

S15-4 Large body size in island-dwelling passerines: the roles of insular specialization, niche expansion and ecological release

Ian P.F. OWENS^{1,2*}, Susan N. SCOTT³, Sarah I. ROBINSON^{3,4}, Sonya M. CLEGG¹, Jiro KIKKAWA³

1. Dept. of Biological Sciences, Imperial College London, Silwood Park, Ascot, Berkshire SL5 7PY, UK; *i.owens@imperial.ac.uk

2. Natural Environment Research Council Centre for Population Biology, Silwood Park, Ascot, Berkshire SL5 7PY, UK

3. Dept. of Zoology and Entomology, The University of Queensland, St. Lucia, QLD 4072, Australia

4. Dept. of Animal Ecology, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18D, SE-756 46, Sweden

Abstract Birds follow the “island rule”, under which small-bodied forms tend to get larger on islands and large-bodied forms tend to get smaller. The traditional explanation for larger island relatives of small-bodied forms is based on ecological release on islands: islands support relatively few species, interspecific competition thus is weak, selection therefore favors niche expansion and ecological generalism, and ecological generalism is facilitated by larger body size. Anecdotal observations that island-dwelling populations sometimes have unusual feeding habits support this. However, important predictions arising from this hypothesis remain untested, namely that (1) island populations will display a greater range of foraging behaviors than mainland populations, and (2) generalist island populations will be made up of individual generalists rather than a diversity of individual specialists. We tested these predictions using the island-dwelling white-eyes (*Zosteropidae*) of the Southwest Pacific region, and the Heron Island population of the Capricorn silvereve (*Zosterops lateralis chlorocephalus*) in particular. Results show that island-dwelling populations of silvereves are indeed consistently more generalistic than their mainland counterparts when viewed *en masse*. Contrary to the generalist foraging hypothesis, however, individual island-dwelling silvereves are actually more specialized than expected by chance alone. Thus generalist foraging and ecological release are not the full explanation for increased body size in these birds.

Key words Niche expansion, Ecological release, Body size, Specialization, *Zosterops*

1 Introduction

Island-dwelling birds have long proved a fruitful source of inspiration to evolutionary biologists and ecologists (MacArthur and Wilson, 1967; Carlquist, 1974; Lack, 1976; Grant, 1998). There are at least two particular reasons for this. First, island communities are often made up of a different mix of species from mainland communities, leading to a string of theories on biogeography and the evolution of biodiversity. Secondly, island-dwelling forms are often different — in terms of morphology, behavior and ecology — from their mainland counterparts. We will focus on the second of these phenomena, using observations and tests on a particular species, the silvereve (*Zosterops lateralis*), to illustrate general patterns in the way island- and mainland- populations differ in ecology and morphology.

In his overview, Grant (Grant, this symposium) stressed the importance of distinguishing between evolutionary shifts in populations on solitary islands versus adaptive radiations in archipelagos, and explained why we might expect to find different patterns and mechanisms in these separate situations. Darwin’s finches of the Galapagos are the classic case of adaptive radiation in archipelago-dwell-

ing birds.

We have been studying evolutionary shifts of the other type, on solitary islands. Our subject populations are, in most cases, the only representatives of their family — the *Zosteropidae* or white-eyes — on the island in question, and may well represent a single colonization event. It is true that in several cases more than one *Zosterops* species occurs on a single island, but even here available evidence suggests that the sympatric species arose through separate colonization events. The evolutionary story that we are exploring, therefore, is very different to that illustrated by Darwin’s finches. We are examining instead the ecological basis of what has been called the “island rule”, with particular emphasis on the role of niche expansion and ecological generalism in promoting morphological evolution on solitary islands.

2 The “island rule” in birds

On first inspection, the literature on morphological evolution on solitary islands might suggest that island-dwelling birds follow a remarkably different pattern of insular evolution from that of other vertebrates, particularly mammals. Mammals follow a general “island rule”, with large

forms evolving towards dwarfism and small forms evolving towards gigantism (Lomolino, 1985). In birds, however, it is generally accepted that there is no general trend for insular shifts in body size (Case, 1978; Grant, 1998). Instead, the general trend among passerine birds is only towards large bills, a trend typically explained as an adaptation towards ecological generalism under “ecological release” (Case, 1978; Grant, 1965, 1998).

