Hawkesbury	*Canis lupus*	Darimont and Paquet 2002
	Martes americana	Hall 1981
	Ursus americanus	Royal BC Museum
Hawkins	*Ursus arctos*	WorldWideWeb
Heceta	*Canis lupus*	UAF Museum
	Mustela erminea	UAF Museum
	Ursus americanus	Conroy et al. 1999
Hiiumaa	*Felis lynx (lynx)*	Mitchell-Jones et al. 1999
	Martes martes	Mitchell-Jones et al. 1999

Island	Species	Specimen / Reference
	Meles meles	Mitchell-Jones et al. 1999
	Mustela nivalis	Mitchell-Jones et al. 1999
	Mustela putorius	Mitchell-Jones et al. 1999
	Ursus arctos	Mitchell-Jones et al. 1999
	Vulpes vulpes	Mitchell-Jones et al. 1999
Hinchinbrook	*Lontra canadensis*	Smithsonian
	Mustela erminea	MVZ
	Mustela vison	Smithsonian
	Ursus arctos	UAF Museum
Hokkaido	*Canis lupus*	Millien-Parra and Jaeger 1999
	Lutra lutra	Abe et al. 1994
	Martes zibellina	Wilson & Reeder 1993
	Meles meles	Millien-Parra and Jaeger 1999
	Mustela erminea	Millien-Parra and Jaeger 1999
	Mustela nivalis	Tokyo
	Mustela sibirica	Sasaki 1991
	Nyctereutes procyonoides	Nowak 1991
	Ursus arctos	Matsuhashi et al. 1999
	Vulpes vulpes	Millien-Parra and Jaeger 1999
Hong Kong	*Felis bengalensis*	Goodyear 1992, Lai et al. 2002
	Herpestes urva	Goodyear 1992
	Melogale moschata	Goodyear 1992, Lai et al. 2002
	Mustela kathiah	Lai et al. 2002
	Paguma larvata	Lai et al. 2002
	Viverricula indica	Goodyear 1992, Lai et al. 2002
	Vulpes vulpes	Goodyear 1992
Honshu	*Canis lupus*	Abe et al. 1994
	Lutra lutra	Sasaki 1991
	Martes melampus	British Museum
	Meles meles	Sasaki 1991
	Mustela erminea	Wilson & Reeder 1993
	Mustela nivalis	Dobson 1994
	Mustela sibirica	British Museum
	Nyctereutes procyonoides	British Museum
	Ursus malayanus	Abe et al. 1994
	Ursus thibetanus	Millien-Parra and Jaeger 1999
	Vulpes vulpes	British Museum
Hoste	*Lontra provocax*	Harris 1969
	Pseudalopex culpaeus	Smithsonian
Ibiza	*Genetta genetta*	Michaux et al. 2002
	Martes foina	Nowak 1999
Iceland	*Alopex lagopus*	British Museum
Ikaria	*Canis aureus*	Krystufek et al. 1997
	Martes foina	Masseti 1995
Iki	*Mustela sibirica*	British Museum
Ios	*Mustela nivalis*	Mitchell-Jones et al. 1999

Island	Species	Specimen / Reference
Ireland	*Canis lupus*	Long 2003
	Lutra lutra	British Museum
	Martes martes	Dayan & Simberloff 1994
	Meles meles	Dayan & Simberloff 1994
	Mustela erminea	Dayan & Simberloff 1994
	Vulpes vulpes	British Museum
Iriomote	*Felis iriomotensis*	Nowak 1991
Isla Bastimentos	*Procyon lotor*	Smithsonian
Isla de los estados	*Lontra felina*	Medina-Vogel et al. 2004
	Lontra provocax	Medina-Vogel et al. 2004
Isla parida	*Potos flavus*	British Museum
Isla Popa	*Nasua narica*	Smithsonian
	Potos flavus	Smithsonian
	Procyon lotor	Smithsonian
Isla San Cristobal	*Potos flavus*	Smithsonian
	Procyon lotor	Smithsonian
Islay	*Lutra lutra*	Corbet & Harris 1991
	Mustela erminea	Smithsonian
Isle au Haut	*Lontra canadensis*	Crowell 1986
	Mustela vison	Crowell 1986
	Vulpes vulpes	Crowell 1986
Ithaca	*Martes foina*	Masseti 1995
Iturup	*Martes zibellina*	Novosibirsk
	Mustela erminea	Hoekstra and Fagan 1998
	Mustela nivalis	Hoekstra and Fagan 1998
	Ursus arctos	Novosibirsk
	Vulpes vulpes	Kostenko 2002
Java	*Aonyx cinerea*	British Museum
	Arctictis binturong	Wilson & Reeder 1993
	Arctogalidia trivirgata	Nowak 1991
	Cuon alpinus	British Museum
	Felis bengalensis	British Museum
	Felis viverrina	Nowak 1999
	Herpestes javanicus	Kansas
	Lutra perspicillata	Berlin
	Lutra sumatrana	Gathorne 1991
	Martes flavigula	British Museum
	Melogale orientalis	British Museum
	Mustela lutreolina	Wilson & Reeder 1993
	Mustela nudipes	British Museum
	Mustela sibirica	Kanchanasakha et al. 1998
	Mydaus javanensis	British Museum
	Panthera pardus	British Museum
	Panthera tigris	Wilson & Reeder 1993
	Paradoxurus hermaphroditus	British Museum

