THE ROYAL SOCIETY

Received 19 February 2002
Accepted 20 March 2002

The 'island rule' in birds: medium body size and its ecological explanation

Sonya M. Clegg[1*] **and Ian P. F. Owens**[1,2]

[1]*Department of Biological Sciences, and* [2]*NERC Centre for Population Ecology, Imperial College at Silwood Park, Ascot, Berkshire SL5 7PY, UK*

Do birds show a different pattern of insular evolution from mammals? Mammals follow the 'island rule', with large-bodied species getting smaller on islands and small-bodied species getting bigger. By contrast, the traditional view on birds is that they follow no general island rule for body size, but that there is an insular trend for large bills. Insular shifts in feeding ecology are, therefore, widely assumed to be the primary cause of divergence in island birds. We use a comparative approach to test these ideas. Contrary to the traditional view, we find no evidence for increased bill size in insular populations. Instead, changes in both bill size and body size obey the 'island rule'. The differences between our results and the traditional view arise because previous analyses were based largely on passerines. We also investigate some ecological factors that are thought to influence island evolution. As predicted by the traditional view, shifts in bill size are associated with feeding ecology. By contrast, shifts in body size are associated with the potential for intraspecific competition and thermal ecology. All these results remain qualitatively unchanged when we use different methods to score the ecological factors and restrict our analyses to taxa showing pronounced morphological divergence. Because of strong covariation between ecological factors, however, we cannot estimate the relative importance of each ecological factor. Overall, our results show that the island rule is valid for both body size and bill length in birds and that, in addition to feeding ecology, insular shifts in the level of intraspecific competition and the abiotic environment also have a role.

Keywords: bill size; birds; body size; ecology; evolution; islands

1. INTRODUCTION

The literature suggests that birds and mammals show different patterns of island evolution. On the one hand, mammals follow the 'island rule', with large-bodied taxa evolving towards smaller size on islands and small-bodied taxa evolving towards larger size (Foster 1964; Van Valen 1973; Heaney 1978; Williamson 1981; Lawlor 1982; Lomolino 1985; Brown *et al.* 1993; Damuth 1993; Alroy 1998). On the other hand, in birds it is generally believed that there is no general island trend for body size (Carlquist 1974; Case 1978; Gaston & Blackburn 1995; Grant 1966*a*, 1998; Blondel 2000; but see Lack 1974). Instead, the general island trend in birds is thought to be for large bill size (e.g. Mayr 1942, 1963; Lack 1947; Grant 1965*a*,*b*, 1998; Keast 1968; Carlquist 1974; Abbott 1980; Case 1978; Williamson 1981; Whittaker 1998; Blondel 2000).

This traditional view is based, in large part, on Grant's (1965*a*,*b*, 1966*a*) classic comparisons between mainland- and island-dwelling taxa in North America and Mexico. Grant found no general trend with respect to wing length, which he used as an index of body size, but there was a significant tendency for island forms to have longer bills. Subsequently, these findings have given rise to the idea that changes in feeding ecology are the prime force in driving morphological divergence in island birds (e.g. Keast 1968; Mayr 1963; Abbott 1980; Grant 1998; Blondel 2000). The most noteworthy exception to this interpretation was a later paper by Grant (1968) himself, in which he indicated that a general island trend in body size may be obscured through complex interactions with other variables, and discussed the potential role of thermal ecology in island biology. Such subtlety has, however, often been lost in subsequent reviews, which have continued to report that there is no general island trend for body size in birds, and that changes in feeding ecology are the primary agent of change.

The overall aims of this study were to collate newly available data on the morphological characteristics of insular races of birds and use it to test: (i) whether there is a consistent trend for large bill size in insular populations; (ii) whether the 'island rule' applies to either body size or bill size in birds; (iii) whether previous analyses on insular birds were based on taxonomically representative databases; and (iv) whether insular shifts in avian morphology are correlated with three ecological factors suggested to be important in the insular evolution of birds—feeding ecology, thermal ecology and the potential for intraspecific competition.

2. METHODS

(a) *Database*

We collated a database of comparison between island taxa (subspecies or species) and their mainland counterparts. Where information from more than one mainland taxon was available, we used data from the population at the most similar latitude to the insular population. Data were collated from handbooks and reviews (Grant 1965*a*; Cramp & Simmons 1977, 1980, 1983; Cramp 1985, 1988, 1992; Madge & Burn 1988; Marchant & Higgins 1990*a*,*b*, 1993; Cramp & Perrins 1993, 1994; Taylor & Van Perlo 1998), including the first nine

---

[*] Author for correspondence (sonya.clegg@ic.ac.uk).

