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Functional Ecology, Vol. 6, No. 3 (1992), 265-273.

Functional Ecology 1992
6, 265–273

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Summary

1. Body size influences the physiology, behaviour and community level interactions of organisms, but little is actually known about the factors that determine it. Close examination of evolution on islands may allow identification of pressures selecting on size.
2. In this study, I collected and analysed body length data for 13 insular populations of a small mammalian herbivore (genus *Neotoma*). I found a significant tendency for insular woodrats to be larger than mainland forms, and this outcome is significantly related to the absence of mammalian predation pressure.
3. Since gigantism may be a common phenomenon among small insular herbivores, I suggest that large size may be of physiological advantage under stressful conditions. The allometric relationship between metabolism and body mass predicts that larger animals will have lower specific metabolic rates, yet their gut size increases isometrically. Consequently, they may be able to obtain more energy from the microbial fermentation of plant fibres than smaller herbivores.

Key-words: Gigantism, Gulf of California, herbivory, islands, *Neotoma*

Functional Ecology (1992) **6**, 265–273

Introduction

The size of an organism affects virtually every aspect of its existence. Despite this, and considerable conjecture regarding the 'right size' (e.g. Haldane 1928; Rosenzweig 1968; Van Valen 1973a; Bourleire 1975; Case 1979), very little is actually known about why organisms are as large or small as they are. The study of insular animals, with their frequent incidences of dwarfism or gigantism (Foster 1964; Sondaar 1977), would seem to provide an ideal opportunity to investigate this fundamental property.

Foster (1964) was among the first to summarize information on trends in the body size evolution of insular mammals. He suggested that observed patterns could be explained in terms of trophic levels, with carnivores and ungulates showing consistent decreases. The strongest tendency was exhibited by small rodents, primarily cricetids and microtines (Case 1978), which in 60 of 69 instances increased in body length. Similar patterns have been reported elsewhere, including Britain (Corbet 1961) and the Gulf of California (e.g. Case 1978; Lawlor 1982), leading Van Valen (1973a,b) to generalize the phenomenon as the 'island rule'. Numerous theories incorporating factors such as predation, competition and limited resources have been proposed to explain such observations (cf. Grant 1965; Stanley 1973; Van Valen, 1973a,b; Case 1978; Heaney 1978; Lawlor 1982, 1983; Angerbjorn 1985; Lomolino 1985). At the same time, however, many investigators have drawn upon data that are limited due to small sample sizes and lack of replicate populations. Both problems have hindered the application of detailed statistics.

Here the body length measurements were collected and analysed for several species of a small mammalian herbivore (genus *Neotoma*) found on numerous landbridge islands off the Coast of Baja California, Mexico. Through a combination of museum visits and field trapping, it has been possible to enlarge the available data set by more than an order of magnitude. Statistical analyses corroborate Lawlor's overall observation (1982) that insular woodrats exhibit gigantism, although calculated changes for each island differ considerably from his. The relationship between body length variation and commonly cited influences such as predation, competition and island area are also examined. Results support the hypothesis that relaxation or amelioration of predation pressure is correlated with occurrence of gigantism. Finally, mechanisms that may partially explain the apparent propensity towards gigantism in small herbivorous rodents are discussed.

Materials and methods

Woodrats are small herbivorous mammals distributed throughout North America (Hall 1981); they