Island	Species	Specimen / Reference
	Prionodon linsang	Wilson & Reeder 1993
	Viverra tangalunga	Leiden
	Viverricula indica	Wilson & Reeder 1993
Jersey	*Mustela erminea*	British Museum
Jura	*Lutra lutra*	Corbet & Harris 1991
	Mustela erminea	Corbet & Harris 1991
Kangean	*Paradoxurus hermaphroditus*	British Museum
	Viverricula indica	Wilson & Reeder 1993
Karaginskij	*Canis lupus*	Stroganov 1969
	Gulo gulo	WorldWideWeb
	Martes zibellina	WorldWideWeb
	Mustela erminea	Schreiber et al. 1989
	Ursus arctos	Stroganov 1969
	Vulpes vulpes	WorldWideWeb
Karimata	*Aonyx cinerea*	Meijaard 2003
	Felis bengalensis	Meijaard 2003
	Viverra tangalunga	Smithsonian
Karimon	*Aonyx cinerea*	Smithsonian
Karimunjawa	*Aonyx cinerea*	Corbet & Hill 1992, Meijaard 2003
	Felis bengalensis	Meijaard 2003
Karpathos	*Martes foina*	Mitchell-Jones et al. 1999
Kayak	*Ursus arctos*	WorldWideWeb
	Vulpes vulpes	WorldWideWeb
Kefalonia	*Canis aureus*	Krystufek et al. 1997
	Martes foina	WorldWideWeb
	Meles meles	WorldWideWeb
	Mustela nivalis	WorldWideWeb
	Vulpes vulpes	WorldWideWeb
King (BC)	*Mustela vison*	Canadian Museum of Nature
Kiska	*Alopex lagopus*	UAF, Smithsonian
Kisseraing	*Paradoxurus hermaphroditus*	Schreiber et al. 1989
Kithira	*Martes foina*	Mitchell-Jones et al. 1999
	Meles meles	Mitchell-Jones et al. 1999
	Mustela nivalis	Mitchell-Jones et al. 1999
	Vulpes vulpes	Mitchell-Jones et al. 1999
Knight	*Lontra canadensis*	UAF
Kodiak	*Alopex lagopus*	Forsyth 1985
	Canis lupus	Hall 1981
	Lontra canadensis	Hall 1981, Goldman 1935
	Mustela erminea	Hall 1981
	Ursus arctos	Hall 1981
	Vulpes vulpes	MVZ
Koh Chang	*Herpestes javanicus*	WorldWideWeb
	Viverricula indica	WorldWideWeb

Island	Species	Specimen / Reference
Koh Samui	*Paradoxurus hermaphroditus*	Museum records
Koh yao	*Paguma larvata*	Museum records
	Paradoxurus hermaphroditus	Museum records
Kolgujev	*Canis lupus*	Ellerman & Morison-Scot 1966
	Vulpes vulpes	Ellerman & Morison-Scot 1966
Korcula	*Canis aureus*	Krystufek et al. 1997
	Herpestes Sp.	WorldWideWeb
	Martes foina	WorldWideWeb
	Mustela nivalis	WorldWideWeb
Kos	*Martes foina*	Mitchell-Jones et al. 1999
	Vulpes vulpes	Mitchell-Jones et al. 1999
Kosciusko	*Canis lupus*	UAF Museum
	Ursus americanus	Conroy et al. 1999
Krestof	*Lontra canadensis*	UAF Museum
	Ursus arctos	Smithsonian
Krk	*Felis silvestris*	WorldWideWeb
	Martes foina	WorldWideWeb
	Vulpes vulpes	WorldWideWeb
Kruzof	*Lontra canadensis*	UAF Museum
	Mustela erminea	Macdonald and Cook 1996
	Mustela vison	Conroy et al. 1999
	Ursus arctos	Smithsonian
Kuiu	*Canis lupus*	Conroy et al. 1999
	Gulo gulo	Conroy et al. 1999
	Lontra canadensis	Carnegie, MVZ
	Martes americana	Conroy et al. 1999
	Mustela vison	MVZ
	Ursus americanus	Conroy et al. 1999
Kunashir	*Martes zibellina*	Kostenko 2002
	Mustela erminea	Kostenko 2002
	Mustela nivalis	Abramov & Baryshnikov 2000, Kostenko 2002
	Ursus arctos	Kostenko 2002, Hoekstra and Fagan 1998
	Vulpes vulpes	Novosibirsk
Kundur	*Arctictis binturong*	Meijaard 2003
	Arctogalidia trivirgata	Meijaard 2003
	Mydaus javanensis	Meijaard 2003
	Paradoxurus hermaphroditus	Corbet and Hill 1992
	Viverra tangalunga	Meijaard 2003
Kupreanof	*Canis lupus*	Conroy et al. 1999
	Gulo gulo	Conroy et al. 1999
	Lontra canadensis	Macdonald and Cook 1996
	Martes americana	UAF Museum, Carnegie
	Mustela vison	Carnegie Museum, Smithsonian
	Ursus americanus	Smithsonian, MVZ

