Island/mainland body size differences in Australian varanid lizards

Ted J. Case[1], Terry D. Schwaner[2]

[1] Department of Biology, C-016, University of California at San Diego, La Jolla, CA 92093, USA
[2] Alabama School of Mathematics and Science, PO Box 161628, Mobile, AL 36616, USA

Abstract. Island varanids seem to be an exception to the rule that territorial vertebrate taxa often become gigantic relative to mainland relatives when on islands, whereas non-territorial species become dwarfed (Case 1978). However, no systematic island/mainland studies have examined the empirical size trends in this group of carnivorous lizards. We perform such an analysis for the Australian region and critically evaluate various selective agents that might be responsible for size changes in several island populations. Insular gigantism occurs at least four times among the island populations examined. The magnitude of size change is positively correlated to prey abundance on the islands (as indirectly measured through a condition index of the lizards, essentially a measure of how fat they are) and the size of prey: islands with large prey have large varanids and vice versa. Since the island population with the largest size change, the Reevesby *Varanus rosenbergi*, was introduced less than 100 years ago, these size changes can be quite rapid. This might indicate that selective coefficients are strong; however, we can not exclude the possibility that these size differences have no genetic component and simply reflect environmental differences in growth rate and shifts in age structure between island and mainland locations.

Key words: Lizards – Islands – Gigantism *Varanus*

Body size is an easily measured phenotypic trait that often shows tremendous inter- and intraspecific variation from island to island or island to mainland. Many vertebrate groups display predictable and striking differences in body size between closely related island and mainland forms (Foster 1964; Case 1978; Carlquist 1965; Reese 1989; Hooijer 1951). For example, among cricetid rodents, island forms are typically larger than mainland relatives while among artiodactyls, elephants, hippos, and carnivores, the reverse is often the case (Foster 1964; Angerbjörn 1986; Lister 1989). Among reptiles, some taxa like

tortoises and iguanid lizards are typically large on islands while other groups like snakes are often dwarfed (Reese 1989; Soulé 1966; Schoener 1969, 1970). Case (1978) reviewed these varied size trends and found a loose association between insular gigantism and territorial taxa, on the one hand, and insular dwarfism and non-territorial taxa, on the other.

Models of optimal body size predict that optimal body size should be directly related to food availability (Schoener 1969; Case 1978) and therefore, given heritable variation in body size, size might evolve to be larger in isolated populations with sustained higher food levels. Food availability may be greater on islands because of the loss of competitors, a more benign maritime climate, or reduced threat from predation leading to more freedom in foraging activities. Yet, in the absence of much predation and competition, island population sizes are expected to rise. In turn, this higher population size could mitigate any enhanced food productivity: more consumers would make larger demands on their food supply. Territoriality would dampen this density compensation so that a higher ratio of food supply per consumer would still exist in islands compared to mainland populations. Non-territorial species are in potential danger of seriously over-exploiting their island resources (once freed from predators) and should exist at lower levels of food supply/consumer than mainland populations. All this assumes that consumers have some impact on the growth rate of their resources and this may not be the case in many situations (Andrewartha and Browning 1961).

As with other biogeographic rules, Case (1978) also found numerous exceptions to the association of relatively large size in island races or species that are territorial compared to mainland relatives. Social structure also affects optimal body size. For promiscuous/polygamous species, intraspecific competition among males for females may become intensified if densities are high as in insular situations. Since larger males are usually socially dominant, hold larger territories, and mate with more females (Stamps 1983, Brattstrom 1974), selection may act directly on males leading to larger male body size; female size might also increase simply as a correlated character

Correspondence to: T.J. Case

(females share the same genes as males except on the sex chromosomes).

For species in which prey handling ability is closely related to prey size, body size may shift in response to a shift in the size spectrum of their food. For example, if a small-sized competitor was missing from an island, the availability of small-sized prey might be greater, in turn, favoring a decrease in body size even in territorial species (i.e. character displacement or conversely character relaxation). In this way, a species' body size might be more closely related to the body size of available prey than overall prey abundance. For example, this appears to be the case for black tiger snakes (*Notechis ater niger*) on islands off southern Australia (Schwaner 1985, 1990; Schwaner and Sarre 1988, 1990; Williams et al. 1988; Shine 1987).

Exceptions might also arise because of differences in the numbers and variety of predators. The common defense of small animals is to escape into numerous hiding places since their small size allows quick entry. The smaller the animal, the greater the availability of predator-proof refuges and the greater importance of hiding as a predator defense. The absence of large predators on islands may allow larger size in their prey.

Varanids are wide-ranging, active foraging, carnivorous lizards that generally do not defend exclusive feeding territories (Pianka 1968; Green and King 1969; Auffenberg 1981). Examples of dwarfism among varanids were mentioned by Mertens (1934). He included instances in Indonesia (*Varanus salvodori*), the Bismarks (*V. indicus*), and Monte Bello island off Western Australia (*V. gouldii*). In the latter case, however, Mertens' conclusion seems to be based on a single specimen (pg 67).

Here, we quantify the island-mainland size differences in three Australian varanid species and examine two alternative food-based hypotheses for their possible origin. Our focus on food-based hypotheses, rather than predators, is because in the Australian fauna today the most serious predators of large varanids are humans and introduced dingos. All the islands that we discuss lack these predators. All the islands in this study are xeric, post-Pleistocene land bridge islands with isolation times from the mainland of only 5–15 thousand years (Robinson et al. 1985).