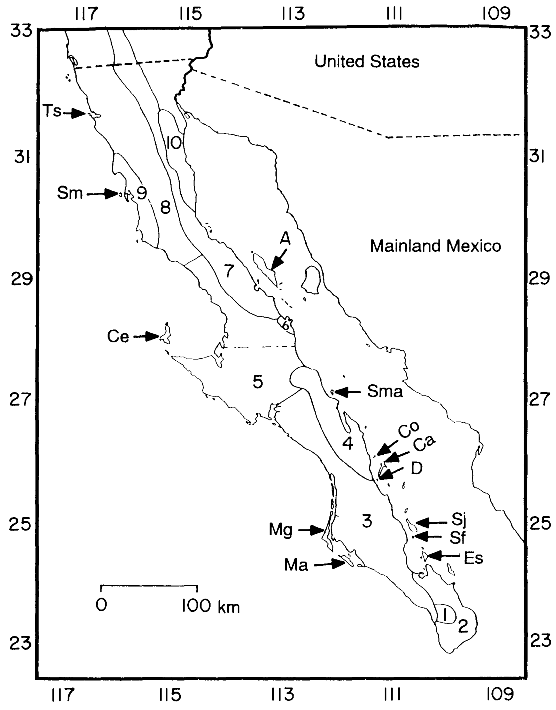

Fig. 1. Map of Baja California, Mexico. Islands: A, Angel de la Guarda; Sma, San Marcos; Co, Coronados, Ca, Carmen; D, Danzante; Sj, San José; Sf, San Francisco; Es, Espíritu Santo; Ma, Santa Margarita; Mg, Magdalena; Ce, Cedros; Sm, San Martín; Ts, Todos Santos. Mainland subspecies are represented by numbers: 1, *Neotoma lepida notia*; 2, *N. lepida arenacea*; 3, *N. lepida pretiosa;* 4, *N. lepida ravida*; 5, *N. lepida molagrandis;* 6, *N. lepida aridicola;* 7, *N. lepida gilva;* 8, *N. lepida intermedia;* 9, *N. lepida egressa*; 10, *N. lepida felipensis*. Species distributions are redrawn from Hall (1981).

also inhabit 15 islands off the coast of Baja California, Mexico (Fig. 1). With the exception of Angel de la Guarda, which is of oceanic origin, the islands were isolated from the mainland by the rising of the sea level some 5800–11 000 years ago (Durham & Allison 1960; Wiggins 1960; Milliman & Emery 1968; Gastil, Minch & Phillips 1983). Only the 13 populations derived from *N. lepida* (Huey 1964) and located off the coast of Baja California were studied, although two additional islands situated off mainland Mexico house a Sonoran species, *N. albigula*. Gigantism was reported in this genus by Burt (1932), Huey (1964) and Lawlor (1982, 1983).

During the course of the project over 1200 woodrat mounts were examined, of which 991 were suitable for inclusion in the final data set. Study skins were from collections housed at: Museum of Vertebrate Zoology (University of California Berkeley); Museum of Systematic Biology (University of California Los Angeles); San Diego Natural History Museum; Los Angeles County Natural History Museum; Museum of Zoology (University of Michigan); Museum of Zoology (University of Arizona); United States National Museum; and the American Museum of Natural History. Information recorded from each tag included the (sub)species, location trapped, museum catalogue number, sex, date of capture, total length, tail length, ear length, hindfoot length, mass (if reported), reproductive condition, collector and collector catalogue number. Skulls were measured for greatest length and zygomatic breadth. Body length was determined by subtracting the tail measurement from total length. When available, the original collectors' notes were consulted for additional information with respect to habitat, reproductive condition or exact trapping locality.

Juveniles, as determined by a combination of pelage condition/colour, collector notation, or skull morphology were excluded from the analyses. It was occasionally not possible to differentiate between a small adult and a subadult individual. Such specimens were retained in the data set.

Species lists for each island were compiled from published accounts (Burt 1932; Orr 1960; Wiggins 1960; Huey 1964; Soule & Sloan 1966; Vaughan & Schwartz 1980; Lawlor 1982; Cody 1983; Cody, Moran & Thompson 1983; Lawlor 1983; Murphy 1983), and verified in some instances by personal observations. Islands were then scored as to presence or absence of other rodent species, potential herbivorous competitors and potential predators.

Univariate and multivariate statistical analyses were performed, using both body and skull length. Overall conclusions were not particularly sensitive to the measure used, however, so only body length is reported here. Because significant heterogeneity of variance existed among the data, non-parametric statistics were employed whenever possible.

Statistics were calculated on mean body length and/or per cent change relative to the mainland, and performed separately for each sex to avoid spurious results attributable to skewed sex ratios. The most probable mainland source population was determined for each island by a combination of ocean depth profiles and data available from the literature (Durham & Allison 1960; Milliman & Emery 1968; Gastil, Minch & Phillips 1983; Maluf 1983). Procedures were conducted both with and without Angel de la Guarda but results did not vary with the inclusion of this oceanic island.