Being curious about such a different pattern, we re-examined morphological patterns of evolution in island-dwelling birds by compiling a new database of 110 phylogenetically matched-pairs of species and subspecies, each comprising an isolated island- and a mainland-dwelling form. We then used this database to search for general patterns of morphological change in island birds (Clegg and Owens, 2002).

Contrary to common perceptions, we found no overall tendency for the island birds to have large bills (paired t -test: $t = 0.13$, $n = 92$, $P = 0.90$). Instead, we found that island birds, like mammals, followed the “island rule” with respect

to both body and bill size (Fig. 1). For both body size and bill length we found a significant trend for small-bodied species to become bigger on islands and for large-bodied forms to become smaller. Of course, there were exceptions to this rule, causing us to control carefully for a ‘regression effect’. But the overall support for the classic island rule was robust (Clegg and Owens, 2002).

Why has the rule been overlooked in previous analyses on morphological shifts in insular birds? The main reason seems to be bias from a disproportionately large number of passerine species in databases. If we confine our own data set to oceanic island-dwelling passerines alone, we also find a strong trend for increased bill size ($t = 2.0$, $n = 28$, $P = 0.05$); yet this pattern is only half of the island rule. The whole pattern is for both large and small-bodied birds to converge towards a body size of around 100 g, with an independent but parallel island rule for bill size (Fig. 1).

3 The role of niche expansion and ecological generalism

As Grant (Grant, this symposium) points out, the traditional explanation for the island rule is that morphological shifts are adaptations to facilitate ecological niche expansion, with selection favoring generalism because insular populations typically experience relatively weak interspecific competition and a relatively depauperate environment (reviewed in Grant, 1998). In insular passerines, for example, it has often been suggested that larger bill size — and, by extension, larger body size — allows access to a wider range of resources and, ultimately, more efficient generalist behavior (Grant, 1965, 1968, 1998; Carlquist, 1974).

There is abundant circumstantial evidence to support the generalist foraging explanation with respect to morphological shifts in insular passerines. Most strikingly, island populations appear to have wider ecological niches than their mainland counterparts (e.g., Diamond, 1970; Lack, 1976), and there is experimental evidence showing that, in at least one case, such niches are shaped by interspecific competition, or lack of it (Alatalo et al., 1985).

Taken together, these studies make a strong case for associating morphological shifts in island birds with the development of more generalist foraging habits under competitive release. Tests of the generalist foraging explanation remain uncommon, however. Few systematic studies, for example, have compared multiple island with multiple mainland morphologies. Rather, evidence for insular niche expansion has been based largely on qualitative descriptions of habitat use by island forms (e.g., Lack, 1969), on observations of the ecology of island races alone (e.g., Diamond, 1970), or on single mainland-island comparisons (e.g., Alatalo et al., 1985).

In addition to the problem of replication, it has rarely been tested whether apparently generalist island populations are actually made up of individual generalists. An apparently “generalist” population may be made up of individual