Methods

Rationale

If body size in varanids increases with increases in the per-capita food supply (Case 1978), then populations of relatively large body size will be a) insular; b) associated with higher food levels and c) occur at lower population densities. If body size in varanids responds more to changes in the body size of available prey, then large-body-sized varanid populations will be a) insular or mainland depending on the available prey size distributions in the two places; b) associated with large-sized prey; and c) uncorrelated with varanid population density.

Notice that these two mechanisms are not mutually exclusive. To distinguish relative role of the two, it is necessary to have measures of both prey abundance and prey size distributions in both island and mainland sites. With most lizards it is difficult to get an accurate measure of prey abundance. Defining what is an acceptable and "available" prey demands a keen understanding of the animal's gestalt. More fundamentally, prey abundance is subject to much environmental variability in desert habitats. It may be impossible to extrapolate from present differences in prey abundance between populations to those in the distant past. Here we use the animal's body fat condition as a bio-assay of recent-term food availability. Animals that have been successful foragers during their recent life (at least one growing season) will have more food in their stomachs and more stored food in the form of fat bodies. They will be relatively heavy for their length compared to animals that have been unsuccessful foragers. Thus the y-axis deviations from the y = log body mass versus x = log snout-vent length is a useful measure of body condition and indirectly of recent food abundance, provided that these residuals are homoscedastic. Condition of different populations of the same species (e.g. insular and mainland) can be compared by examining the log weight-residuals of animals from that location to the regression line (log weight vs log snout-vent length) based on all populations pooled.

This condition index would fail as a practical measure of food abundance if all excess food beyond maintenance costs was converted immediately into linear growth, rather than fat storage or egg production. Lizard linear growth rates are positively correlated with food availability (Schoener and Schoener 1978; Dunham 1978; Andrews 1979, 1982; Roughgarden and Fuentes 1977; Case 1982), however, there is nearly always a lag time between assimilation and growth and reproduction in poikilotherms and fat and/or glycogen storage is the intervening step (Andrews 1982).

The range of prey size available eaten by a varanid species is determined from stomach contents of lizards from all pooled populations. The range of prey sizes available for a given species in a given local is then determined by faunal surveys using the potential prey lists compiled from stomach contents. Pianka (1970, 1982), Shine (1986), James et al. (1992), Losos and Greene (1988), and King and Green (1979) present exhaustive lists of prey items for many varanid species and the museum specimens that we have examined add no qualitatively new items. We use our own faunal surveys supplemented with published faunal records from each island location to make a list of the available prey items at each site. For example, the largest individuals of *V. rosenbergi*, which happen to be insular, can eat penguin chicks but not adult penguins. We therefore consider penguin chicks an available prey item when they are present at a location, even if the local population of *V. rosenbergi* at that site is too small to consume them. Adult penguins are never considered as available prey. We have not determined the relative abundance of different-sized prey at each location. Varanids may kill their own prey as well as scavenge on already-dead items. Large prey items are more frequently scavenged than small. For example, on Kangaroo island, *V. rosenbergi* will scavenge on road-kill kangaroos, yet adult kangaroos are too large to be killed by these varanids. Prey items that are solely scavenged are not included.

Phenotypic mean body size differences between populations may be purely environmental responses to differences in food availability with no evolutionary and genetic differentiation. It is especially difficult to distinguish between genetic and environmental causes of body size differences in slow and continuous growing reptiles such as these varanid lizards. Barnett and Schwaner (1985) were able to demonstrate that new-born tiger snakes from an island of giant adults, raised in the laboratory and fed *ad libitum*, grow significantly faster than those in the field. Schwaner (unpublished) has also found that in young snakes raised in the laboratory and fed similar diets, snakes from populations with large adult size grow significantly faster than those from dwarfed populations indicating that these size differences are at least partly genetic. We have not attempted such studies with varanids so our study is, by itself, mute on this important distinction.

Museum specimens

We measured all the island and mainland varanids available in the South Australia Museum, Adelaide and the Western Australia

Museum, Perth in the following species: *V. gouldii*, *V. rosenbergi*, and *V. acanthurus* (sample sizes appear in Tables 1 and 2). The first two of these species are similar in size and habits and were formerly considered as only subspecies of *V. gouldii* (Storr 1980). In varanids, sex determination is difficult because there are no outward secondary sexual characteristics in most species. Reliable sex determination is based on the presence or absence of a hemi-penis and testes or ovaries. Since this often entails destructive sampling, sex was not determined on all individuals. Snout-vent length was measured to the nearest mm using a meter stick. Specimens from the South Australia Museum were then blotted dry of alcohol and weighed using spring scales, usually to the nearest gm. We could not locate two specimens of *V. gouldii* that were measured by Storr (1980) at the Museum of Western Australia and included in his monograph. These two specimens (Nos. 14666 and 24811) apparently no longer exist.