Results

SIZE CHANGES AMONG *NEOTOMA*

Table 1a summarizes woodrat body sizes on islands off the coast of Baja California. The change in body length relative to the most probable mainland source population is also given. Lengths of mainland forms are reported in Table 1b, with proposed island derivatives indicated. Means have not been adjusted for skewed population sex ratios, which in most instances would give larger positive deviations from

Table 1. (a) Body size (head–rump length excluding tail in mm±95% confidence interval) and sexual dimorphism in adult woodrats inhabitating islands off the coast of Baja California

		Male		Female		Unweighted mean*			%
Island	Species/subspecies	*n*	Length	*n*	Length	*n*	Length	Ratio	Change
Coronados	*Neotoma bunkeri* Burt	1	222·0±	5	216·4±14·55	6	217·3±11·26	2·59%	27·5%
Danzante	*N. lepida latirostra*	3	217·0±19·87	5	201·8±4·16	8†	207·5±7·78	7·53%	21·7%
Carmen	*N. lepida nudicauda*	3	181·7±18·97	8	191·5±8·90	11	188·8±7·12	−5·12%‡	10·7%
Angel de la Guarda	*N. lepida insularis*	7	186·9±10·88	4	172·5±10·75	11	181·7±8·21	8·35%	10·3%
Cedros	*N. bryanti* Merriam	27	200·1±7·22	31	192·0±4·72	58	195·8±4·20	4·22%	9·5%
San Marcos	*N. lepida marcosensis*	8	188·1±15·85	6	183·5±16·43	14	186·1±9.89	2·51%	9·2%
San Martín	*N. martinensis* Goldman	19	193·6±4·03	10	175·7±3·85	29	187·4±4·32	10.19%	8·5%
Todos Santos	*N. anthonyi* J.A. Allen	22	182·3±6·83	38	177·1±3·88	60	179·2±3·46	2·94%	6·2%
Sta Margarita	*N. lepida pretiosa*	8	198·4±9·52	13	191·5±5·49	21	194·1±4·70	3·60%	3·4%
Magdalena	*N. lepida pretiosa*	12	194·4±7·46	18	186·9±6·98	30	189·8±5·02	3·85%	1·1%
San José	*N. lepida perpallida*	13	183·9±9·14	16	172·3±4·74	29	177·5±5·03	6·73%	−5·5%
Espíritu Santo	*N. lepida vicina*	10	174·2±13·55	9	174·0±9·96	19	174·1±7·68	0·12%	−7·3%
San Francisco	*N. lepida abbreviata*	10	165·2±5·00	14	158·0±5·28	24	161·0±3·77	4·56%	−14·3%

Comparisons were made between insular derivatives and most probable mainland source population.

* Unweighted mean has not been adjusted for differences in sex ratios. Ratio represents degree of sexual dimorphism.

† Mass data available for an additional 41 animals.

‡ Negative ratios probably represent inclusion of subadults in the data set.

Table 1. (b) Body size (head–rump in mm±95% confidence interval) and sexual dimorphism of mainland subspecies of adult woodrats in Baja California

	Males		Females		Unweighted mean			Island
Subspecies	*n*	Length	*n*	Length	*n*	Length	Ratio	derivatives
Neotoma lepida arenacea	83	186·5±3·59	74	179·8±3·58	157	183·4±2·56	3·73%	
N. lepida aridicola	4	157·5±23·90	3	159·7±15·97	7	158·4±10·46	−1·38%	
N. lepida egressa	41	177·1±4·35	42	168·6±3·37	83	172·8±2·84	5·04%	*N. martinensis*
N. lepida felipensis	11	170·5±6·00	16	159·1±4·31	28	164·2±3·94	7·17%	
N. lepida gilva	17	168·2±3·74	8	156·9±5·61	26	164·7±3·50	7·20%	*N. lepida insularis*
N. lepida intermedia	13	173·8±7·46	14	164·1±8·35	27	168·7±5·54	5·91%	*N. anthonyi*
N. lepida molagrandis	46	182·4±3·74	48	175·3±4·36	94	178·8±2·92	4·05%	*N. bryanti*
N. lepida notia	27	174·9±5·43	26	169·7±4·43	53	172·3±3·48	3·06%	
N. lepida pretiosa	41	192·7±4·68	35	181·9±4·92	76	187·8±3·54	5·93%	*N. lepida abbreviata* *N. lepida perpallida* *N. lepida vicina*
N. lepida ravida	49	172·4±4·82	37	168·1±3·01	86	170·5±3·02	2·56%	*N. bunkeri* *N. lepida latirostra* *N. lepida nudicauda* *N. lepida marcosensis*