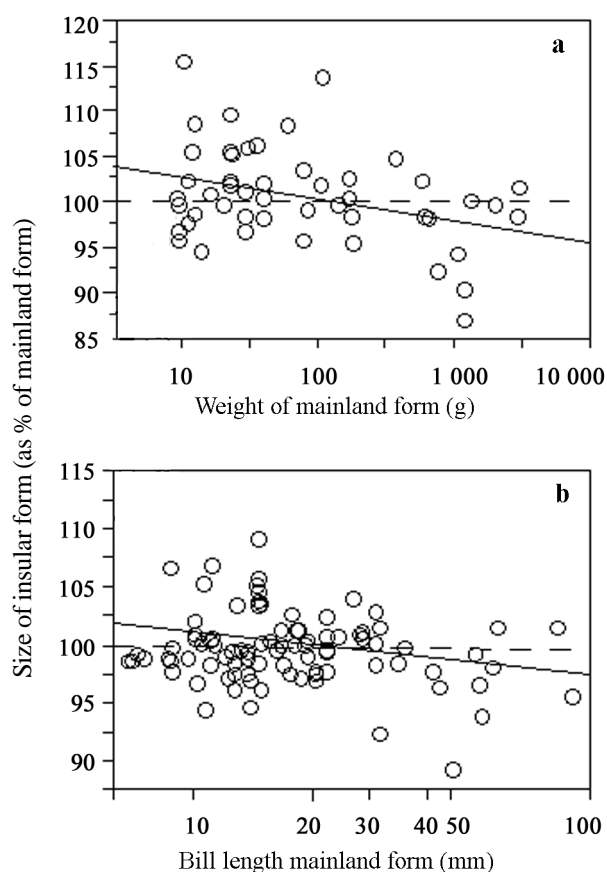


Fig. 1 The island rule in birds

Graphs show the relationship between the size of the mainland form and the relative size of the insular form, with respect to (a) body weight ($r^2 = 0.12$, $n = 51$, $P < 0.01$) and (b) bill length ($r^2 = 0.07$, $n = 92$, $P < 0.05$). In both cases, there is a significant negative relationship, which in the case of the body weight graph crosses the 100% line at approximately 100 g. The lines result from simple linear regression models fitted to log data. See Clegg and Owens (2002) for further details.

generalists or, equally plausibly, of a variety of individual specialists. The distinction between these two types of population has important consequences for understanding how generalist behavior may lead to morphological divergence on islands. If selection for generalist behavior explains the morphological shifts, then individuals should be generalists. If it is found that individuals are, in fact, specialists, then the traditional “niche expansion” explanation for the island rule stands contradicted.

4 A test species: the silvereeye, *Zosterops lateralis*

The family Zosteropidae contains a large number of successful island colonizers (Mees, 1969), many of which have repeatedly undergone insular differentiation in morphology, ecology and behavior. For example, the south-west Pacific members of the silvereeye species complex (*Zosterops lateralis*) have repeatedly invaded islands from the Australian mainland. Many of these isolated populations represent ancient invasions, having diverged into species and subspecies with very distinct phenotypes, while others are more recent and barely incipient species (Mees, 1969; Degnan, 1993). We have therefore made use of this group for a replicated study of island evolution.

One member of the complex — the Capricorn silvereeye *Zosterops lateralis chlorocephalus* — also presents an unusual opportunity to examine niche shifts at the level of individual island-dwelling birds. This race is 40% heavier than its mainland counterpart, with proportionally longer and thicker bill, and has been the subject of a long-term study of behavior and ecology on Heron Island, southern Great Barrier Reef, Australia. The Heron Island population shows strikingly generalist foraging behavior, and its large body size is unlikely to reflect neutral genetic mechanisms such as drift and founder events (Kikkawa, 1980; Degnan, 1993; Clegg et al., 2002a, b). So it was used to test whether population-level generalism is based on individual-level generalism or on a diversity of individual specialists.

5 Are island-dwelling populations more generalist?

We conducted a replicated test of the prediction that island-dwelling populations exhibit a wider range of foraging behaviors than comparable populations on the mainland. We compared the foraging ecology of silvereeyes at five mainland sites with that of silvereeyes at five island sites. The five mainland sites were at Oxley Creek, Brisbane, Queensland (27°32'S, 153°00'E), Mooloolaba, Queensland (26°41'S, 153°08'E), Lamington National Park, Queensland (28°15'S, 153°08'E), Lake Wellington, Victoria (38°06'S, 147°20'E), and Wilson's Promontory, Victoria (39°03'S, 146°24'E). In summer, the race of the silvereeye at mainland sites in Queensland is *Zosterops lateralis cornwalli*, and that in Victoria is *Z. l. westernensis* (Schodde and Mason, 1999). The five island sites are Hobart, Tasmania (42°53'S,

147.20E), Palmerston North, New Zealand (40°21'S, 175°36'E), Chatham Island, New Zealand (44°00'S, 176°30'W), Lord Howe Island, New South Wales (31°33'S, 159.05'E), and Heron Island, Queensland (23°26'S, 151°55'E). The first three of these island populations are of the race *Z. l. lateralis*, while the Lord Howe Island race is *Z. l. tephroleurus* and that on Heron Island *Z. l. chlorocephalus* (Schodde and Mason, 1999).