Island	Species	Specimen / Reference
Kythnos	*Martes foina*	Masseti 1995
Kyushu	*Canis lupus*	Abe et al. 1994
	Lutra lutra	Abe et al. 1994
	Martes melampus	British Museum
	Meles meles	British Museum
	Mustela sibirica	British Museum
	Nyctereutes procyonoides	Nowak 1991
	Ursus thibetanus	Millien-Parra and Jaeger 1999
	Vulpes vulpes	Millien-Parra and Jaeger 1999
Lamukotan	*Mydaus javanensis*	Meijaard 2003
Langkawi	*Arctogalidia trivirgata*	Corbet & Hill 1992, Meijaard 2003
	Lutra perspicillata	Smithsonian
	Paradoxurus hermaphroditus	British Museum
	Viverra tangalunga	Corbet & Hill 1992, Meijaard 2003
Lantau	*Lutra lutra*	Goodyear 1992
	Melogale moschata	Lai et al. 2002, Porcupine! 24
	Mustela kathiah	Lai et al. 2002
	Paguma larvata	Marshall 1967
Laut (Borneo)	*Aonyx cinerea*	Corbet & Hill 1992, Meijaard 2003
	Viverra tangalunga	Corbet & Hill 1992, Meijaard 2003
Laut (Natuna)	*Aonyx cinerea*	Meijaard 2003
	Lutra sumatrana	British Museum
	Viverra tangalunga	Meijaard 2003
Lefkada (Levkas)	*Canis aureus*	Giannatos 2004
	Martes foina	Mitchell-Jones et al. 1999
	Mustela nivalis	Mitchell-Jones et al. 1999
	Vulpes vulpes	Mitchell-Jones et al. 1999
Lesbos	*Lutra lutra*	Mitchell-Jones et al. 1999
	Martes foina	Mitchell-Jones et al. 1999
	Meles meles	Mitchell-Jones et al. 1999
	Mustela nivalis	De Marinis and Masseti 2003
	Vulpes vulpes	Peabody Museum
Lewis	*Lutra lutra*	Corbet and Southern 1977
Leyte	*Paradoxurus hermaphroditus*	Smithsonian
	Viverra tangalunga	Smithsonian
Lingga	*Aonyx cinerea*	Meijaard 2003
	Arctogalidia trivirgata	Field Museum
	Viverra tangalunga	Smithsonian
Lolland	*Martes foina*	Copenhagen
	Mustela erminea	Copenhagen
	Mustela nivalis	Copenhagen
	Vulpes vulpes	Mitchell-Jones et al. 1999
Lombok	*Felis bengalensis*	Corbet & Hill 1992
	Paradoxurus hermaphroditus	Corbet & Hill 1992

Island	Species	Specimen / Reference
Long (Alexander Archipelago)	*Lontra canadensis*	Macdonald and Cook 1996
	Mustela erminea	Cook et al. 2001
	Mustela vison	Macdonald and Cook 1996
Long (Maine)	*Mustela vison*	Crowell 1986
	Vulpes vulpes	Crowell 1986
Louise	*Lontra canadensis*	Hall 1981
	Martes americana	Royal BC Museum
	Mustela erminea	Reid et al. 2000
	Ursus americanus	Cowan and Guiget 1956
Lowther	*Alopex lagopus*	Canadian Museum of Nature
Luzon	*Paradoxurus hermaphroditus*	AMNH, British, Leiden, Smithsonian
	Viverra tangalunga	AMNH, Field, Smithsonian
Lyo	*Mustela erminea*	Angerbjorn 1986
Madagascar	*Cryptoprocta ferox*	Wilson & Reeder 1993
	Eupleres goudotti	Wilson & Reeder 1993
	Fossa fossana	Wilson & Reeder 1993
	Galidia elegance	Wilson & Reeder 1993
	Galidictis fasciata	Wilson & Reeder 1993
	Galidictis grandidieri	Wilson & Reeder 1993
	Mungotictis decemlineata	Wilson & Reeder 1993
	Salanoia concolor	Wilson & Reeder 1993
Madura	*Herpestes javanicus*	British Museum
	Panthera pardus	Meijaard 2003
	Paradoxurus hermaphroditus	nature conservation in indonesia web site
Magdalena	*Canis latrans*	Smithsonian
Mallorca	*Felis silvestris*	Massety 1995
	Genetta genetta	Michaux et al. 2002
	Martes martes	Michaux et al. 2002
	Mustela nivalis	British Museum
Man	*Lutra lutra*	Corbet and Southern 1977
	Mustela erminea	Corbet & Harris 1991
Marble	*Lontra canadensis*	Smithsonian
Margarita	*Conepatus semistriatus*	WorldWideWeb
	Felis pardalis	Linares 1998, Sunquist and Sunquist 2002
Maria Madre	*Procyon lotor*	Smithsonian
Maria Magdalena	*Procyon lotor*	Wilson 1991
Marinduque	*Paradoxurus hermaphroditus*	Heaney 1986
Maripipi	*Paradoxurus hermaphroditus*	Heaney 1986
Mayne	*Lontra canadensis*	Royal BC Museum
McCauley	*Canis lupus*	Darimont and Paquet 2002
	Martes americana	Hall 1981
Melville	*Alopex lagopus*	Smithsonian