DOI 10.1098/rspb.2002.2024

volumes of *The birds of North America* (American Ornithological Union, Cornell Laboratory for Ornithology and the Academy of Natural Sciences of Philadelphia). We excluded seabirds and swifts because in these groups it is not clear that insular and mainland forms experience a substantially different environment. We also excluded flightless species, because morphological changes may be due to flightlessness rather than island dwelling *per se*.

Our two measures of morphology were body weight (g) and bill-to-skull length (mm). For both traits, we used data exclusively from adults and, where possible, we used data on females. In total, our database contained 110 comparisons, among which mainland body weight ranged from 8.99 to 2897 g and mainland bill length ranged from 6.7 to 99.1 mm.

We collated data on three ecological factors that are suggested to be linked to morphological evolution in island vertebrates: feeding ecology, thermal ecology and potential for intraspecific competition (see Grant 1968; Case 1978; Abbott 1980; Lomolino 1985; Whittaker 1998; Blondel 2000). For each factor, we used two separate indices to minimize the risk that our results were artefacts of any particular scoring method (Bennett & Owens 2002).

Our two indices of feeding ecology were 'trophic level' and 'food-type specialization' (e.g. Grant 1965*b*, 1968; Abbott 1980; Blondel 2000). Trophic level was scored as being either 'low' or 'high', where 'low' corresponded to comparisons where the diet of the mainland form largely consisted of vegetable matter and/or herbivorous invertebrates. Vegetable matter and herbivorous invertebrates were pooled in the low trophic level category to ensure sufficient species in each category for two-way analyses. Mainland species were considered to feed largely on vegetable matter and/or herbivorous invertebrates if the handbook account indicated that these items comprised over 50% of the diet in terms of volume, weight, calorific intake or number of food items. Where percentage figures were not provided, we assumed that words such as 'largely', 'mostly', 'predominantly', 'exclusively' and 'entirely' meant greater than 50%. Food-type specialization was scored as being either 'low' or 'high', where 'high' corresponded to comparisons in which the diet of the mainland form regularly consisted of only one food type. Food-type categories were leaves and shoots, seeds, fruit, nectar and pollen, invertebrates, vertebrates and vertebrate carrion (Arnold & Owens 1999; Owens *et al.* 1999). Species were categorized as regularly including a food type in their diet if that item comprised more than 25% of their diet, in terms of volume, weight, calorific content or number of food items. Where percentage figures were not available, we assumed that words such as 'regularly', 'usually' and 'commonly' meant greater than 25%. Again, this criterion was used to ensure sufficient species for two-way analyses. Information was obtained from the same handbooks from which we obtained morphological information.

Our two indices of thermal ecology were 'latitude of island population' and latitudinal shift between the island and mainland populations (henceforth 'latitudinal shift') (e.g. Grant 1968). Latitude of island populations was scored as 'low' or 'high', where 'low' corresponded to comparisons where the latitudinal midpoint of the geographical breeding range of the insular form was between the Tropic of Capricorn and the Tropic of Cancer. This criterion satisfied the sample size requirement of two-way analysis. Latitudinal shift was scored as either 'decrease' or 'increase', where 'decrease' corresponded to comparisons where the latitudinal midpoint of the geographical breeding range of the island population was at a lower latitude than the corresponding midpoint for the mainland population. Information was obtained from the handbooks from which we obtained morphological information.

Our two indices of the potential for intraspecific competition were 'group foraging' and 'all-purpose territoriality' (e.g. MacArthur *et al.* 1972; Case 1978; Whittaker 1998). We assumed that the potential for such competition is greatest in species that forage in groups and/or defend all-purpose breeding territories. Group foraging was scored as 'present' or 'absent', where 'present' indicated a comparison in which, in the mainland species, individuals regularly compete with members of the same species for access to a particular food item or access to particular feeding site. Species were classified as foraging in a group if they were described as regularly feeding in 'groups', 'flocks' or 'parties'. All-purpose territoriality was scored as either 'present' or 'absent'. Comparisons were classified as showing all-purpose breeding territoriality if the mainland taxon's breeding territories typically contained regular feeding sites. Information was obtained from the handbooks from which we obtained morphological data.

(b) *Analyses*

The first stage of our study was to use paired *t*-tests to test whether there was a general tendency for island-dwelling birds to be either larger, or smaller, than their mainland-dwelling counterparts. Because many of the morphological differences between island and mainland forms were small (less than 2%), and we were concerned that sampling error may obscure weak relationships, we repeated these analyses using only those comparisons in which the divergence between the island and mainland form was at least 2.5% of the mainland figure for body weight and bill length, respectively (2.5% was the highest value for which we could retain a sufficiently large database to perform statistically meaningful two-way analyses). Henceforth, this is referred to as the 'restricted database'.