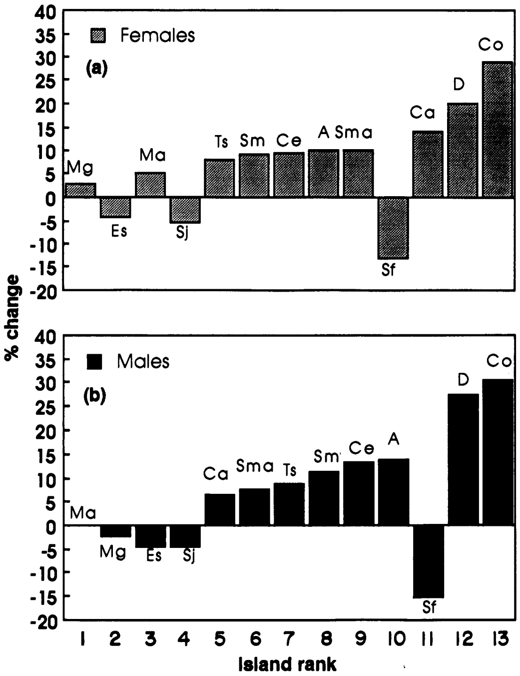

Fig. 2. Body length changes among insular *Neotoma*. A Wilcoxon signed-rank test ($n=13$, $P<0{\cdot}01$ for both sexes) suggests that there is a significant tendency for woodrats to increase in length when isolated on islands. The y-axis represents the per cent change of island woodrat with respect to presumed mainland counterpart; x-axis represents the absolute rank order — from smallest to largest deviations, irrespective of sign. Body length fluctuations were calculated separately for each sex. (a) Females only; (b) males. Mg, Magdalena; Es, Espíritu Santo; Ma, Santa Margarita; Sj, San José; Ts, Todos Santos; Sma, San Marcos; Ce, Cedros; A, Angel de la Guarda; Sm, San Martín; Sf, San Francisco; Ca, Carmen; D, Danzante; Co, Coronados.

the mainland. Sample sizes are small for both Coronados and Danzante islands. Only six specimens (five female, one male) are known from Coronados, and several recent expeditions to this island have failed to yield any further animals (K. Kleyboecker, personal communication; F.A. Smith, unpublished observations 1989, 1990). Live trapping of an additional 41 woodrats on Danzante, however (Vaughan & Schwartz 1980; F.A. Smith, unpublished observation), confirms the body size estimates suggested by the museum skins.

The per cent deviation in body length from the adjacent mainland population was calculated for each island. If size has altered randomly due to processes such as genetic drift or adaptation to heterogeneous selective pressures, then equal numbers of islands should demonstrate positive and negative changes of approximately the same magnitude. A one-tailed Wilcoxon's signed rank test rejects this null hypothesis (Fig. 2; females, $P<0{\cdot}01$; males, $P<0{\cdot}025$).

The paired comparisons are necessarily sensitive to the mainland subspecies chosen as ancestor, yet definitive information is lacking regarding not only the systematics of the group, but also subsequent evolution within it. For example, relatively shallow waters occur between several neighbouring islands. San José and San Francisco are separated by only 11 m, while the nearest mainland peninsula lies across a channel 64 m in depth (Gastil *et al.* 1983). In the absence of sedimentation or other geological processes, this suggests that the two constituted a single land mass until fairly recently, and thus may share a common evolutionary history for some portion of their isolation. The precise identification of 'source' populations awaits as yet unconducted genetic analysis. Accordingly, the data were pooled to test the more conservative hypothesis that *overall* insular *Neotoma* are larger than mainland forms. A one-tailed Mann–Whitney U-test was performed (Fig. 3) using the mean body length of each population. The null hypothesis of equivalent body size was rejected ($P<0{\cdot}01$ for both males and females), suggesting that insular woodrats have a significant tendency to exhibit gigantism. A two-way analysis of variance indicates that although males are significantly larger than females ($P<0{\cdot}001$), there is no interaction between species and degree of sexual dimorphism among either mainland or insular populations ($P>0{\cdot}8$; Table 1).

Measurements of both length and mass were available for approximately one-third ($n=370$) of the study skins. As expected, there is a significant regression of mass on body length (Fig. 4, $r^2=0{\cdot}64$, $P<0{\cdot}0001$). Although a linear model corroborates the prediction of a 1% length increase representing a 3% change in mass (cf. McMahon 1973), a second order model provides a significantly better fit (partial F-test, $P<0{\cdot}05$) and suggests for the range plotted, a 3–6% increase in mass for each 1% increment in length. This indicates that the largest insular woodrats (*c.* 230 mm) can exceed 400 g. Skull length is a slightly better predictor of mass than is body length ($r^2=0{\cdot}69$ *vs* $r^2=0{\cdot}64$). Presumably this is due to the reduced variation inherent in measurements made by a single researcher.