Island	Species	Specimen / Reference
	Canis lupus	Anderson 1943, Hall 1981
	Gulo gulo	Hall 1981
Menorca	*Martes martes*	Michaux et al. 2002
	Mustela nivalis	Michaux et al. 2002
Mindanao	*Paradoxurus hermaphroditus*	Heaney 1986
	Viverra tangalunga	Heaney 1986
Mindoro	*Paradoxurus hermaphroditus*	Heaney 1986
	Viverra tangalunga	Smithsonian
Mitkof	*Canis latrans*	Conroy et al. 1999
	Canis lupus	UAF
	Gulo gulo	Carnegie, Kansas
	Martes americana	UAF Museum, Carnegie
	Mustela erminea	UAF Museum
	Mustela vison	UAF Museum
	Ursus americanus	UAF Museum, MVZ
Mljet	*Martes foina*	WorldWideWeb
Montague	*Lontra canadensis*	Smithsonian, MVZ
	Ursus arctos	Smithsonian, MVZ
Moresby	*Lontra canadensis*	Royal BC Museum
	Martes americana	Royal BC Museum
	Mustela erminea	Smithsonian
	Ursus americanus	Cowan and Guiget 1956
Mount Desert Island	*Felis rufus*	Hall 1981
	Lontra canadensis	Crowell 1986
	Martes pennanti	Crowell 1986 Hall 1981
	Mephitis mephitis	Crowell 1986
	Mustela erminea	Crowell 1986
	Mustela frenata	Crowell 1986
	Mustela macrodon	MCZ
	Mustela vison	MCZ
	Procyon lotor	Crowell 1986
	Ursus americanus	Crowell 1986
	Vulpes vulpes	Hall 1981
Mull	*Lutra lutra*	Corbet & Harris 1991
	Mustela erminea	King and Moors 1979
Nagai	*Lontra canadensis*	Hall 1981, Goldman 1935
Navarino	*Pseudalopex culpaeus*	Darwin 1845
Naxos	*Martes foina*	British Museum
	Mustela nivalis	Mitchell-Jones et al. 1999
Negros	*Felis bengalensis*	British, Field, Smithsonian
	Paradoxurus hermaphroditus	Field, Smithsonian
	Viverra tangalunga	Heaney 1986
Newfoundland	*Alopex lagopus*	Hall 1981

Island	Species	Specimen / Reference
	Canis latrans	Canadian Museum of Nature
	Canis lupus	Smithsonian
	Felis lynx (Canadensis)	Hall 1981
	Gulo gulo	Hall 1981
	Lontra canadensis	Hall 1981
	Martes americana	MCZ, Smithsonian
	Mustela erminea	Hall 1981
	Ursus americanus	Wilson & Reeder 1993
	Vulpes vulpes	Munchen
Nias	*Arctictis binturong*	Corbet & Hill 1992, Meijaard 2003
	Felis bengalensis	Meijaard 2003
Nootka	*Canis lupus*	WorldWideWeb
	Felis concolor	Royal BC Museum
	Mustela vison	WorldWideWeb
	Ursus americanus	WorldWideWeb
North Twin	*Alopex lagopus*	Canadian Museum of Nature
North Uist	*Lutra lutra*	WorldWideWeb
Novosibirskiye Ostrova	*Alopex lagopus*	Boitani & Bartoly 1983
Nunivak	*Alopex lagopus*	Smithsonian
	Mustela vison	UAF Museum
Nusa barung	*Viverricula indica*	Meijaard 2003
Oki	*Nyctereutes procyonoides*	Millien-Parra and Jaeger 1999
Oland	*Lutra lutra*	Angerbjorn 1985
	Martes martes	Angerbjorn 1985
	Meles meles	Angerbjorn 1985
	Mustela erminea	Angerbjorn 1985
	Mustela nivalis	Angerbjorn 1985
	Vulpes vulpes	Mitchell-Jones et al. 1999
Orcas	*Lontra canadensis*	British Museum
Orkney	*Lutra lutra*	Mitchell-Jones et al. 1999
Padang	*Paradoxurus hermaphroditus*	Schreiber et al. 1989
	Ursus malayanus	Meijaard 2003
Padre	*Canis latrans*	British Museum
	Canis rufus	Kansas
	Felis rufus	US National parks service
	Procyon lotor	US National parks service
	Taxidea taxus	The Mammals of Texas - Online Edition
Pag	*Canis aureus*	Krystufek et al. 1997
Palau pagai utara (North pagai)	*Paradoxurus lignicolor*	AMNH
Palawan	*Aonyx cinerea*	Wilson & Reeder 1993
	Arctictis binturong	Wilson & Reeder 1993
	Felis bengalensis	British Museum
	Felis planiceps	Alderton 1993
	Herpestes brachyurus	Corbet & Hill 1992, Meijaard 2003