The second stage was to test whether the 'island rule' was valid for either body weight or bill length. We followed Lomolino's (1985) methodology. For body weight and bill length, we constructed a regression model of log (island value) on log (mainland value) and then tested whether the slope coefficient of this model was significantly different from unity. The island rule predicts that the regression slope should be significantly less than one. In addition, we used ANOVAs to test whether there was a difference between 'large' and 'small' mainland taxa in terms of the relative size of their insular forms. For both body weight and bill length, mainland taxa were classified as being either large or small on the basis of whether they were above or below the average size in our database. Again, all of these analyses were repeated on the restricted database.

The third stage of our study was to test for either taxonomic or morphological differences between our own database and that used by Grant (1965*a*,*b*, 1966*a*). We did this in four steps. First, we used a χ^2-test to determine if there was a significant difference between these databases in the proportion of passerine taxa used. Second, we used a one-sample binomial test to assess whether the proportion of passerines in these databases was significantly different from that expected by chance, given that 59% of all bird species are passerines (5712 passerines, 3960 non-passerines: Sibley & Monroe 1990). Third, we used unpaired *t*-tests to assess whether there was a difference between these with respect to the mean body weight and bill length. Finally, we used paired *t*-tests to test whether there was a significant difference between island and mainland forms with respect to body weight and bill length when we performed our analyses on oceanic island-dwelling passerines alone.

The final stage of our study was to test for ecological correlates of the relative size of insular forms. We used two-way ANOVA models of relative insular body weight and relative insular bill length, respectively, to test for significant interactions between the body weight or bill length of the corresponding mainland taxa and the ecological index in question. These ANOVA models were repeated for each ecological index in turn, and repeated on the restricted database. Ideally, we would have gone on to construct simultaneously multi-way ANOVA models to test for the relative effects of mainland body size and all six ecological variables. These analyses were not possible, however, because high covariance between categorical variables led to a large number of empty cells.

All continuous variables were log-transformed prior to statistical analysis. All tests are two-tailed. All statistical analyses were carried out using JMP v. 4.1 (SAS Institute 2001).

3. RESULTS

We found no evidence of any consistent difference between island- and mainland-dwelling taxa in bill length (paired t-test: $t = 0.13$, $n = 92$, $p > 0.8$); nor did we find a consistent pattern for body weight ($t = 0.01$, $n = 51$, $p > 0.9$). Both of these results remained qualitatively unchanged when we used the restricted database (body weight: $t = 0.13$, $n = 21$, $p > 0.9$: bill length: $t = 0.15$, $n = 30$, $p > 0.8$).

As predicted by the island rule, the lines of regression were significantly less than unity for both body weight ($r^2 = 0.98$, $n = 51$, regression slope = 0.95 (s.e ± 0.02), t-test against slope of unity $p < 0.001$) and bill length ($r^2 = 0.98$, $n = 92$, regression slope = 0.95 (s.e. ± 0.02), t-test against slope of unity $p < 0.001$). The same was true when we used the restricted database (body weight: $r^2 = 0.96$, $n = 22$, regression slope = 0.86 (s.e. ± 0.04), $p < 0.001$; bill length: $r^2 = 0.93$, $n = 31$, regression slope = 0.84 (s.e ± 0.04), $p < 0.001$). One-way ANOVA models confirmed that, for both body weight (figure 1*a*) and bill length (figure 1*b*), 'large' mainland forms tended to be associated with decreases in the relative size of insular forms, whereas 'small' mainland forms tended to be associated with increases in the relative size of insular forms. Again, this pattern remained qualitatively unchanged when we repeated the analyses on the restricted database (body weight: $F = 5.90$, d.f. = 20,1, $p < 0.05$; bill length: $F = 7.89$, d.f. = 29,1, $p < 0.05$).

Our database contained a significantly lower proportion of comparisons based on passerines (55 out of 110; 50% of comparisons) than did Grant's (1965*a*,*b*) database (82 out of 98; 82% of comparisons) ($\chi^2 = 26.14$, d.f. = 1, $p < 0.001$). In our database, the proportion of passerines was not significantly different from that expected by chance (binomial test: $p > 0.25$), whereas the proportion of passerines in Grant's database was significantly higher than that expected by chance (binomial test: $p < 0.01$). Also, the mean size of the mainland species used by Grant (1965*a*) in his Tres Marías comparisons was significantly smaller than the mean size of the mainland species in our database with respect to both body weight (Grant's database: $n = 6$, mean = 50.18; our database: $n = 71$, mean = 321.44, $t = 2.13$, $p < 0.05$) and bill length (Grant's database: $n = 19$, mean = 14.86; our database: $n = 79$, mean = 24.15, $t = 2.81$, $p < 0.01$). Finally, when we restricted our database to oceanic island-dwelling passerines alone, we found that there was a significant island trend for increases in both bill length (paired t-test: $t = 2.00$, $n = 28$, $p < 0.05$) and body weight ($t = 3.01$, $n = 16$, $p < 0.01$). These two results remained qualitatively unchanged when we repeated our analyses on the restricted database (body weight: $t = 2.60$, $n = 7$, $p < 0.05$; bill length: $t = 3.51$; $n = 13$, $p < 0.05$).

