

## MORPHOLOGICAL SHIFTS IN ISLAND-DWELLING BIRDS: THE ROLES OF GENERALIST FORAGING AND NICHE EXPANSION

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**Abstract.**—Passerine birds living on islands are usually larger than their mainland counterparts, in terms of both body size and bill size. One explanation for this island rule is that shifts in morphology are an adaptation to facilitate ecological niche expansion. In insular passerines, for instance, increased bill size may facilitate generalist foraging because it allows access to a broader range of feeding niches. Here we use morphologically and ecologically divergent races of white-eyes (*Zosteropidae*) to test three predictions of this explanation: (1) island populations show a wider feeding niche than mainland populations; (2) island-dwelling populations are made up of individual generalists; and (3) within insular populations there is a positive association between size and degree of foraging generalism. Our results provide only partial support for the traditional explanation. In agreement with the core prediction, island populations of white-eye do consistently display a wider feeding niche than comparative mainland populations. However, observations of individually marked birds reveal that island-dwelling individuals are actually more specialized than expected by chance. Additionally, neither large body size nor large bill size are associated with generalist foraging behavior per se. These latter results remained consistent whether we base our tests on natural foraging behavior or on observations at an experimental tree, and whether we use data from single or multiple cohorts. Taken together, our results suggest that generalist foraging and niche expansion are not the full explanation for morphological shifts in island-dwelling white-eyes. Hence, we review briefly five alternative explanations for morphological divergence in insular populations: environmental determination of morphology, reduced predation pressure, physiological optimization, limited dispersal, and intraspecific dominance.

**Key words.**—Foraging, generalism, islands, morphology, niche, *Zosterops*.

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“Subspecies on small islands tend to be larger, as in *Z[osterops] lateralis* on islets off Australia. This is a widespread trend in island songbirds, and the usual explanation is that it enables them to take a wider range of foods from the limited number available on small islands; but while this seems reasonable, it has not been tested in the field.” (Lack 1971, p. 216)

Island populations are often morphologically and ecologically distinct from their mainland counterparts and such differences have played an important role in stimulating ecological and evolutionary theory (see reviews by Carlquist 1970; Lack 1971, 1976; Case 1978; Williamson 1981; Alder and Levins 1994; Brown 1995; Grant 1998; Whittaker 1998; Blondel 2000; McNab 2002). One particularly robust rule is that, among small-bodied animals, insular forms tend to be larger than their mainland counterparts (van Valen 1965; Lomolino 1985; Damuth 1993; Clegg and Owens 2002). This pattern has been shown with respect to body size in insular rodents (Foster 1964; Heaney 1978; Lomolino 1985; Alder and Levins 1994) and both bill size and body size in insular passerines (Grant 1965, 1968; Mees 1969; Keast 1970, 1996; Abbott 1974; Clegg and Owens 2002). One explanation for these insular shifts in morphology is that they 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; Whittaker 1998). Among passerine birds, for instance, it has often been suggested that larger bill size allows access to a

wider range of resources and, ultimately, more efficient generalist behavior (Grant 1965, 1968, 1998; Carlquist 1970; Keast 1970, 1996; Abbott 1974). This argument has also been extended to other morphological traits, such as tarsus length, where longer, more robust tarsi have been hypothesized to allow more efficient use of a broader range of perching substrates (Grant 1965; Keast 1996, p. 388). We refer to this hypothesis as the “generalist foraging” explanation, and the overall aim of this study is to test its validity with respect to the morphological variation shown in one group of island-dwelling passerines, the white-eyes (*Zosteropidae*).

There is abundant circumstantial evidence in support of the generalist foraging explanation with respect to morphological shifts in insular passerines. Most strikingly, many ornithologists have reported that island populations appear to have wider ecological niches than their mainland counterparts (e.g., Diamond 1970; Keast 1970; Alerstam et al. 1974; Lack 1976; Cox and Ricklefs 1977; Diamond and Marshall 1977). Also, insular shifts in morphology are particularly well documented for aspects of morphology known to be associated with foraging ecology, such as bill size and bill shape (Murphy 1938; Grant 1965, 1968, 1979; Lack 1971; Abbott 1974; Clegg and Owens 2002). One of the best studied examples of insular differentiation in feeding ecology among birds concerns the comparison between the tit species (*Parus* spp.) of the Fennoscandinavian mainland and those of the Baltic island of Gotland (Alerstam et al. 1974; Alatalo et al. 1986). On the mainland, several species of tit regularly feed in the same woodland habitat, with feeding positions