Island	Species	Specimen / Reference
	Lutra perspicillata	Paris
	Mydaus marchei	Wilson & Reeder 1993
	Paradoxurus hermaphroditus	Corbet & Hill 1992
	Viverra tangalunga	Corbet & Hill 1992, Meijaard 2003
Panaitan	*Cuon alpinus*	nature conservation in indonesia web site
	Herpestes javanicus	Meijaard 2003
	Panthera pardus	nature conservation in indonesia web site
	Paradoxurus hermaphroditus	nature conservation in indonesia web site
	Viverricula indica	Meijaard 2003
Panay	*Felis bengalensis*	Heaney 1986
	Paradoxurus hermaphroditus	Heaney 1986
	Viverra tangalunga	Heaney 1986
Panebangan	*Viverra tangalunga*	Smithsonian
Papa Stour	*Lutra lutra*	British Museum
Paramushir	*Mustela erminea*	Hoekstra and Fagan 1998 Kostenko 2002
	Mustela nivalis	Kostenko 2002
	Ursus arctos	Hoekstra and Fagan 1998
	Vulpes vulpes	Kostenko 2002
Pemba	*Atilax paludinosus*	Kingdon 1977
Pender	*Mustela erminea*	Banfield 1974
	Procyon lotor	Cowan and Guiget 1956
Phuket	*Felis bengalensis*	WorldWideWeb
Pinang	*Felis bengalensis*	Smithsonian
	Paradoxurus hermaphroditus	British Museum
	Viverra megaspila	British Museum
	Viverra tangalunga	Singapore
	Viverricula indica	Corbet & Hill 1992
Pini	*Arctogalidia trivirgata*	Corbet & Hill 1992
Pitt	*Canis lupus*	Darimont and Paquet 2002
	Gulo gulo	COSEWIC 2003
	Martes americana	Hall 1981
	Ursus americanus	Hall 1981
Polillo	*Viverra tangalunga*	Heaney 1986
Pooley	*Canis lupus*	Darimont and Paquet 2002
	Ursus americanus	Marshall and Ritland 2002
Porcher	*Canis lupus*	WorldWideWeb
	Lontra canadensis	WorldWideWeb
	Mustela erminea	WorldWideWeb
	Mustela vison	WorldWideWeb
Price	*Mustela vison*	Royal BC Museum
Prince Edward	*Canis latrans*	Appleyard et al. 1998
	Canis lupus	Smithsonian

Island	Species	Specimen / Reference
	Felis lynx (Canadensis)	Forsyth 1985
	Lontra canadensis	Hall 1981
	Martes americana	Hall 1981
	Martes pennanti	Hall 1981
	Mustela erminea	Hall 1981
	Mustela vison	Hall 1981
	Ursus americanus	Hall 1981
	Vulpes vulpes	Hall 1981
Prince of Wales	*Canis lupus*	MVZ
	Lontra canadensis	UAF Museum
	Mustela erminea	UAF Museum, Smithsonian
	Mustela vison	Smithsonian, MVZ
	Procyon lotor	Eder and Pattie 2001
	Ursus americanus	Smithsonian
Prince of Wales - Nunavut	*Alopex lagopus*	Canadian Museum of Nature
Prince Patrick	*Alopex lagopus*	Smithsonian
	Canis lupus	Smithsonian
Princess Royal	*Canis lupus*	Darimont and Paquet 2002
	Ursus americanus	British, Kansas
Qeshm	*Felis silvestris*	WorldWideWeb
	Herpestes edwardsi	WorldWideWeb
	Herpestes javanicus	WorldWideWeb
	Vulpes rueppelli	WorldWideWeb
Quadra	*Canis lupus*	Royal BC Museum
	Felis concolor	Hall 1981
Raasay	*Lutra lutra*	Corbet and Southern 1977
	Vulpes vulpes	WorldWideWeb
Rab	*Martes foina*	WorldWideWeb
	Mustela nivalis	WorldWideWeb
Raspberry	*Ursus arctos*	WorldWideWeb
Read	*Canis lupus*	Royal BC Museum
	Felis concolor	WorldWideWeb
	Lontra canadensis	WorldWideWeb
	Mustela erminea	WorldWideWeb
	Mustela vison	WorldWideWeb
Revillagigedo	*Canis lupus*	Conroy et al. 1999
	Gulo gulo	Conroy et al. 1999
	Martes americana	UAF
	Mustela erminea	UAF Museum, Smithsonian
	Mustela vison	Smithsonian, MVZ
	Ursus americanus	Conroy et al. 1999
Rhodes	*Martes foina*	Mitchell-Jones et al. 1999, Schreiber et al. 1989
	Meles meles	Mitchell-Jones et al. 1999, Schreiber et al. 1989
	Mustela nivalis	Mitchell-Jones et al. 1999
	Vulpes vulpes	Mitchell-Jones et al. 1999
Rhum	*Lutra lutra*	Corbet and Southern 1977

Island	Species	Specimen / Reference
Rishiri	*Mustela sibirica*	Tokyo
	Vulpes vulpes	Millien-Parra and Jaeger 1999
Roderick	*Canis lupus*	Darimont and Paquet 2002
	Ursus americanus	Marshall and Ritland 2002
Roti	*Paradoxurus hermaphroditus*	Leiden
Rugen	*Vulpes vulpes*	Kube and Probst 1999
Rupat	*Ursus malayanus*	Meijaard 2003
	Viverra tangalunga	Meijaard 2003
Saaremaa	*Canis lupus*	WorldWideWeb
	Felis lynx (lynx)	Mitchell-Jones et al. 1999
	Lutra lutra	Burton 1979
	Martes martes	Mitchell-Jones et al. 1999
	Meles meles	Mitchell-Jones et al. 1999
	Mustela erminea	WorldWideWeb
	Mustela nivalis	Mitchell-Jones et al. 1999
	Mustela putorius	Mitchell-Jones et al. 1999
	Ursus arctos	Mitchell-Jones et al. 1999
	Vulpes vulpes	Mitchell-Jones et al. 1999
Sado Shima	*Mustela sibirica*	Tokyo
	Nyctereutes procyonoides	Tokyo
Saint Lawrence	*Alopex lagopus*	British Museum
	Canis lupus	Hall 1981
	Ursus arctos	Smithsonian
	Vulpes vulpes	Smithsonian
Saint Matthew	*Paradoxurus hermaphroditus*	Smithsonian
Saint Matthew Isl.	*Alopex lagopus*	Hall 1981
Saint Paul Isl. (Pribilof Isls.)	*Vulpes vulpes*	Smithsonian
Sakhalin	*Canis lupus*	Ellerman & Morison-Scot 1966
	Cuon alpinus	Dobson 1994
	Felis lynx (lynx)	Wilson & Reeder 1993
	Gulo gulo	Ellerman & Morison-Scot 1966
	Lutra lutra	Tokyo, Novosibirsk
	Martes zibellina	Kansas, Novosibirsk
	Mustela erminea	Ellerman & Morison-Scot 1966
	Mustela nivalis	Abramov & Baryshnikov 2000, Stroganov 1969
	Nyctereutes procyonoides	WorldWideWeb
	Ursus arctos	Anatomie comparee
	Vulpes vulpes	British Museum
Saltspring	*Felis concolor*	Hall 1981
	Mustela erminea	Royal BC Museum
	Procyon lotor	Cowan and Guiget 1956
Samar	*Viverra tangalunga*	Field Museum
Samos	*Canis aureus*	Mitchell Jones et al. 1999, Giannatos 2004
	Martes foina	Giannatos 2004