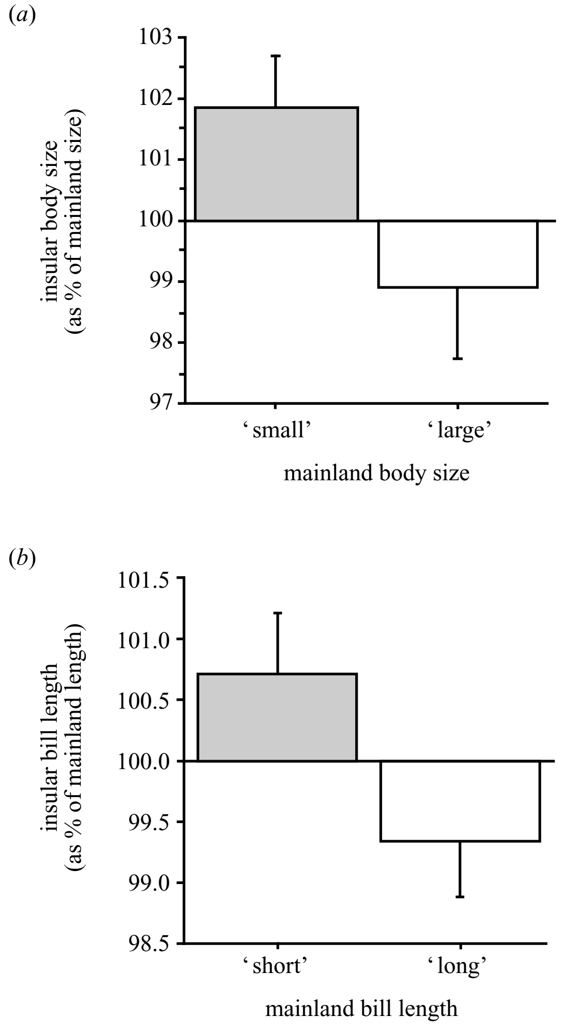

Figure 1. Insular changes in body size and bill length in birds. (*a*) Association between body size of mainland form and relative body size of insular form, where 'small' and 'large' refer to less than, and greater than, mean body size, respectively (one-way ANOVA: $F = 4.70$, d.f. = 50,1, $p < 0.05$). (*b*) Association between bill length of mainland form and relative bill length of insular form, where 'short' and 'long' refer to greater than, and less than, mean bill length, respectively ($F = 4.92$, d.f. = 91,1, $p < 0.05$). Error bars show standard errors.

Using two-way ANOVA models, we found significant interactions between variation in mainland body size and variation in both indices of thermal ecology (table 1*b*) and both indices of the potential for intraspecific competition (table 1*c*). Decreases in body weight among large-bodied forms were strongly associated with low latitudes and shifts towards the equator (figure 2*a*,*b*), and more weakly associated with the absence of group feeding and all-

Table 1. Ecological correlates of changes in body weight and bill length in island birds.
(Two-way ANOVA models. In models of relative insular body weight and relative insular bill length, 'size of mainland form' was measured in terms of body weight and bill length, respectively. Asterisks denote level of significance: $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.)