An underlying assumption in interpretation of the statistics is that potential collector biases or environmental heterogeneity are randomy distributed with respect to islands and mainland. In an effort to obtain information about the consistency of body length within a given geographical area, time analyses were performed on populations for which sufficient data existed. Collections in many instances spanned 100 or more years, although sampling periods were sporadic. The following criteria were used in compiling data for a one-way ANOVA:

1. Three or more sampling periods separated by at least 5 years.

2. A minimum sample size of five individuals of the same sex.

3. For mainland populations, trapping that was conducted at the same locality.

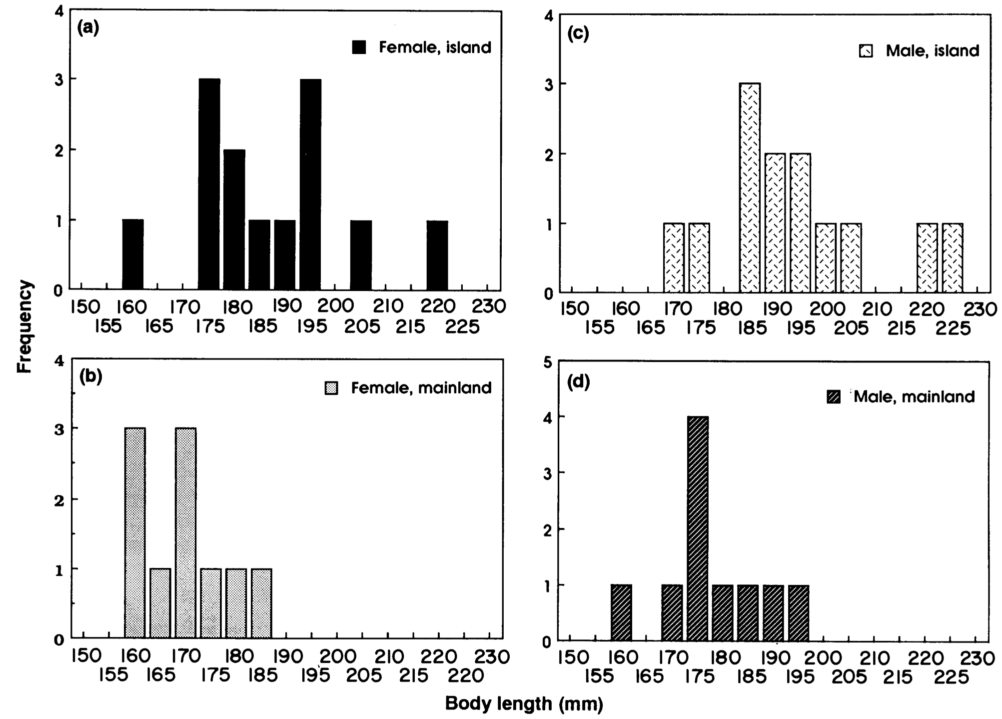

Fig. 3. Histograms of body length among populations of *Neotoma lepida*: (a,b) females, (c,d) males. Top graphs in each set refer to island populations, bottom graphs, adjacent mainland populations. The group mean for insular woodrats is significantly different than that of mainland populations (one-tailed Mann–Whitney *U*-test, $n_1=13$, $n_2=10$, $P<0{\cdot}01$ for both sexes).

Only four populations met such stipulations, and no significant increase in explained variation was found with the inclusion of time as an independent variable. Within the limitations of the data set, body size within a locality was remarkably consistent.

PHYSICAL AND BIOTIC FACTORS

Multiple regressions were performed to identify possible relationships between the degree of body size change and physical factors such as island area, time since isolation and distance of island from mainland (Table 2). No significant relationship was found between these variables and the degree of gigantism ($P>0{\cdot}1$; ratio data arcsine transformed). Likewise, the absence or presence of other rodent species (e.g. *Peromyscus, Perognathus*) is unrelated to the level of body size change (Mann–Whitney *U*-test, $P>0{\cdot}1$). Animals that could be construed as potential competitors include members of the genera: *Lepus, Sylvilagus, Thomomys, Odocoileus* and *Sauromalus* (Table 2). The latter is sympatric