Island	Species	Specimen / Reference
	Mustela nivalis	De Marinis and Masseti 2003, Giannatos 2004
Samothraki (Samothrace)	*Martes foina*	Masseti 1995
San Clemente	*Urocyon littoralis*	Smithsonian
San Jose	*Bassariscus astutus*	Field, MCZ, MVZ
San Miguel	*Spilogale gracilis*	Schreiber et al. 1989
	Urocyon littoralis	Smithsonian, MVZ
San Nicholas	*Urocyon littoralis*	Smithsonian
Sanga-Sanga	*Paradoxurus hermaphroditus*	Field Museum website
Sanibel	*Procyon lotor*	Field Museum
Santa Catalina	*Urocyon littoralis*	Field, Smithsonian
Santa Cruz	*Spilogale gracilis*	Smithsonian, MVZ
	Urocyon littoralis	Smithsonian
Santa Rosa	*Spilogale gracilis*	Nowak 1999
	Urocyon littoralis	Smithsonian
Sardinia	*Felis silvestris*	British Museum
	Martes martes	Brussels
	Mustela nivalis	British Museum, Brussels
	Vulpes vulpes	Michaux et al. 2002
Saturna	*Procyon lotor*	Cowan and Guiget 1956
Sebangka (Lingga Isl.)	*Aonyx cinerea*	Meijaard 2003
Seguam	*Alopex lagopus*	Smithsonian
Semisopochnoi	*Alopex lagopus*	Smithsonian
Serifos	*Martes foina*	Masseti 1995
Setoko	*Aonyx cinerea*	Meijaard 2003
	Panthera tigris	Meijaard 2003
Severnaya Zemlya	*Alopex lagopus*	Boitani & Bartoly 1983
Shantar	*Gulo gulo*	an action plan for mustelids and viverrids
	Martes zibellina	Berlin
	Mustela erminea	Berlin
	Ursus arctos	Hall 1981
Sheppey	*Meles meles*	Harris et al. 1995
	Mustela erminea	Corbet & Harris 1991
	Mustela nivalis	Corbet & Harris 1991
Shetland	*Lutra lutra*	British Museum
Shikoku	*Canis lupus*	Abe et al. 1994
	Lutra lutra	Sasaki 1991
	Martes melampus	Wilson & Reeder 1993
	Meles meles	British Museum
	Mustela sibirica	British Museum
	Nyctereutes procyonoides	Nowak 1991
	Ursus malayanus	Abe et al. 1994
	Ursus thibetanus	Millien-Parra and Jaeger 1999
	Vulpes vulpes	Millien-Parra and Jaeger 1999
Shrubby /Shruby	*Lontra canadensis*	Goldman 1935
	Mustela vison	Macdonald and Cook 1996

Island	Species	Specimen / Reference
Shumshu	*Lutra lutra*	Kostenko 2002
	Mustela nivalis	Kostenko 2002
	Ursus arctos	Kostenko 2002
	Vulpes vulpes	Kostenko 2002
Shuyak	*Lontra canadensis*	Hall 1981
	Ursus arctos	Rausch 1963, Servheen 1989
Siberut	*Hemigalus derbyanus*	Schreiber et al. 1989
	Paradoxurus lignicolor	Nowak 1999, Schreiber et al. 1989
Sibuyan	*Paradoxurus hermaphroditus*	Field Museum website
	Viverra tangalunga	Field Museum website
Sicily	*Canis lupus*	Ellerman & Morison-Scot 1966
	Felis silvestris	Michaux et al. 2002
	Lutra lutra	Burton 1979
	Martes martes	Mitchell-Jones et al. 1999
	Meles meles	Nowak 1999
	Mustela nivalis	British Museum
	Vulpes vulpes	Michaux et al. 2002
Sidney	*Mustela vison*	Royal BC Museum
Siguijor	*Viverra tangalunga*	Field Museum website
Simeulue	*Paradoxurus hermaphroditus*	Smithsonian
Singapore	*Aonyx cinerea*	British Museum
	Arctogalidia trivirgata	British Museum
	Cynogale bennettii	British Museum
	Felis bengalensis	Singapore
	Felis planiceps	Animal Diversity web
	Felis viverrina	Leiden
	Herpestes brachyurus	Wilson & Reeder 1993
	Lutra perspicillata	Singapore
	Lutra sumatrana	British Museum
	Martes flavigula	Smithsonian
	Neofelis nebulosa	Corbet & Hill 1992
	Paguma larvata	British Museum
	Panthera pardus	Corbet & Hill 1992
	Panthera tigris	AMNH
	Paradoxurus hermaphroditus	British Museum
	Viverra megaspila	Medway 1969, Meijaard 2003
	Viverra tangalunga	Corbet & Hill 1992, Meijaard 2003
	Viverra zibetha	Singapore
	Viverricula indica	Corbet & Hill 1992, Meijaard 2003
Singkep	*Arctogalidia trivirgata*	Meijaard 2003
Sipura	*Hemigalus derbyanus*	Heaney 1986
	Paradoxurus lignicolor	Smithsonian, Singapore
Sitkalidak	*Mustela erminea*	Ann Arbor Museum of Zoology
	Ursus arctos	WorldWideWeb