Field work

King and Green (1979) and Green and King (1978) conducted a long-term study of *V. rosenbergi* on Kangaroo island and *V. gouldii* on coastal South Australia. King (pers. comm.) has generously supplied us with his raw size data. Many animals in his study were placed in

Table 1. Snout-vent length comparisons for lizards of different sexes, species, regions, and collected from different seasons for *Varanus rosenbergi* and *V. gouldii*. Only individuals greater than 240 mm snout vent are included in the comparisons ($N > 240$ mm). Snout-vent (SV) is log-transformed. Unpaired t-test comparisons are made between pairs of populations or ANOVAS if more than two groups are compared

Group	N	Mean log SV	p
Comparison: SEASON; Group: Kangaroo Island V. rosenbergi.			
Spring/Summer	203	2.602	0.170
Fall/Winter	69	2.611	
Comparison: SEX; Group: Kangaroo Island V. rosenbergi			
Males	27	2.588	0.0017
Females	13	2.529	
Comparison: SEX; Group: Mainland V. rosenbergi			
Males	26	2.521	0.050
Females	10	2.481	
Comparison: SEX; Group: Mainland V. gouldii			
Males	58	2.458	0.0028
Females	30	2.491	
Comparison: REGION; Group: Mainland V. rosenbergi			
South Australia	10	2.540	0.058
Western Australia	33	2.504	
Comparison: REGION; Group: Mainland V. gouldii			
South Australia	48	2.490	0.032
Western Australia	71	2.473	
Northern Territory	15	2.512	
Comparison: SPECIES; Group: South Australia V. rosenbergi and V. gouldii			
V. rosenbergi	10	2.540	0.014
V. gouldii	48	2.490	
Comparison: SPECIES; Group: Western Australia V. rosenbergi and V. gouldii			
V. rosenbergi	33	2.504	0.013
V. gouldii	71	2.473	

the South Australia Museum and we can thus compare masses and lengths before and after fixing; this allows an estimate of live body sizes of animals from populations for which we only have preserved specimens.

Additionally, we personally studied and collected *V. rosenbergi* from Thistle Island, Spilsby Island, and Reevesby Island as well as from South Australia and Western Australia mainland locations. Mass, length, and sex were determined from live animals collected during 1984–1985. During this field work we estimated the relative abundance of varanids based on timed encounters with animals or animal signs (burrows, scats, and tail drags). TJC counted the number of such signs seen in three hours of search per site. Such are very crude abundance estimates can not be converted into absolute densities. We use them only as a way of crudely comparing the relative rank abundance of animals between island-mainland pairs.

Body-size comparisons between populations

Mean body size for lizards is not a useful index of the maximum size attainable in a population because it is highly influenced by the age distribution of the population when it was sampled. On the other hand, the maximum body size is highly sensitive to the total sampling effort. Case (1976) used the upper decile body size as a compromise but this measure lacks confidence intervals and straightforward statistical comparisons are lacking. Here we use the mean body size of all individuals which are greater than a threshold size, T; The actual minimum size for reproductive maturity is difficult to know with certainty because reproduction in these varanids is highly seasonal (King and Green 1979). Many individuals that do not show enlarged testes or ova could still be reproductively mature. The smallest gravid female of *V. gouldii* and *V. rosenbergi* in our sample was 250 mm and 255 mm respectively. For *V. rosenbergi* and *V. gouldii*, we chose T as 240 mm, which was the lower trecile of the mainland populations for both these species (see Fig. 1). We refer to animals above size T as "adults". For *V. acanthurus*, we excluded individuals below T = 130 mm, which again was the lower trecile of the size distribution, however size at reproductive maturity here is unknown. (Fig. 1).

In comparing size differences between populations, we chose to keep a constant T, rather than a relative value, even though populations may differ in mean and maximum body size. This means that dwarf populations will have fewer individuals and only the largest individuals will be included in the sample of "adults"; "gigantic" populations will have relatively more individuals included in the "adult" sample than should be. In both cases, the bias is such to make it more difficult to prove directional size changes: i.e. significant dwarfism or significant gigantism compared to an intermediate sized population. Thus by using a fixed T, we provide a conservative test of between-population body size differences compared to that of using a sliding T, different for different populations. We feel that this conservative statistical approach is justified because we will be making multiple comparisons and there is the possibility that Type I errors may slip in.

Results

Sexual dimorphism in size

To compare size differences between populations we must be aware of potential size differences between the sexes that could confound comparisons between populations with different sex ratios. The sex ratio is usually skewed toward males (Fig. 2, Table 1). For mainland *V. rosenbergi* and *V. gouldii*, males reach adult snout-vent lengths that are about 12% larger than females (t-tests < 0.05). The

Table 2. Island/Mainland size contrasts for varanid populations. Snout-vent lengths were first log transformed. Only individuals whose snout vent exceeds T are considered. The "Trend" indicates the direction of size differences for islands relative to mainland populations (ND = no significant difference) and the size ratio shows the island population's mean adult sv (before log transformation) divided by that of the constrasting mainland population.

Species/Group	N (after truncation)	Mean log SV	p (t-test)	Trend (size ratio)
V. rosenbergi:				
Mainland South Australia	10	2.540		
Islands:				
Kangaroo Island	309	2.600	0.0003	Giant (1.15)
Reevesby Island	4	2.697	0.0001	Giant (1.43)
Thistle Island	16	2.575	0.061	ND
Spilsby Island	4	2.624	0.0275	Giant (1.21)
Taylors	4	2.542	0.936	ND
V. gouldii				
Mainland Western Australia	71	2.472		
Islands:				
Wardang	4	2.590	0.0002	Giant (1.31)
Bernier	4	2.453	0.534	ND
V. acanthurus				
Mainland Western Australia	63	2.230		
Islands				
Barrow	3	2.150	0.039	Dwarf/ND (0.83) (see discussion)

same is true for the *V. rosenbergi* population on Kangaroo Island. Below, before we compare body sizes, we first perform a contingency analysis to determine whether the sex ratio is significantly different between comparison populations. If not, we combine both sexes. In Fig. 3 we show the length/weight (log transformed) relationship for the two sexes. Neither slopes nor intercepts for the sexes are significantly different (ANCOVA; $p > 0.5$).