	dependent variables					
	relative body weight of island form			relative bill length of island form		
independent variables	d.f.	*F*-ratio	*p*-value	d.f.	*F*-ratio	*p*-value
(*a*) analyses based on indices of feeding ecology						
size of mainland form	1	2.87	0.10	1	2.33	0.13
trophic level	1	0.32	0.57	1	0.31	0.57
size of mainland form × trophic level	1	3.03	0.09	1	6.49	$< 0.01^{**}$
residual	48	—	—	89	—	—
size of mainland form	1	0.83	0.37	1	1.33	0.25
food-type specialization	1	0.01	0.91	1	0.10	0.75
size of mainland form × food-type specialization	1	0.89	0.35	1	3.87	$< 0.05^{*}$
residual	48	—	—	89	—	—
(*b*) analyses based on indices of thermal ecology						
size of mainland form	1	15.55	$< 0.001^{***}$	1	1.60	0.21
latitude of island form	1	8.99	$< 0.01^{**}$	1	0.60	0.44
size of mainland form × latitude of island form	1	10.54	$< 0.01^{**}$	1	3.63	0.06
residual	48	—	—	89	—	—
size of mainland form	1	16.78	$< 0.01^{**}$	1	3.53	0.07
latitudinal shift	1	11.05	$< 0.01^{**}$	1	0.92	0.34
size of mainland form × latitudinal shift	1	10.79	$< 0.01^{**}$	1	0.31	0.58
residual	48	—	—	89	—	—
(*c*) analyses based on indices of the potential for intraspecific competition						
size of mainland form	1	0.31	0.58	1	1.01	0.32
group feeding	1	8.55	$< 0.01^{**}$	1	2.06	0.16
size of mainland form × group feeding	1	4.20	$< 0.05^{*}$	1	0.06	0.81
residual	48	—	—	89	—	—
size of mainland form	1	0.03	0.87	1	1.32	0.26
all-purpose territoriality	1	14.35	$< 0.05^{*}$	1	1.13	0.29
size of mainland form × all-purpose territoriality	1	8.08	$< 0.01^{**}$	1	1.90	0.19
residual	48	—	—	89	—	—

purpose territoriality (figure 2*c*,*d*). Increases in body weight among small-bodied forms were strongly associated with the presence of group feeding and all-purpose territoriality (figure 2*c*,*d*). There were no significant associations or interactions with the two indices of feeding ecology (table 1*a*). These results remained qualitatively unchanged when we used the restricted database (for all analyses based on an index of thermal ecology or the potential for intraspecific competition: interaction $F > 6.21$, $p < 0.02$; for all analyses based on an index of feeding ecology: interaction $F < 1.22$, $p > 0.29$).

The pattern for bill length was very different, with no significant associations between variation in the relative bill length of insular forms and variation in either of the two indices of thermal ecology (table 1*b*) or either of the two indices of the potential for intraspecific competition (table 1*c*). There were, however, significant interactions between variation in mainland bill length and variation in both indices of feeding ecology (table 1*a*). Increases in bill length in short-billed taxa and decreases in bill length in large-billed taxa are associated with low trophic levels (figure 3*a*) and low food-type specialization (figure 3*b*). These results remained qualitatively unchanged when we used the restricted database (for all analyses on an index of feeding ecology: interaction $F > 5.38$, $p < 0.03$; for all analyses on an index of thermal ecology or potential for intraspecific competition: interaction $F < 1.35$, $p > 0.26$).

4. DISCUSSION

Contrary to the traditional view on insular evolution in birds, we found no consistent evidence for a general trend towards large bill size in island-dwelling birds. Instead, our results suggest strongly that birds follow the 'island rule' previously identified in mammals. That is, on islands, large birds evolve towards smaller size and small birds evolve towards larger size. This pattern is true for both body weight and bill length. It remains true whether we