Island	Species	Specimen / Reference
Sjaelland	*Lutra lutra*	Pertoldi et al. 2003
	Martes foina	Copenhagen
	Martes martes	Copenhagen
	Mustela erminea	Copenhagen
	Mustela nivalis	Copenhagen
	Mustela putorius	Copenhagen
	Vulpes vulpes	British Museum
Skaro	*Mustela erminea*	Angerbjorn 1986
Skopelos	*Martes foina*	Masseti 1995
	Mustela nivalis	Masseti 1995
Skye	*Lutra lutra*	Corbet & Harris 1991
	Martes martes	Art Gallery & Museum, Glasgow
	Mustela erminea	Corbet & Harris 1991
	Mustela nivalis	Corbet & Harris 1991
	Vulpes vulpes	Corbet & Harris 1991
Somerset	*Alopex lagopus*	Smithsonia
South Pagai	*Hemigalus derbyanus*	Smithsonian
	Paradoxurus lignicolor	Smithsonian
South Twin	*Alopex lagopus*	Carnegie Museum
South Uist	*Lutra lutra*	British Museum
Southampton	*Alopex lagopus*	Carnegie Museum
	Canis lupus	Banfield 1974
	Mustela erminea	Carnegie Museum
Sri lanka	*Canis aureus*	British Museum
	Felis chaus	Nowak 1991 , Sunquist and Sunquist 2002
	Felis rubiginosus	British Museum
	Felis viverrina	British Museum
	Herpestes edwardsi	British Museum
	Herpestes fuscus	British Museum
	Herpestes smithii	British Museum
	Herpestes vitticollis	British Museum
	Lutra lutra	British Museum
	Panthera pardus	British Museum
	Paradoxurus hermaphroditus	British Museum
	Paradoxurus zeylonensis	British Museum
	Ursus ursinus	Wilson & Reeder 1993
	Viverricula indica	British Museum
Suemez	*Canis lupus*	Macdonald and Cook 1996
	Mustela erminea	UAF Museum, MVZ
	Mustela vison	MVZ
Sugi	*Arctogalidia trivirgata*	Meijaard 2003
Sullivans	*Paradoxurus hermaphroditus*	Smithsonian
Sumatra	*Aonyx cinerea*	British Museum
	Arctictis binturong	British Museum

Island	Species	Specimen / Reference
	Arctogalidia trivirgata	Nowak 1991
	Arctonyx collaris	British Museum
	Cuon alpinus	British Museum
	Cynogale bennettii	British Museum
	Felis bengalensis	British Museum
	Felis marmorata	Wilson & Reeder 1993
	Felis planiceps	British Museum
	Felis temminckii	British Museum
	Felis viverrina	Brussels
	Hemigalus derbyanus	Wilson & Reeder 1993
	Herpestes brachyurus	Wilson & Reeder 1993
	Herpestes javanicus	Leiden
	Herpestes semitorquatus	Berlin
	Lutra lutra	British Museum
	Lutra perspicillata	British Museum
	Lutra sumatrana	Wilson & Reeder 1993
	Martes flavigula	British Museum
	Mustela lutreolina	Leiden, AMNH
	Mustela nudipes	British Museum
	Mydaus javanensis	British Museum
	Neofelis nebulosa	British Museum
	Paguma larvata	Wilson & Reeder 1993
	Panthera tigris	Wilson & Reeder 1993
	Paradoxurus hermaphroditus	British Museum
	Prionodon linsang	Wilson & Reeder 1993
	Ursus malayanus	Wilson & Reeder 1993
	Viverra tangalunga	Wilson & Reeder 1993
	Viverricula indica	Wilson & Reeder 1993
Swindle	*Canis lupus*	Cowan and Guiget 1956
Taiwan	*Aonyx cinerea*	Wilson & Reeder 1993
	Felis bengalensis	British Museum
	Felis viverrina	Wilson & Reeder 1993
	Herpestes urva	Wilson & Reeder 1993
	Lutra lutra	British Museum
	Martes flavigula	British Museum, Smithsonian
	Melogale moschata	British Museum
	Mustela sibirica	Wilson & Reeder 1993
	Neofelis nebulosa	Wilson & Reeder 1993
	Nyctereutes procyonoides	British Museum
	Paguma larvata	Smithsonian
	Ursus malayanus	Wilson & Reeder 1993
	Ursus thibetanus	Wilson & Reeder 1993
	Viverricula indica	British Museum
Tebing tinggi	*Arctictis binturong*	Meijaard 2003
	Arctogalidia trivirgata	Meijaard 2003