Size/Weight relationships

Since we use lengths and weights of preserved museum specimens as well as freshly-caught field animals in our analyses, we must first determine the average degree of shrinking in length and weight so that we can correct for differences in size due to preservation. We have both fresh and preserved lengths and weights for a subsample of 5 Kangaroo Island *V. rosenbergi*. These were collected by Dennis King during 1966–1972 and were preserved for roughly 14–18 years before they were again measured at the South Australian Museum. We also have lengths and weights for two Reevesby Island *V. rosenbergi* alive and after being preserved for 2 weeks. We have determined that shrinkage is about two percent in snout-vent length and is independent of body size. Below when we compare sv between populations we multiply the lengths of museum specimens by this small correction factor (1.02). Interestingly, the length-weight relationship for preserved and field collected specimens are nearly identical so the condition indices of the two groups can be lumped (ANCOVA; $p > 0.8$).

Specimens have been collected during many times of the year and this could potentially confound size differ-

ences and the condition indices of the individuals. On Kangaroo Island, Green and King (1978) made a systematic effort to collect *V. rosenbergi* specimens from all times of the year so we can test for season effects at this site. We lumped specimens into two groups Fall/winter (April–August) and Spring/Summer (September–March) and performed a t-test on log snout-vent (Table 1). There are no significant differences ($p > 0.17$, $N = 203$, 69).

We examined residuals from log weight vs log sv regressions in mainland *V. gouldii* and mainland and Kangaroo Island *V. rosenbergi* to see if the linear regression provided a good fit and to see if there was any systematic relationship between the value of residuals and log body length. There is no tendency for residuals to change in value with log sv in animals above size T (linear regression, $p > 0.8$ in all three species). The squared deviations (residual variance) decreases slightly but significantly in *V. gouldii*, increases slightly but significantly in Kangaroo Island *V. rosenbergi*, and is statistically independent of log sv in mainland *V. rosenbergi*. In short we find no reason to expect a systematic bias in the condition index with a lizard's body length.

Regional differences in mainland populations

Mainland specimens have been collected from different parts of their ranges so it is necessary to determine if size and weight differences exist before comparing different mainland populations to off-shore island populations. The largest mainland *V. gouldii* occur in the Northern Territory where we have no islands from which lizards were measured. Table 1 shows a tendency, although not quite significant, for both *V. rosenbergi* and *V. gouldii* to be
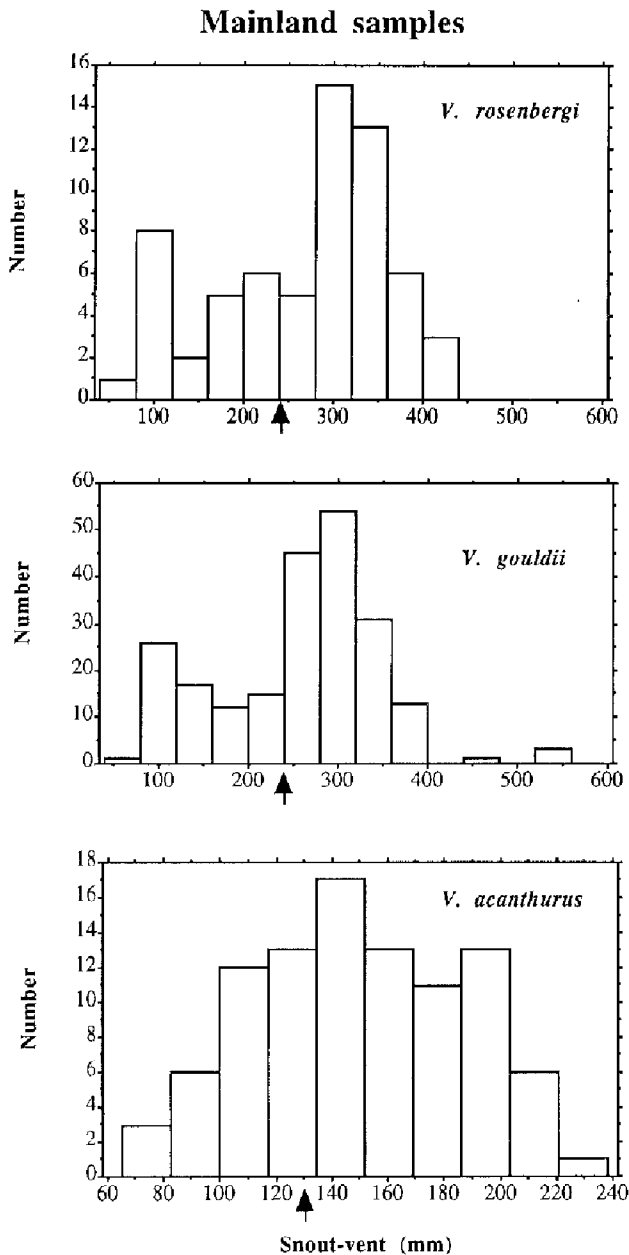
Mainland samples