At each of these sites we quantified the foraging ecology of the silvereeye population in terms of both foraging height and foraging substrate (for detailed methodology, see Scott et al., 2003). We then compared the distribution of foraging activities among mainland and island populations

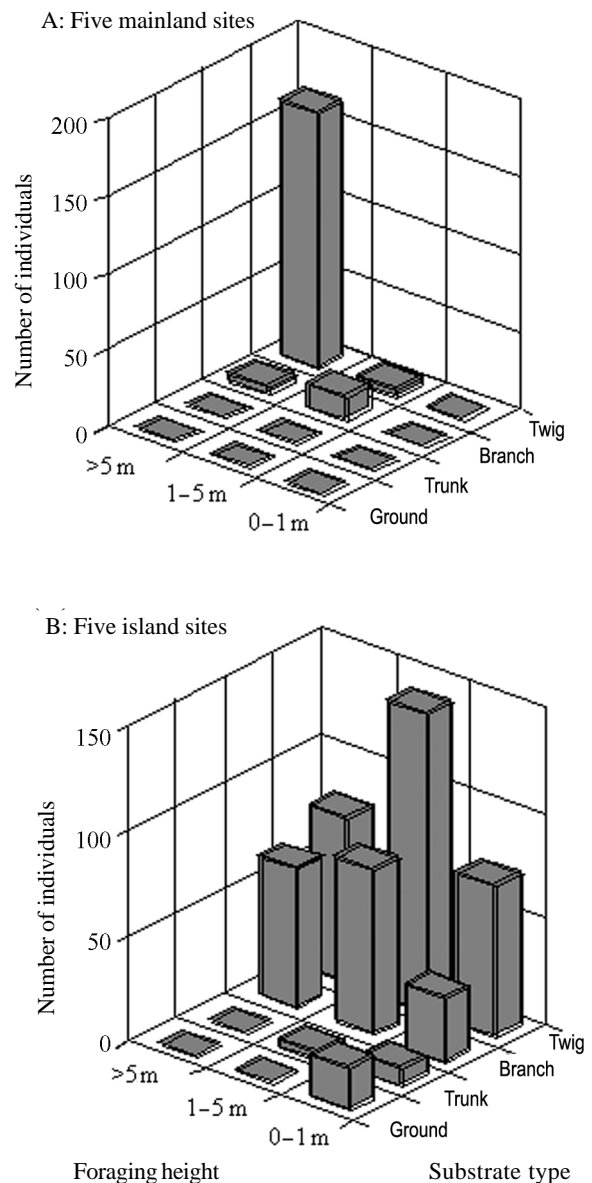


Fig. 2 Foraging behavior of silvereeyes at (A) five mainland sites and (B) five island sites

Foraging position is categorized on a 3-point scale with respect to height, and a 4-point scale with respect to substrate. See Scott et al. (2003) for further details.

by using the Shannon-Wiener Index to quantify the extent of foraging specialization within each population. From there we compared the extent of specialization among mainland populations with that among island populations.

The results supported the traditional, niche expansion explanation for the island rule. In general, island populations showed a greater range of foraging behaviors than mainland populations (Fig. 2).

6 Are individuals generalists?

We then investigated whether the degree of foraging specialization shown by Heron Island silvereyes was consistent with that expected by chance alone. Data on foraging behavior were collected from two sources: from ‘natural’ observations of foraging behavior under normal field conditions, and from ‘experimental’ observations of foraging on an experimental tree, to control for effects of variation in habitat structure (for methodology, see Scott et al., 2003).

We again recorded behavior with respect to foraging height and foraging substrate, and quantified the degree of individual foraging specialization using a Shannon-Wiener Index. In this case, however, an index known as an ‘equally common behavior’ or ECB (Werner and Sherry, 1987) was calculated. ECB values are based on the degree of utilization of available heights and substrates and range between 0 (extreme specialist) and infinity (extreme generalist). It was used as an index of the degree of foraging specialization shown by an individual in any one foraging period. We then used Kolmogorov-Smirnov one-sample tests to compare the shape of the observed ECB frequency distribution (across individuals) with expected distribution resulting from the Monte Carlo bootstrap procedure.