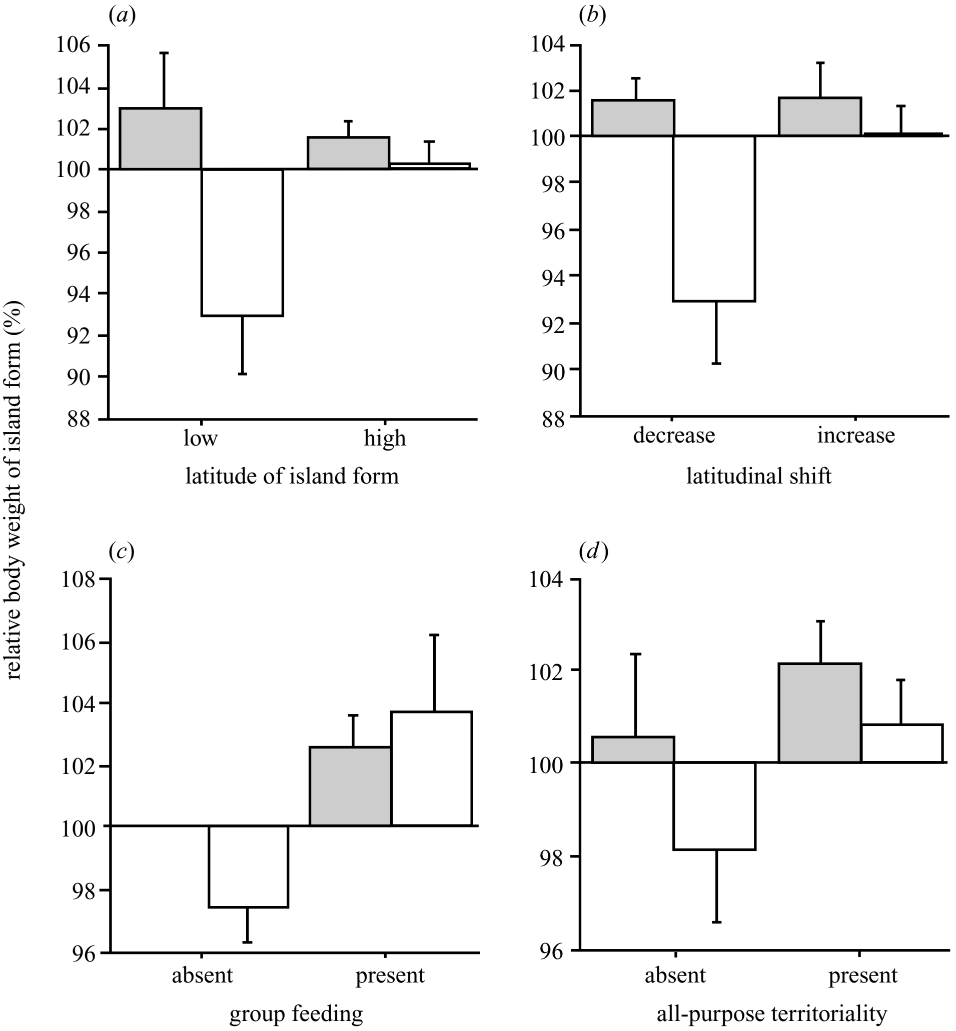

Figure 2. Variation in the relative body weight of island birds versus variation in the body weight of their mainland counterparts and variation in (*a*) latitude of the island form, (*b*) latitudinal shift, (*c*) group feeding and (*d*) all-purpose breeding territoriality (shaded bars, smalled-bodied birds; white bars, large-bodied birds). Error bars show standard errors.

perform our analyses on the entire dataset or on our restricted database, where the morphological divergence between the island and mainland forms is at least 2.5% of the mainland value.

Why are our findings so different from those of previous analyses of insular birds? Our tests indicate that previous databases contained a disproportionately large number of passerine species. In Grant's (1965*a*,*b*) classic study, over 80% of comparisons were based on passerines, which is significantly higher than expected by chance given that only 59% of bird species are passerines. Compared to our database, therefore, Grant's database contained a significantly greater proportion of small-bodied forms. We suggest that such differences had a substantial effect on the results obtained in previous studies. Indeed, if we restrict our analyses to oceanic island-dwelling passerines, we find that there is a significant general trend towards large bill size and heavier body mass. Our other tests reveal, however, that this trend towards large size in insular passerines is only half of the island rule.

Why do birds follow the island rule? Our, albeit preliminary, ecological analyses indicate that there is no single ecological explanation, with different ecological factors affecting different morphological characters in large- and small-bodied taxa, respectively. With respect to body size, changes towards large size in small-bodied forms are associated with intense intraspecific competition and may be adaptations for the high population densities known to characterize island populations (Crowell 1962; Grant 1966*b*; MacArthur *et al.* 1972; Wright 1980; Blondel *et al.* 1988). Changes towards small body size in large-bodied birds, however, are associated with our indices of thermal ecology and may be adaptations for heat dissipation at low latitudes (Grant 1968; Case 1978).

In the case of bill length, both increases in length among short-billed forms and decreases in length among long-billed forms are associated with our indices of foraging ecology. The island rule is most pronounced in species that specialize in eating seeds and small invertebrates, suggesting that medium bill size may be an adaptation for generalism in the absence of interspecific competition (see Grant 1965*a*,*b*, 1968, 1998; Lack 1971, 1976; Mayr 1963; Abbott 1980; Blondel 2000).

As we have already pointed out, an important limitation of our study is that strong covariance between ecological factors meant that we were not able to construct more complex statistical models to estimate the relative role of each factor. Given this limitation, we have to be cautious