Fig 1. Histograms of the snout-vent lengths of mainland populations of three species of *Varanus*. Only animals larger than T (the arrow) are used in latter statistical comparisons. Note the change in scale of the x-axis in the bottom subfigure

V. rosenbergi

Fig 2. A histogram of the snout-vent lengths of *Varanus rosenbergi*. This is the pooled sample of all specimens (from both islands and mainland sites) whose length and sex is known. Males tend to be more numerous in the population and average slightly larger in body size

Fig 3. The relationship between log weight (g) and log snout-vent (mm) for both sexes of *V. rosenbergi*. This is the pooled sample of all specimens whose lengths, weights, and sexes are known. The dotted regression line is for males and the solid line is for females. The two regression lines are not significantly different from each other

larger in South Australia than Western Australia. Since we have islands off both these coasts, we only compare insular populations of both species to the mainland population from the same state. Also within the same mainland region, *V. rosenbergi* is slightly larger than *V. gouldii*.

Island/Mainland size contrasts

Table 2 summarizes those comparisons that can be made between island and mainland populations. In each case we compare the island population to the mainland population in the adjacent mainland state. However, none of our
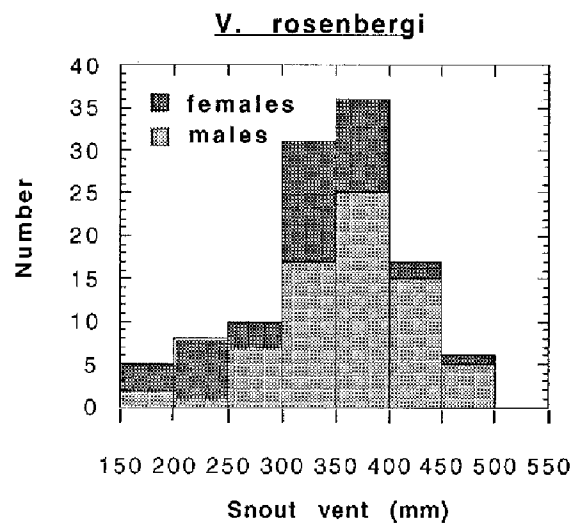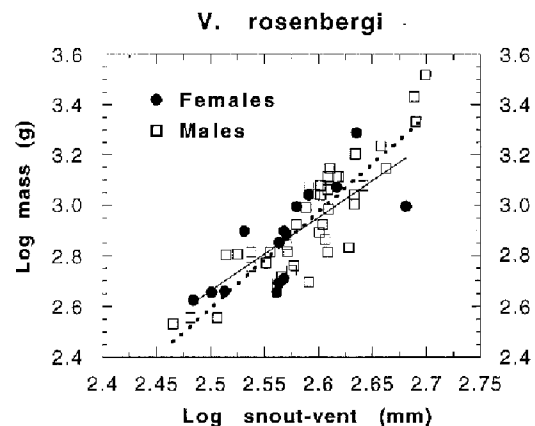
results are substantially altered if we use the entire mainland population instead of just the adjacent state. For *V. rosenbergi* we find examples of significant gigantism on Kangaroo Island, Reevesby Island, and Spilsby Island. On Thistle, the gigantism is less and not quite significant ($p = 0.061$). We find no cases of dwarfism in *V. rosenbergi* although two (out of five) insular populations do not differ significantly from mainland populations. Among the gigantic insular populations, *Varanus gouldii* is relatively gigantic on Wardang Island (even though we only have four animals whose size exceeds T) but not significantly different on Bernier (but again N is only 4). The apparent dwarfism of *Varanus acanthurus* on Barrow island is based on only three adult specimens and collecting bias could have produced this apparent trend (see discussion). The magnitude of island/mainland size differences, where significant, exceed those realized between different

geographical regions of the mainland for *V. gouldii* and *V. rosenbergi* (Table 1 compared to Table 2).

Body size and body condition index

Figure 4 contrasts the log sv vs log wt residuals of all *V. rosenbergi* populations for which we have simultaneous weight and snout vent data. Populations which have heavier, more robust lizards for their length appear higher on the y-axis. Populations with thinner individuals are lower. For both axes, the mean plus and minus one st. error is shown. The largest sample available for *V. rosenbergi* is the Kangaroo Island population ($N = 296$ individuals whose weight and snout vent are known). There is a significant linear correlation between a population's mean condition index and its mean snout-vent length ($p < 0.025$).
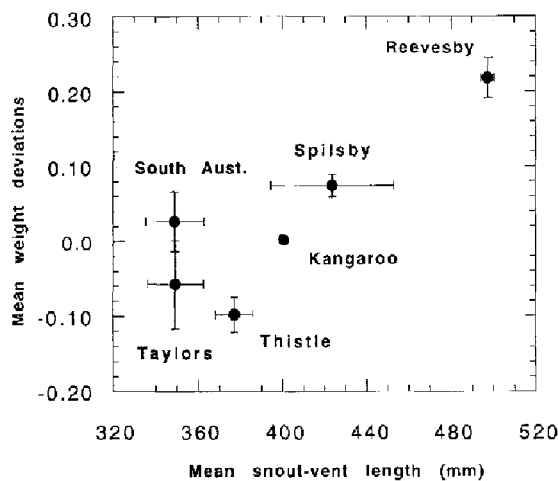

Fig 4. The average condition indexes (log weight residuals) for various *V. rosenbergi* populations are compared to their mean adult log snout-vent lengths (sv in mm). Populations which have heavier, more robust lizards after controlling for sv appear higher on the y-axis. Populations with thinner individuals are lower on the y-axis. For both axes, the mean value plus and minus one st. error is shown. There is a significant linear correlation across population between their mean condition index and their mean adult snout-vent length

A one tailed *t*-test was used to compare the residuals for *V. gouldii* adults on Wardang Island to those of mainland *V. gouldii* adults. In spite of the small sample size for Wardang ($N = 4$), the contrast was significant at $p < 0.035$; the mean residual for Wardang was significantly greater, implying that the relatively gigantic Wardang animals also have a higher condition index on average than conspecifics on the mainland.