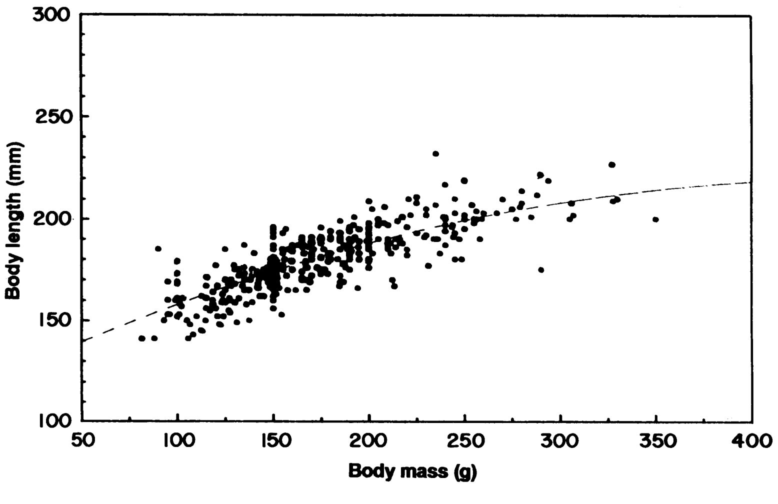

Fig. 4. Body length *vs* mass of *Neotoma*. Regressions were calculated separately for each sex, but since slopes were not significantly different, data are pooled. Equation of curve: $\text{length}=118{\cdot}23+0{\cdot}448x-0{\cdot}000494x^2$ ($r^2=0{\cdot}64$, $P<0{\cdot}0001$).

Table 2. Physical characteristics and biota of woodrat-inhabited islands off the coast of Baja California, Mexico

Island	Area (km^2)	Rank*	D† (km)	Time (years)‡	Type§	Competitors¶			Predators**		
						H	Pm	Pg	M	R	S
Todos Santos	1·2	8	6	9800	P	0††	×	0	0	—	—
San Martín	2·3	7	5	7500	P	0	×	0	0	—	—
San Francisco	2·6	13	8	—		G	×0	0	×	0	×
Danzante	4·9	2	2	8000	G	0	0	×	0	×	×
Coronados	8·5	1	2	6400	G	0	×	×	0	×	×
San Marcos	32	4	5	5600	G	0	0	×	0	×	×
Espíritu Santo	99	11	6	9800	G	×	×	×	×	×	×
Carmen	151	3	6	9300	G	×	×	×	0	×	×
San José	194	12	5	10 600	G	×	×	×	×	×	×
Sta Margarita	205	9	1	6800	P	×	×	×	0	—	—
Magdalena	290	10	1	6800	P	×	×	×	×	—	—
Cedros	348	6	24	9100	G	×	×	×	0	—	—
Angel de la Guarda	895	5	13	—		O	××	×	×	0	×

* Rank is body length of female woodrats from largest (1) to smallest (13).

† D represents the shortest distance from island to mainland, but may not necessarily be the last point of connection between the two land masses.

‡ Time of isolation is calculated from estimated divergence from the nearest adjacent mainland; in some instances islands may have remained connected with each other until fairly recently.

§ Type: G, gulf; P, pacific, O, oceanic island.

¶ Competitors: H, herbivores (*Lepus, Sylvilagus, Thomomys* and *Odocoileus*); Pm, *Peromyscus* spp.; Pg, *Perognathus* spp.

** Predators: M, mammals (*Canis, Bassariscus* and *Urocyon*); R, raptors (*Buteo jamaicensis, Falco peregrinus, Falco sparverius, Tyto alba, Bubo virginianus, Speotyto cunicularia*); S, snakes (*Crotalus* spp., *Elaphe rosalie, Hypsiglena* spp., *Lampropeltis* spp., *Lichanura* spp., *Masticophis* spp., *Pituophis* spp., *Salvadora hexalepis*).

†† ×, present; 0, absent; —, data unavailable.

with *Neotoma* on all Gulf islands and so was excluded from further analysis. There is a slight, non-significant trend towards decreased body size on islands with potential herbivorous competitors (Fig. 5a, $P>0{\cdot}1$), but when islands also containing mammalian predators (Table 2) are removed from the analysis (Fig. 5b), mean body size is essentially equivalent. The only factor tested that is significantly correlated with gigantism is the absence of mammalian predators, as illustrated in Fig. 5c ($P<0{\cdot}025$ for both sexes).

There was no significant correlation between the presence of avian or snake species and the degree of gigantism ($P>0{\cdot}1$). This is perhaps not surprising given the nearly ubiquitous distribution of snake species on islands (Soule & Sloan 1966; Murphy 1983; Table 2). It was difficult, however, to accurately compile species lists for raptors given their high mobility and ephemeral use of some islands.