Island	Species	Specimen / Reference
	Felis bengalensis	Meijaard 2003
Telebon (Telibon)	*Paradoxurus hermaphroditus*	Smithsonian
Terutao (Ta Ru Tao)	*Arctogalidia trivirgata*	British Museum, Singapore
	Paradoxurus hermaphroditus	British Museum, Singapore
Texada	*Procyon lotor*	WorldWideWeb
Thasos	*Canis aureus*	Krystufek et al. 1997
	Martes foina	Masseti 1995
Thera (Santoríni)	*Martes foina*	Masseti 1995
	Mustela nivalis	Masseti 1995
Tiburon	*Bassariscus astutus*	MVZ
	Canis latrans	Kansas, MVZ
	Urocyon cinereoargenteus	Collins 1993
Tierra del fuego	*Conepatus humboldti*	Field
	Felis concolor	AMNH
	Lontra felina	Nowak 1991
	Lontra provocax	Redford & Eisenberg 1992
	Pseudalopex culpaeus	Smithsonian
	Pseudalopex griseus	British Museum
Tinos	*Meles meles*	Masseti 1995
Tioman	*Arctictis binturong*	Meijaard 2003
	Arctogalidia trivirgata	Meijaard 2003
	Paradoxurus hermaphroditus	British Museum
Tobago	*Procyon cancrivorus*	Wilson & Reeder 1993
Trinidad	*Eira barbara*	British Museum
	Felis pardalis	Wilson & Reeder 1993
	Lontra longicaudis	Redford & Eisenberg 1992
	Procyon cancrivorus	British Museum
Tukarak	*Alopex lagopus*	Carnegie Museum
	Mustela erminea	Carnegie Museum
	Vulpes vulpes	Carnegie Museum
Tuxekan	*Ursus americanus*	Conroy et al. 1999
Unalaska	*Mustela erminea*	Smithsonian
Unimak	*Canis lupus*	Smithsonian
	Gulo gulo	Peterson 1967
	Lontra canadensis	Peterson 1967
	Mustela erminea	Smithsonian
	Mustela nivalis	Smithsonian
	Mustela vison	Peterson 1967
	Ursus arctos	Peabody Museum
Urup	*Vulpes vulpes*	Kostenko 2002
Vancouver island	*Canis lupus*	Royal BC Museum, Smithsonian
	Felis concolor	Hall 1981
	Gulo gulo	Royal BC Museum
	Lontra canadensis	Royal BC Museum

Island	Species	Specimen / Reference
	Martes americana	Royal BC Museum, Amsterdam
	Mustela erminea	Hall 1981
	Mustela vison	Royal BC Museum, MVZ
	Procyon lotor	Hall 1981
	Ursus americanus	Hall 1981
Vargas	*Mustela vison*	Royal BC Museum
Victoria	*Gulo gulo*	Hall 1981
	Mustela erminea	Smithsonian
Vinal haven	*Lontra canadensis*	Crowell 1986
	Mustela vison	Crowell 1986
	Vulpes vulpes	Crowell 1986
Warren	*Canis lupus*	Melton 1982
	Lontra canadensis	Macdonald and Cook 1996
Whidby	*Mustela erminea*	Smithsonian
Wight	*Lutra lutra*	Corbet and Southern 1977
	Meles meles	Corbet & Harris 1991
	Mustela erminea	Corbet & Harris 1991
	Mustela nivalis	King and Moors 1979
	Vulpes vulpes	Harris et al. 1995
Woewodski	*Canis lupus*	UAF Museum
	Martes americana	Macdonald and Cook 1996
Wolin	*Martes martes*	WorldWideWeb
	Meles meles	WorldWideWeb
	Vulpes vulpes	WorldWideWeb
Woronkofski	*Lontra canadensis*	UAF Museum
Wrangell	*Canis lupus*	MVZ
	Gulo gulo	Conroy et al. 1999
	Lontra canadensis	UAF Museum
	Martes americana	Conroy et al. 1999
	Mustela erminea	UAF Museum, Smithsonian
	Mustela vison	Smithsonian
	Ursus americanus	MVZ
Yakushima	*Mustela sibirica*	British Museum
Yeo	*Canis lupus*	Darimont and Paquet 2002
	Ursus americanus	Marshall and Ritland 2002
Zakynthos	*Martes foina*	Mitchell-Jones et al. 1999
	Mustela nivalis	Mitchell-Jones et al. 1999
Zanzibar (Unguja)	*Bdeogale crassicauda*	British Museum
	Civettictis civetta	Haltenorth & Diller 1980, Kingdon 1977
	Galerella sanguinea	British Museum
	Genetta servalina	Van Rompaey & Colyn 1998
	Panthera pardus	British, MCZ
Zarembo	*Canis lupus*	Conroy et al. 1999
	Mustela erminea	Hall 1981
	Mustela vison	Conroy et al. 1999

Island	Species	Specimen / Reference
	Ursus americanus	Conroy et al. 1999

References are based on museum specimens I measured and then on literature sources, but a literature soure does not necessarily mean specimens were not measured. Nor is the list of souces or museums exhaustive – in many cases I measured specimens in more collection and/or obtained data on their presence on a particular island in more sources tan I list.