being divided among species: willow tits (*Parus montanus*) and crested tits (*P. cristatus*) feed nearer to the trunk of trees, whereas coal tits (*P. ater*) feed away from the trunk toward the end of branches (Alerstam et al. 1974). There is strong experimental evidence that these differences in feeding ecology are due to interspecific competition because, when crested and willow tits are removed, the coal tits expand their foraging repertoire to include sites closer to the trunks (Alatalo et al. 1985). It therefore comes as no surprise that on the island of Gotland, where there are no willow tits or crested tits, the coal tit typically occupies an expanded foraging niche (Alatalo et al. 1986) and shows a pattern of morphological divergence consistent with becoming a more generalist forager (Gustafsson 1988). Moreover, a subsequent comparative study has shown that, among these species of tit, morphology is closely linked to behavior even after the effects of phylogeny have been removed (Suhonen et al. 1994). Taken together, therefore, these studies make a strong case for morphological divergence in these island tits being associated with the adoption of more generalist foraging habits under competitive release.

Replicated tests of the generalist foraging explanation remain uncommon, however. In particular, there have been relatively few systematic studies that quantitatively describe insular niche expansion by comparing multiple islands with multiple mainland areas. Rather, evidence for insular niche expansion tends to be based on qualitative descriptions of habitat use by island forms (e.g., Lack 1969), observations of the ecology of island races alone (e.g., Diamond 1970; Diamond and Marshall 1977), or single mainland-island comparisons (e.g., Keast 1970; Alerstam et al. 1974; Cox and Ricklefs 1977; Alatalo et al. 1985, 1986).

In addition to the problem of replication, it has very rarely been tested whether apparent generalist island populations are actually made up of individual generalists. As van Valen (1965) pointed out, an apparent generalist population may be made up of individual generalists or, equally plausibly, from a variety of individual specialists. The distinction between these two types of generalist populations has important consequences for understanding how generalist behavior may lead to morphological divergence in insular populations. If selection for generalist behavior is to be used to explain morphological shifts, then individuals should be generalists. If each individual is a different type of specialist, however, there need not be a consistent shift in morphology as a direct consequence of a niche expansion with a large variance at the population level. Finally, although there is sound evidence for a causal link between morphology and feeding ecology in passerine birds, there is little direct proof that differences between individuals in overall bill size or overall body size are linked to the degree of foraging generalism per se.

One of the rare quantitative studies of the ecology of generalist foraging in island passerines is Werner and Sherry's (1987) study of the Cocos finch, *Pinaroloxias inornata*, which is a close relative of the Darwin's finches of the Galapagos islands. As has been noted for many other populations of insular passerines, Cocos finches show a huge range of foraging behaviors when viewed en masse. However, when Werner and Sherry (1987) followed uniquely marked individuals

they found that each bird was a specialist, with individuals often using only a single foraging technique. The generalist population was, therefore, made up from a diversity of individual specialists. Also, when Werner and Sherry (1987) tested for a link between foraging niche breadth and morphology, they found no significant associations. Although it is not yet possible to compare the foraging ecology of Cocos finches with their direct mainland counterparts, Werner and Sherry's (1987) results suggest that the ecology of generalist foraging and niche expansion found in insular passerines may be more complex than assumed by the traditional generalist foraging explanation.

Given the lack of quantitative investigations of the generalist foraging explanation for insular shifts in morphology, we examined the nature of niche expansion and generalist foraging behavior in the silvereye species complex (*Zosterops lateralis*) in Australia and southwestern Pacific islands. This species complex contains classic examples of island-colonizing forms that tend to evolve into single insular races with distinctive morphology and ecology (Mees 1969; Lack 1971, 1976; Clegg et al. 2002a,b). Also, as shown by the quote at the beginning of this section, morphological divergence among island forms of this group have been directly linked to generalist foraging behavior (Lack 1971). To establish if island-dwelling silvereyes are consistently more generalist than mainland silvereyes, we compare foraging ecology of populations at five mainland sites and five island populations. We then focus on one particularly well-studied insular race to test, first, whether individuals are generalist or specialist foragers, and second, whether individual variation in the degree of foraging generalism is associated with individual variation in morphology.