Discussion

MAJOR FINDINGS

The results from this study clearly demonstrate that insular *Neotoma* exhibit gigantism in the Gulf of California (Figs. 2 and 3), confirming Lawlor's earlier prediction for the genus (1982, 1983). The significant relationship found between gigantism and the absence of mammalian predators (Fig. 5c) supports the frequent assertion that predation counters selection for larger body size in rodents (i.e. Falconer 1953; Cook 1961; Kurten 1971; Sondaar 1977; but see Lomolino 1985). Because small mammals generally cannot outrun predators, their usual strategy is to bolt down a burrow (Kurten 1971; Bourliere 1975; Heaney 1978; Lawlor 1982). Not only does a larger body render this behaviour more difficult, but a bigger animal is both more conspicuous and a more profitable food package (Kurten 1971; Stanley 1973; Bourliere 1975). Amelioration of predation may well allow expression of positive selective pressures acting on body size, but offers few clues to their nature. The identification of factors favouring larger body size has engendered a lively discussion in the literature. Many diverse factors have been proposed, including competition, thermoregulation, resource limitations, water conservation, and/or phylogenic constraints (Grant 1965; Kurten 1971; Stanley 1973; Van Valen 1973a,b; Case 1978, 1979; Heaney 1978; Lawlor 1982, 1983).

Interestingly, the results of this study suggest that the presence of other herbivores and/or rodents does not influence body size change in *Neotoma* (Fig. 5a,b). It could be argued that species composition on landbridge islands has altered since the time of their isolation from the mainland. Lawlor (1983) has in fact proposed that some insular fauna may be supersaturated with respect to classical island biogeography theory (MacArthur & Wilson 1967). Nevertheless, a more parsimonious explanation is that interspecific competition is not the driving factor behind island gigantism in woodrats.

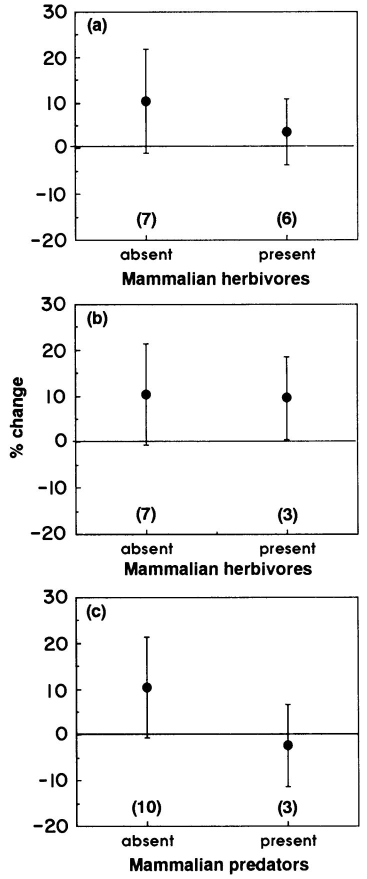

Fig. 5. Per cent change from mainland *vs* presence or absence of: (a) mammalian herbivores (predators also present); (b) mammalian herbivores only; (c) predators (herbivores also present). No island that contained predators lacked herbivores. A Mann–Whitney *U*-test fails to reject the null hypothesis for graphs (a) and (b) ($P>0{\cdot}1$, both sexes), but for graph (c) reveals a significant increase in woodrat body size on islands without predators ($P<0{\cdot}025$, both sexes). Data are presented only for females, results for males were similar. Values enclosed in parentheses are numbers of islands. Error bars are 95% confidence intervals.

RESOURCE AVAILABILITY AND BODY SIZE FLUCTUATIONS

In light of the apparent tendency within trophic levels for a common evolutionary response to isolation on islands (Foster 1964), many investigators have considered resource availability to be of primary importance in determining the direction of body size changes (Kurten 1971; Case 1978; Heaney 1978; Wassersug *et al.* 1979; Lawlor 1982). The lower diversity and abundance of insular food items is often cited as an explanation for dwarfism in carnivores and ungulates (Foster 1964; Kurten 1971; Sondaar 1977; Lawlor 1982). Conversely, gigantism in rodent species is frequently attributed to an expanded food base resulting from reduced competitive pressures, lack of predators (permitting access to previously restricted items) or the greater mobility of a larger animal (Grant 1965; Kurten 1971; Stanley 1973; Van Valen 1973a,b; Case 1978, 1979; Heaney 1978). Lawlor (1982, 1983) predicted that the dietary strategy of rodents would influence the direction of subsequent body size evolution. He argued that for specialists, metabolic conservation would drive dwarfism because of the overall level of depressed resources. Generalist species, however, would evolve larger size because it allows exploitation of a greater array of food sources.