Body size and prey size

Table 3 shows the range of prey sizes available on islands where the insular population is either gigantic, dwarfed, or similar in size to the same species on the mainland. For the set of species for which we have adequate size data, the relatively gigantic individuals occur exclusively on islands where large prey items are available (e.g. rabbits, mutton birds, petrels, rats, etc). However, large prey are available for the *V. acanthurus* on Barrow Island, yet this population is dwarfed relative to the mainland. Another deviation is the *V. gouldii* on Bernier Island. Although we only have four adult specimens from this island (large than size T), their average snout-vent length is slightly smaller than mainland forms, although not significantly so, even though this island has large prey in the form of bandicoots and breeding seabird populations.

Discussion

Based on eight island/mainland contrasts we find significant insular gigantism in half the populations and significant dwarfism in one. The one case of dwarfism occurs in *V. acanthurus*, which is the smallest of the three species considered here, so the different size trends are not simply a reflection of niche relaxation, in which smaller species become large on islands while larger species reduce to intermediate sizes. The gigantism in *V. rosenbergi* can be quite dramatic; the 43% snout vent increase on Reevesby Island reflects more than a doubling in average adult body weight.

Table 3. The prey sizes available to varanids on different islands and the body size of the endemic insular varanid relative to their mainland relatives

Island	*Varanus* species	Large prey	Small prey	Relative size
Kangaroo, SA	Rosenb.	carrion, penguin chicks, rats	mice, lizards, arthropods	Giant
Spilsby, SA	Rosenb.	rabbits	mice, lizards, arthropods	Giant
Wardang, SA	Gouldii	rabbits, penguin chicks	mice, lizards, arthropods	Giant
Reevsby, SA	Rosenb.	storm petrels and chicks	mice, lizards, arthropods	Giant
Thistle, SA	Rosenb.	none	mice, lizards, arthropods	No diff
Taylors, SA	Rosenb.	none	mice, lizards, arthropods	No diff
Bernier, WA*	Gouldii	bandicoot, seabird chicks	mice, lizards, arthropods	No diff
Barrow, WA†	Acanth.	rats, seabird chicks (bandicoots)	mice, lizards, arthropods	No diff/dwarf

Notes: "Giant", "Dwarf", or "No diff" refer to significant body size differences between the island and adjacent mainland populations at $p < 0.05$. The dwarf trend of *V. acanthurus* on Barrow island is based on a sample of three adult individuals. Bandicoots are present on Barrow but are too large for consumption by *V. acanthurus*

Rats include *Rattus fucipes* and *Rattus rattus*

* Bernier Island also has a sympatric population of the similar sized species *Varanus panoptes*

One note of caution is that of the eight insular populations, six are represented by sample sizes of 3 of 4 individuals above the threshold size T. With such small samples sizes, we must ask whether there might be collecting bias in these insular populations. A sex bias seems unlikely since our statistical tests of sex ratio reveal no differences between islands and mainlands. A seasonal bias is unlikely to lead to a body size bias, since our island samples are (like the mainland samples) predominantly from spring/summer. Moreover, on Kangaroo Island, where Green and King (1978) and King and Green (1979) collected individuals throughout the year, there was no seasonal fluctuation in mean snout-vent length. It is our belief that the most likely bias for island populations, is one in which collectors might avoid taking the very large individuals for lack of storage space for preservative and specimens on boat trips under cramped conditions. In the case of Reevesby Island, where we did field work in two separate years, we saw but did not capture, two additional specimens of *V. rosenbergi* that visually appeared to be as large (if not larger) than the specimens that we did manage to capture and measure. We therefore believe that the cases of insular gigantism are most probably real, and not a sample bias. However, it is difficult to be as sanguine for the solitary case of dwarfism in Barrow Island *V. acanthurus*.

These body size differences are paralleled by geographic differences in the amount of available prey, as revealed by the condition index of the animals and by differences in the body size of the available prey, but in neither case is the association perfect. We are unable to reject the null hypothesis that these factors do not influence body size. The hypotheses are not mutually exclusive and both may be operating to different degrees in different places. However, we are unable to tease apart the relative contribution of these two factors based on the set of islands that we have studied.

Where we have conducted field work, it is our distinct impression that the abundance of varanids is higher in island situations than on the adjacent mainland. However, there is no clear relationship between abundance and body size. For example, on both Kangaroo Island and Reevesby Island, *V. rosenbergi* is relatively gigantic, but it is common on Kangaroo Island while scarce on Reevesby. Neighboring Thistle Island has a smaller body-sized population of *V. rosenbergi*, but they were quite common. In a study of certain island/mainland anoles in the Caribbean region, Andrews (1979) found that island species were larger in adult body size and occurred at greater densities but had lower growth rates associated with lower insect availabilities. Our impressions of varanid abundance may be biased by differences in the activity of animals in different places, although we were careful to only conduct censuses during the peak activity periods; more rigorous density estimates are needed.