## MATERIALS AND METHODS

### *Test 1: Are Island Populations Generalist?*

We compared the foraging ecology of silvereyes at five mainland sites with that of silvereyes at five island sites. The five mainland sites were at Oxley Creek, Brisbane, Queensland (27°28'S, 152°59'E); Mooloolaba, Queensland (26°40'S, 153°07'E); Wilson's Promontory, Victoria (39°03'S, 146°23'E); Lake Wellington, Victoria (38°05'S, 147°19'E); and Lamington National Park, Queensland (28°15'S, 153°08'E). The race of silvereye at all these mainland sites is *Zosterops lateralis familiaris*, except for the race at Wilson's Promontory, which is *Z. l. halmaturinus* (Mees 1969). The five island sites are Hobart, Tasmania (42°52'S, 147°19'E); Palmerston North, New Zealand (40°21'S, 175°36'E); Chatham Island, New Zealand (44°00'S, 176°30'E); Lord Howe Island, New South Wales (31°30'S, 159°04'E); and Heron Island, Queensland (23°27'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. tephrolepous* and the Heron Island race is *Z. l. chlorocephalus* (Mees 1969).

At each of the aforementioned sites the foraging ecology of the silvereye population was quantified by locating birds and recording their initial foraging position, in terms of both height and substrate. We used three height categories: 0–1 m, 1–5 m, and > 5 m; and four substrate categories: ground

(including bare ground, ground vegetation, and fallen pine needles), trunk, branch (> 10-mm diameter); twig (< 10-mm diameter, including intact pine needles, flower buds, flowers, and flower stems). In this part of the study identification of individual birds was not attempted, although we did attempt to avoid collecting data on the same bird more than once by moving at least 100 m between observations. Observations at each site were made within a 24-h period, with all observations taking place within 4 h after dawn. At the end of the observation period at each site, we summed the number of times that silvereyes had been observed to forage in each of the 12 possible foraging position categories (three height categories by four substrate categories). Observations were made through 8× magnification binoculars from a distance of at least 10 m.

We compared the distribution of foraging activities among mainland and island populations by using the Shannon-Wiener index to quantify the extent of foraging specialization within each population and then compared the extent of specialization among mainland populations with that among island populations. A Shannon-Wiener index of specialization,  $H'$ , was calculated for each population,

$$H' = -\sum(p_i \ln p_i), \quad (1)$$

where  $p_i$  is the proportion of observations in foraging position category  $i$  (Werner and Sherry 1987; Wheeler and Calver 1996). The  $H'$  values were then transformed into a  $J'$  value (a measure of relative specialization) using the formula

$$J' = H'/H'_{\max}, \quad (2)$$

where  $H'_{\max} = \ln S$ , where  $S$  is the total number of observational categories (3 height classes × 4 substrate classes = 12 observational categories). Thus,  $J'$  values give an index of the degree of specialization shown by a population with respect to the 12 possible foraging position categories, from extreme specialist ( $J' \rightarrow 0$ ) to extreme generalist ( $J' \rightarrow 1$ ). We then used a Mann-Whitney test to compare the  $J'$  values for the mainland populations with the  $J'$ -values for the island populations.

### Test 2: Individual Generalists or Specialists?

This part of the study was conducted on the Capricorn silvereye (*Z. l. chlorocephalus*) population on Heron Island, located 72 km off the eastern coast of Australia in the southern Great Barrier Reef (Mees 1969; Kikkawa 1973). This island race is largely restricted to Capricorn and Bunker group islands and is significantly larger (40% heavier, 26% thicker bill, 20% longer bill, 28% longer tarsus, 10% longer wing) than the mainland race (*Z. l. familiaris*), to which it is closely related (Mees 1969; Kikkawa 1970, 1976; Degnan 1993; Clegg et al. 2002a,b). The Heron Island population of silvereyes is individually color banded to allow easy identification (Kikkawa 1997). This section of the study was conducted between July 1998 and February 1999.

The objectives of this part of the study were to record the foraging behavior of individually banded silvereyes, quantify the extent of foraging specialization, and determine whether the degree of specialization shown by the Heron Island silvereyes was consistent with that expected by chance alone.

Data on foraging behavior were collected in two forms: through natural observations of foraging behavior under normal field conditions and through experimental observations of foraging on an experimental tree. The experimental tree was used to ensure that variation in foraging behavior between individuals was not simply due to variation of available habitat structure (Partridge 1976; Landmann and Winding 1993; Carrascal et al. 1994; Polo and Carrascal 1999). We report both natural and experimental results throughout because, although the experimental tree eliminated spatial variation in habitat structure, it also had the potential to attract large flocks of silvereyes and thereby cause unnaturally high levels of aggressive interaction at feeding sites.