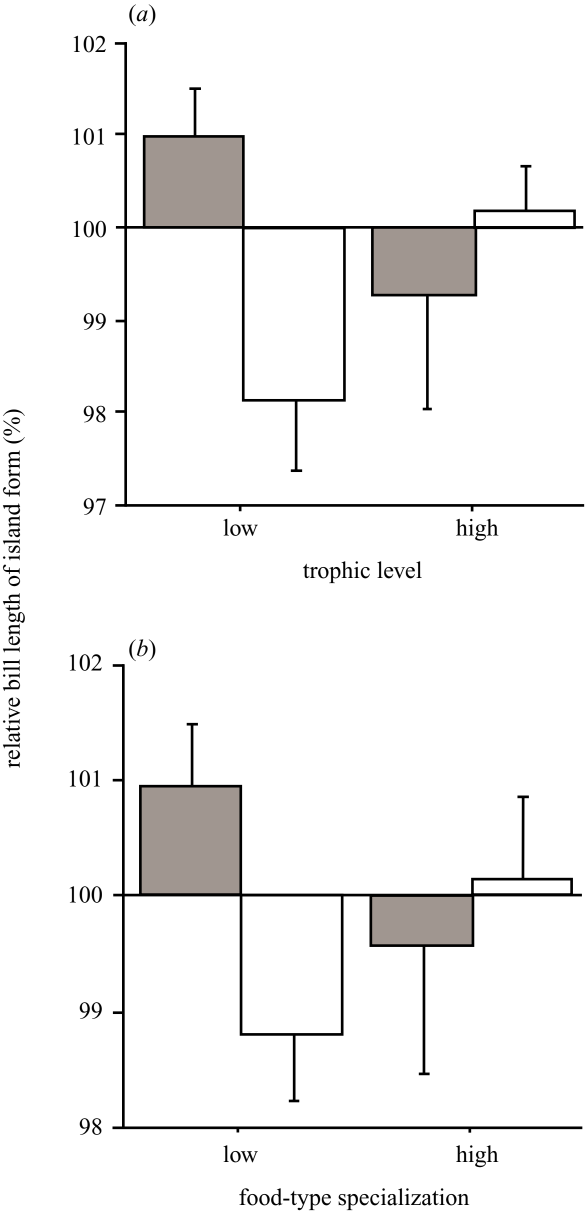

Figure 3. Variation in the relative bill length of island birds versus variation in the bill length of their mainland counterparts and variation in (*a*) trophic level and (*b*) food-type specialization (shaded bars, short-billed birds, white bars, long-billed birds). Error bars show standard errors.

when interpreting our results. Nevertheless, the fact that all of our ecological results remained qualitatively unchanged even if we use subtly different indices of ecological variation suggests that the patterns that we have identified are not artefacts of scoring methods.

Taken together, our analyses indicate that morphological divergence in island birds is not simply due to changes in feeding ecology. It seems likely that harsh intraspecific competition, energetic constraints and physiological optimization also have a role. Despite being much discussed in the mammal-based literature (e.g. Lomolino 1985; Damuth 1993), these sorts of hypotheses have been largely ignored by ornithologists. We hope that our identification of the island rule in birds will lead to renewed interest in the ecological mechanisms underlying insular divergence in birds.

We thank J. Baillie, P. Bennett, J. Blondel, M. Blows, M. Cardillo, T. Case, S. Degnan, F. Frentiu, P. Grant, J. Kikkawa, J. Losos, C. Moritz, T. Price, D. Reznick, S. Robinson, D. Schluter, S. Scott and an anonymous reviewer for discussion and/or comments. This work was supported by grants from the Australian Research Council and the Natural Environment Research Council (UK).

REFERENCES

Abbott, I. 1980 Theories dealing with ecology of landbirds on islands. *Adv. Ecol. Res.* **11**, 329–371.

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

Arnold, K. E. & Owens, I. P. F. 1999 Cooperative breeding in birds: the role of ecology. *Behav. Ecol.* **10**, 465–471.

Bennett, P. M. & Owens, I. P. F. 2002 *Evolutionary ecology of birds*. Oxford University Press.

Blondel, J. 2000 Evolution and ecology of birds on islands: trends and perspectives. *Vie Et Millieu* **50**, 205–220.

Blondel, J., Chessel, D. & Frochot, B. 1988 Bird species impoverishment, niche expansion, and density inflation in Mediterranean island habitats. *Ecology* **69**, 1899–1917.

Brown, J. H., Marguet, P. A. & Tagler, M. L. 1993 Evolution of body size: consequences of an energetic definition of fitness. *Am. Nat.* **142**, 573–584.

Carlquist, S. 1974 *Island biology*. New York: Columbia University Press.

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

Cramp, S. (ed.) 1985 *Handbook of the birds of Europe, the Middle East and North Africa*, vol. 4. Oxford University Press.

Cramp, S. (ed.) 1988 *Handbook of the birds of Europe, the Middle East and North Africa*, vol. 5. Oxford University Press.

Cramp, S. (ed.) 1992 *Handbook of the birds of Europe, the Middle East and North Africa*, vol. 6. Oxford University Press.

Cramp, S. & Perrins, C. M. (eds) 1993 *Handbook of the birds of Europe, the Middle East and North Africa*, vol. 7. Oxford University Press.

Cramp, S. & Perrins, C. M. (eds) 1994 *Handbook of the birds of Europe, the Middle East and North Africa*, vol. 8. Oxford University Press.