The tendency for these non-territorial varanids to often exhibit insular gigantism, rather than the dwarfism predicted from Case's (1978) arguments is interesting. All of Case's dynamic models for population growth assumed that predators would lower the growth rate of their prey and this may not be the case here. It is entirely possible for a predator population to be food-limited (i.e. the population size increases when prey numbers are increased)

without its food prey being predator-limited (Andrewartha and Browning 1961). If a predator does not affect the supply of its food, then predator numbers and territoriality will have little impact on island-mainland differences in food availability. These will be determined more by differences in food productivity rates between locations, perhaps due to edaphic or climatic differences or from differences in the vital rates of still lower trophic levels. Varanids that feed on eggs and chicks of nesting sea birds probably do not have much influence on the size of the next year's nesting bird population since the birds are migratory. Sea bird numbers and thus the number of chicks that are potentially available may be set more by the number of adult birds that return each year to breed, which will be strongly influenced by factors off the island.

Alternatively, it may be that these varanids are more intraspecifically aggressive than is generally thought. As their own densities increase, fighting levels may also increase even though they may not be maintaining exclusive home ranges. This might lead to losses in foraging time and harvested energy as envisioned in Case's (1978) models for situations leading to gigantism. If this sort of process is responsible for gigantism here, then we would expect an association between large size and high food availability and indeed we find it. We would not necessarily expect an association between large varanid size and high varanid densities and we do not see one.

Predators on varanids (except for humans) are generally lacking from all the islands studied, so the striking differences between populations are also not easily assigned to direct size-selection by size-specific predators.

As stated earlier, we have no solid evidence that any of the size differences exhibited between populations have a genetic component or represent local adaptations. Purely phenotypic increases in average size would be expected whenever greater food availability enhances both growth rates and survivorship. The loss of predators would also lead to an age structure more heavily represented by older and consequently larger individuals (Case 1982). Robinson et al. (1985) argue persuasively that the *V. rosenbergi* populations on the South Australian islands of Spilsby, St Peter, Reevesby, and Taylor (but not Thistle and Kangaroo Island) were introduced by human settlers less than 100 years ago. If this is the case, then these size differences have arisen very suddenly over as few as 5–10 generations. This still does not rule out a genetic component to the size differences if selection is strong. Introduced populations of the European tree sparrow in North America and Australia show significant departures from ancestral European populations in morphology and genetics (Barlow 1973; St. Louis and Barlow 1988). Further studies are needed to examine the phylogenetic relationships between the island and mainland populations and to quantify any demographic and ecological differences between these varanid populations before the roots of these size differences will be uncovered.

funds from the Australian Research Grant Scheme. Flinders University of South Australia sponsored TJC as a Visiting Scholar and provided much needed logistical support during the duration of this project. The authors thank the Reserves Advisory Committee (Wildlife Conservation Fund) of South Australia and the South Australia National Parks and Wildlife Service.

References

Andrewartha HG, Browning TO (1961) An analysis of the idea of "resources" in animal ecology. J Theoret Biol 1: 83–97

Andrews RM (1979) Evolution of life histories: a comparison of *Anolis* lizards from matched island and mainland habitats. Breviora 454: 1–51

Andrews RM (1982) Patterns of growth in reptiles. In: Gans C, Pough FH (eds), Biology of the Reptilia, vol 13. Academic Press, New York, pp. 273–320

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

Auffenberg W (1981) The behavioral ecology of the Komodo Monitor. University of Florida Press, Gainesville

Barlow JC (1973) Status of the North American population of the European tree sparrow. Ornithol Monog 14: 10–23

Barnett B, Schwaner TD (1985) Growth in captive born tiger snakes (*Notechis ater serventyi*) from Chappel Island: Implications for field and laboratory studies. Trans Royal Soc S Austr 109: 31 36

Brattsrom BH (1974) The evolution of reptilian social behavior. Am Zool 14: 35–49

Butler WH (1970) A summary of the vertebrate fauna of Barrow Island. West Aust Nat 11: 149–159

Butler WH (1975) Additions to the fauna of Barrow Island. West Aust Nat 78–81

Carlquist S (1965) Island life: a natural history of the islands of the world. Natur Hist Press, Garden City, NY

Case TJ (1975) Species numbers, density compensation, and colonizing ability of lizards on islands in the Gulf on California. Ecology 56: 3–18

Case TJ (1976) Body size differences between populations of the chuckwalla, *Sauromalus obesus*. Ecology 57: 313 323

Case TJ (1978) A general explanation for insular body size trends in terrestrial vertebrates. Ecology 59: 1–18

Case TJ (1982) Ecology and evolution of the insular gigantic *Sauromalus*. In: Burghardt G, Rand AS (eds), Iguanas of the world. Noyes Publ, Park Ridge, NJ, pp. 184 212

Dunham AE (1978) Food availability as a proximate factor influencing individual growth rates in the iguanid lizard *Sceloporus merriami*. Ecology 59: 770–778

Foster JB (1964) Evolution of mammals on islands. Nature 202: 234 235

Fraser AJ (1962) An expedition to Bernier and Dorre Islands. West Aust Fisheries Dept. Fauna Bull No. 2