The observed and expected distributions of ECB values are shown separately in Fig. 3 for natural and experimental observations and for height and substrate. Kolmogorov-Smirnov tests revealed that in all cases there was a significant difference ($P < 0.05$) between observed and expected distributions, the observed distributions consistently containing more specialists than expected by chance (Fig. 3). These results, therefore, do not support the predictions of the traditional explanation of the island rule.

Such findings are in broad agreement with a detailed study of the apparently generalist Cocos finches, which were also revealed to comprise a diversity of extreme specialists. However, no detectable association between foraging behavior and morphology was found at the individual level (Werner and Sherry, 1987). Interestingly, similar overall patterns are found in the true Darwin’s finches of the Galapagos, a group well known for their staggering range of foraging behaviors at the species and population levels but which also often show specialization at the level of individuals (Grant and Grant, 1989). When combined with our own results, these findings suggest that niche expansion and the adoption of generalist foraging behavior do play an important role in insular evolution in passerines,

though perhaps not exactly in the way traditionally envisaged.

7 Conclusions

We have demonstrated that, contrary to existing dogma, birds do follow the ‘island rule’ already established for other vertebrate groups, namely, that small-bodied forms tend to become larger on islands while large-bodied forms become smaller. This is true for size of both body and bill. Our results, however, provide only qualified support for its traditional explanation. It is true that insular populations show a greater diversity of foraging behaviors than do their mainland counterparts overall; but significantly more individual foraging specialists were found in a generalist island population than expected by chance alone. This indicates that the concept of generalist niches is not the full explanation for the island rule in birds. Our ongoing work on insular white-eyes aims to test the relative importance of other factors known to be associated with morphological shifts, such as physiologically optimum body size (Damuth, 1993), reduced risk of predation (Lomolino, 1985), reduced need for dispersal (Alder and Levins, 1994), and increased intraspecific competition in high-density insular populations

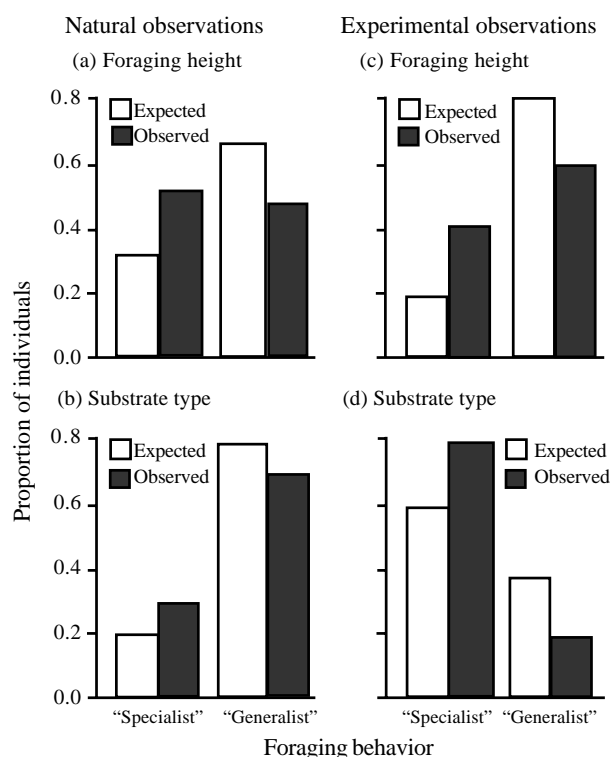


Fig. 3 Comparisons between the observed and expected frequency distributions of feeding specialization for island-dwelling silvereyes foraging under both ‘natural’ and ‘experimental’ conditions

Graphs show specialization with respect to (a) foraging height under natural conditions, (b) foraging substrate under natural conditions, (c) foraging height under experimental conditions, (d) foraging substrate under experimental conditions. See Fig. 2 for height and substrate types, and Scott et al. (2003) for further details.

(Kikkawa, 1980; Robinson and Owens, 2003).

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