Cramp, S. & Simmons, K. E. L. (eds) 1977 *Handbook of the birds of Europe, the Middle East and North Africa*, vol. 1. Oxford University Press.

Cramp, S. & Simmons, K. E. L. (eds) 1980 *Handbook of the birds of Europe, the Middle East and North Africa*, vol. 2. Oxford University Press.

Cramp, S. & Simmons, K. E. L. (eds) 1983 *Handbook of the birds of Europe, the Middle East and North Africa*, vol. 3. Oxford University Press.

Crowell, K. L. 1962 Reduced interspecific competition among the birds of Bermuda. *Ecology* **43**, 75–88.

Damuth, J. 1993 Cope's rule, the island rule and the scaling of mammalian population density. *Nature* **365**, 748–750.

Foster, J. B. 1964 The evolution of mammals on islands. *Nature* **202**, 234–235.

Gaston, K. J. & Blackburn, T. M. 1995 Birds, body size and the threat of extinction. *Phil. Trans. R. Soc. Lond.* B **347**, 205–212.

Grant, P. R. 1965*a* A systematic study of the terrestrial birds of the Tres Marías islands, Mexico. *Yale Peabody Mus. Postillo* **90**, 1–106.

Grant, P. R. 1965*b* The adaptive significance of some size trends in island birds. *Evolution* **19**, 355–367.

Grant, P. R. 1966*a* Further information on the relative length of the tarsus in land birds. *Yale Peabody Mus. Postillo* **98**, 1–13.

Grant, P. R. 1966*b* The density of land birds on the Tres Marías Islands in Mexico. I. Numbers and biomass. *Can. J. Zool.* **44**, 391–400.

Grant, P. R. 1968 Bill size, body size, and the ecological adaptations of bird species to competitive situations on islands. *Syst. Zool.* **17**, 319–333.

Grant, P. R. 1998 Patterns on islands and microevolution. In *Evolution on islands* (ed. P. R. Grant), pp. 1–17. Oxford University Press.

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.

Keast, A. 1968 Competitive interactions and the evolution of niches as illustrated by the Australian honeyeater genus *Melithreptus* (Meliphagidae). *Evolution* **22**, 762–784.

Lack, D. 1947 *Darwin's finches*. Cambridge University Press.

Lack, D. 1971 *Ecological isolation in birds*. Oxford: Blackwell Scientific.

Lack, D. 1974 *Evolution illustrated by waterfowl*. Oxford: Blackwell Scientific.

Lack, D. 1976 *Island biology illustrated by the land birds of Jamaica*. Oxford: Blackwell Scientific.

Lawlor, T. E. 1982 The evolution of body size in mammals: evidence from insular populations in Mexico. *Am. Nat.* **119**, 54–72.

Lomolino, M. V. 1985 Body size of mammals on islands: the island rule re-examined. *Am. Nat.* **125**, 310–316.

MacArthur, R. H., Diamond, J. M. & Karr, J. R. 1972 Density compensation in island faunas. *Ecology* **53**, 330–342.

Madge, S. & Burn, H. 1988 *Wildfowl*. London: Christopher Helm.

Marchant, S. & Higgins, P. J. (eds) 1990*a* *Handbook of Australian, New Zealand and Antarctic birds*, vol. 1, part A. Melbourne, Australia: Oxford University Press.

Marchant, S. & Higgins, P. J. (eds) 1990*b* *Handbook of Australian, New Zealand and Antarctic birds*, vol. 1, part B. Melbourne, Australia: Oxford University Press.

Marchant, S. & Higgins, P. J. (eds) 1993 *Handbook of Australian, New Zealand and Antarctic birds*, vol. 2. Melbourne, Australia: Oxford University Press.

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

Mayr, E. 1963 *Animal species and evolution*. Cambridge, MA: Harvard University Press.

Owens, I. P. F., Bennett, P. M. & Harvey, P. H. 1999 Species richness among birds: body size life history, sexual selection or ecology? *Proc. R. Soc. Lond.* B **266**, 933–939.

SAS Institute 2001 *JMP*, v. 4.1. Cary, NC: SAS Institute.

Sibley, C. G. & Monroe, B. L. 1990 *Distribution and taxonomy of birds of the world*. New Haven, CT: Yale University Press.

Taylor, B. & Van Perlo, B. 1998 *Rails*. Robertsbridge, UK: Pica.

Van Valen, L. 1973 Body size and numbers of plants and animals. *Evolution* **27**, 27–35.

Whittaker, R. J. 1998 *Island biogeography*. Oxford University Press.

Williamson, M. 1981 *Island populations*. Oxford University Press.

Wright, S. J. 1980 Density compensation in island avifaunas. *Oecologia* **45**, 385–389.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.