Green B, King D (1978) Home range and activity patterns of the sand goanna, *Varanus gouldii* (Reptilia: Varanidae). Aust J Wildlife Res 5: 417–424

Heatwole H, Butler H (1981) Structure of an assemblage of lizards on Barrow Island, Western Australia. Aust J Herp 1: 37–44

Hecht MK (1975) The morphology and relationships of the largest known terrestrial lizard, *Megalania prisca* Owen, from the Pleistocene of Australia. Proc Royal Soc. Victoria 87: 239–249

Hooijer DA (1951) Pygmy elephant and giant tortoise. Sci. Monthly 72: 3 8

James CD, Losos JB, and King DR (1992) Reproductive biology and diets of goannas (Reptilia: Varanidae) from Australia. J Herpetol 26: 128–136

King D, Green B (1979) Notes on diet and reproduction of the sand goanna, *Varanus gouldii* rosenbergi. Copeia 1979: 64–70

Lawlor TE (1982) The evolution of body size in mammals: evidence from insular populations in Mexico. Am Nat 119: 54–72

Lister AM (1989) Rapid dwarfing of red deer on Jersey in the last interglacial. Nature 342: 539–542

Losos JB, and Greene HW. Ecological and evolutionary implications of diet in monitor lizards. Biol J Linn Soc 35: 379–407

Mertens R (1934) Die Insel Reptilian. Zoologica 84: 1–205

Pianka ER (1968) Notes of the biology of *Varanus eremius*. West Aust Nat 11: 39–44

Pianka ER (1970) Notes on the biology of *Varanus gouldi flavirufus*. West Aust Nat 11: 141–144

Pianka ER (1982) Observations on the ecology of *Varanus* in the Great Victorian Desert. West Aust Nat 15: 1–8

Pregill GK (1986) Body size of insular lizards: A pattern of Holocene dwarfism. Evolution 40: 997–1008

Reese DS (1989) Tracking the extinct pygmy hippopatamus of Cyprus. Field Mus Nat Hist Bull 60: 22–29

Robinson AC, Canty PD, Mooney PA, Rudduck PM (1986) South Australia's offshore islands. Austr Natl Parks and Wildl Serv Spec Publ.

Robinson AC, Mirtschin PJ, Copley PD, Canty PD, Jenkins RB (1985) The Reevesby Island goanna – a problem in conservation management. S Aust Nat 59: 56–62

Roughgarden J, Fuentes ER (1977) The environmental determinants of size in solitary populations of West Indian *Anolis* lizards. Oikos 29: 44 51

Schoener TW (1969) Models of optimal size for solitary predators. Am Nat 103: 277–313

Schoener TW (1969) Size patterns in West Indian *Anolis* lizards I. Size and specific diversity. Syst Zool 18: 386–401

Schoener TW (1970) Size patterns in West Indian *Anolis* lizards II. Correlations with the sizes of particular sympatric species-displacement and convergence. Am Nat 104: 155–174

Schoener TW, Schoener A (1978) Estimating and interpreting body-size growth in some *Anolis* lizards. Copeia 1978: 390–405

Schoener TW, Schoener A (1980) Densities, sex ratios, and population structure in four species of Bahamian *Anolis* lizards. J Anim Ecol 49: 19–53

Schwaner TD (1985) Population structure of black tiger snakes, *Notechis ater niger*, on offshore islands of South Australia. In: Grigg G, Shine R, Ehrmann H (eds), Biology of Australian frogs and reptiles. Surrey Beatty and Sons, Sydney, pp 35–36

Schwaner TD (1990) Geographic variation in scale and skeletal anomalies of tiger snakes (Elapidae: *Notechis scutatus-ater* complex) in Southern Australia. Copeia 1990: 1138–1143

Schwaner TD, Sarre SD (1988) Body size of tiger snakes in Southern Australia, with particular reference to *Notechis ater serventyi*. J Herpetol 22: 24–33

Schwaner TD, Sarre SD (1990) Body size and sexual dimorphism in mainland and island tiger snakes. J Herpetol 24: 320–323

Shine R (1986) Food habits, habitats, and reproductive biology of four sympatric species of varanid lizards in tropical Australia. Herpetologica 42: 346–360

Shine R (1987) Ecological comparisons of island and mainland populations of Australian tigersnakes (*Notechis*: Elapidae). Herpetologica 43: 233–240

Smith LA (1976) Reptiles of Barrow Island. West Aust Nat 13: 85–108

Soulé M (1966) Trends in the insular radiation of a lizard. Am Midl Nat 100: 47–64

St. Louis VL, Barlow JC (1988) Genetic differentiation among ancestral and introduced populations of the Eurasian tree sparrow (*Passer montanus*). Evolution 42: 266–276

Stamps JA (1983) Sexual selection, sexual dimorphism, and territoriality. In: Huey RB, Pianka ER, Schoener TW (eds), Lizard ecology: studies of a model organism. Harvard Univ. Press, Cambridge, MA, pp 169–204

Storr GM (1980) The monitor lizards (genus *Varanus* Merrem, 1820) of western Australia. Rec West Aust Mus 8: 237–293

Tindale NB (1924) Visit to the islands of the Sir Joseph Banks Group. S Aust Natur 5: 130–132

Williams V, White J, Schwaner TD, Sparrow A (1988) Variation in venom proteins from isolated populations of tiger snakes (*Notechis ater niger*, *N. scutatus*). Toxicon 26: 1067–1075