These ideas do not explain gigantism in insular woodrats, which are dietary specialists. By comparison with mainland animals, they consume a very narrow range of vegetation, with a single species (ironwood), constituting almost three-quarters of the diet (Vaughan & Schwartz 1980; F.A. Smith, unpublished observation). It seems plausible, in fact, that metabolic considerations could also drive gigantism in certain types of specialists. Large size could be a physiological advantage under stressful environmental conditions. Brown & Maurer (1986, 1989), for example, have suggested that larger animals can extract greater amounts of energy and nutrients from a given food supply than can smaller animals, and Justice & Smith (1992) have argued that small herbivores may encounter mechanical limitations in the assimilation of poor-quality forage.

Generally speaking, small 'true' herbivores (e.g. *Neotoma* and *Microtus* species) maintain a hindgut fermentation chamber in the caecum that houses symbiotic microflora capable of digesting plant structural carbohydrates. The maximum chamber size has been empirically demonstrated to be approximately isometric with body mass (Parra 1978; Demment & Van Soest 1985; F.A. Smith, unpublished observations), unlike mass specific metabolic rates that increase allometrically (Kleiber 1961). Consequently, small herbivores typically have faster food passage rates (Parra 1978), a process at odds with the time-dependent nature of microbial fermentation (Justice & Smith 1992). Thus, as herbivores decrease in size, disproportionately less energy can be derived from plant fibres. A larger body permits consumption of low-quality food, which may be more freely available in insular situations. For example, when ironwood (a drought deciduous plant) drops its leaves, woodrats on Isla Danzante subsist primarily on the bark of the plant (T. Vaughan, personal communication), an option potentially unavailable to herbivores of smaller size.

PROBLEMS WITH EARLIER INVESTIGATIONS

Collectively, theories of size fluctuations in the current literature often seem to be in conflict with one another, but at least some of the contradictions might be resolved under closer scrutiny. Although many investigators have linked body size changes to resource availability, there has been a tendency to consider rodents as a unit (i.e. Foster 1964). Moreover, even when rodents have been more fully characterized, it has usually been by family, which does not always accurately describe dietary proclivities (i.e. Lawlor 1982, 1983; Lomolino 1985). The Muridae, for example, contain both the generalist omnivore *Peromyscus*, and *Neotoma*, a true herbivore and quite specialized dietarily. The two genera have sometimes been considered jointly in nutritional explanations for gigantism despite their disparate diets (i.e. Lawlor 1982, 1983). Only Angerbjorn (1985) and Lomolino (1985) calculated comparisons based on individuals of the same sex, and both Lomolino (1985) and Lawlor (1982) have decried the use of inappropriate mainland comparisons with insular forms. In the present work, both paired and pooled comparisons led to the same conclusion.

Small sample sizes have led to conclusions that may be unsubstantiated. Hall's (1938) description of insular body size in *Peromyscus* from Canada has been cited as an example of gigantism (i.e. Case 1978), yet only three of the six islands he discussed contained animals larger than the mainland average. Lawlor (1982, 1983) reported roughly equivalent numbers of increases (seven) and decreases (six) for *Neotoma*, and then suggested that the data support the concept of gigantism in this species. *Peromyscus* in the Gulf of California appear to provide an unequivocal confirmation of gigantism in omnivorous rodents, with size increases reported on 19 of 28 islands (Lawlor 1982, 1983). If data are segregated by island type, however, equivalent numbers of land-bridge islands demonstrate increases as decreases. In fact, body length has only significantly increased on oceanic islands, where migration biases favouring large size (e.g. increased buoyancy, fasting and/or swimming abilities) offer plausible alternative hypotheses. Lastly, it should be noted that analyses of mammalian body size have often relied solely on published species accounts. The present work demonstrates that greatly increased sample sizes can be obtained through the inclusion of museum specimens.

Acknowledgements

I thank D. Tesluk for her assistance in handling museum specimens and R.E. Lenski for helpful advice. R.E. Lenski and S.M. Elliott kindly provided comments on the manuscript. Many thanks to the various curators and curatorial associates I received assistance from during the course of this project; especially J.L. Patton and P.A. Kelly at the MVZ, M.D. Carleton and J. Marshall at the USNM, and G. Musser at the AMNH. Portions of the research reported here were supported by grants from: American Museum of Natural History, National Science Foundation (doctoral dissertation grant BSR-8815175), University of California Consortium on Mexico and the United States, and University of California Intercampus Travel Awards.

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Received 2 March 1991; revised 11 November 1991; accepted 11 November 1991