For our natural observations of foraging behavior, we observed individually banded silvereyes through 8× magnification binoculars as they moved around the island. Individuals were chosen haphazardly from flocks located by their contact calls. Once an individual's identity had been established, we recorded the most recent foraging position at 5-sec intervals, with foraging positions being described by the same height and substrate categories described in the previous section. We continued to follow an individual until we could no longer see it, or until it had ceased to forage for more than five minutes. At the end of each observation period we calculated the proportion of foraging events that had occurred at each height category and the proportion of foraging events that had occurred on each substrate category. The criteria for an individual to be used in the final analysis of natural foraging behavior was that we were able to obtain five such observation periods, each of at least 30 sec duration and each at least 24 h apart. For individuals for which we obtained more than five observation periods, we selected five periods at random to include in the final analyses.

For our experimental observations of foraging behavior, the experimental tree apparatus was 4 m tall, with feeding stations at 0.5-m intervals along its length. At each feeding station there were three baited foraging sites: one on an artificial twig (diameter = 5 mm), one on an artificial branch (diameter = 10 mm) and one on an artificial trunk (flat piece of cork). The feeding sites were baited with quarter-sections of apple, and bait was replaced when exhausted. During any one observation period, individuals were selected haphazardly from foraging flocks and foraging events were categorized with respect to height and substrate. In this case, however, the height categories corresponded with the feeding stations (0.5 m, 1.0 m, 1.5 m, 2.0 m, 2.5 m, 3.0 m, 3.5 m) and our criteria for including an individual in the final analysis was that we were able to obtain five such observation periods, each of at least 20 sec duration and each at least 24 h apart. To maximize the number of individuals that we observed feeding on the tree, we moved the apparatus around the island every few days, thereby covering the range of habitats occurring on the island. Again, for individuals for which we obtained more than five observation periods, we used five randomly selected periods in the final analyses.

The degree of foraging specialization shown by each individual was quantified separately for foraging height and substrate, using a Shannon-Wiener index to quantify the degree of foraging specialization shown by each individual during each foraging period ( $H'$  and  $J'$  values were calculated

as shown previously). An index known as an equally common behavior (ECB) value was calculated by transforming the  $J'$  values, expressing them as a power of  $e$  (Werner and Sherry 1987). ECB values range between zero (extreme specialist) and infinity (extreme generalist) and were used as our index of the degree of foraging specialization shown by an individual in any one foraging period. We compared the observed distribution of ECB values among foraging bouts of a particular individual with the predicted distribution of ECB values randomly distributed among individuals. To do this we used a Monte Carlo simulation to ascertain the likelihood that the overall pattern of individual ECB values could have arisen through chance alone. We precisely followed the simulation procedure of Werner and Sherry (1987), the only exception being that we randomly drew 2000 behaviors for each set of individuals, rather than the 88 behaviors drawn in the Cocos finch study. We then used Kolmogorov-Smirnov one-sample tests to compare the shape of the observed ECB frequency distribution (across individuals) with the expected distribution resulting from the Monte Carlo bootstrap procedure. Separate Kolmogorov-Smirnov tests were performed for natural and experimental observations and for foraging height and foraging substrate categories.

### *Test 3: Morphological Correlates of Specialization*

Using the data on the foraging behavior of individual Heron Island silvereyes, we tested for correlations between variation in morphology and variation in degree of foraging specialization. Degree of individual foraging specialization was quantified by calculating the mean ECB value across all five observations periods. Individual variation in morphology was quantified by taking a standard set of six morphological measurements from each individual at the time of banding: wing length (mm, maximum flattened chord from carpal joint to tip of longest feather); tail length (mm, exposed length of the central feathers); tarsus length (mm, length of the metatarsus); culmen length (mm, culmen tip to posterior end of nostril); culmen depth (mm, measured at the anterior end of the nostril); and culmen width (mm, measured at the anterior end of the nostril; Kikkawa 1997; Clegg et al. 2002a,b). We then used principal component analysis to summarize variation in morphology and multiple linear regression models to test for associations between variation in foraging specialization and variation in morphology. Regression models were built for natural and experimental observations and for foraging height and substrate type, respectively. Initially, all these analyses were performed across all age groups of birds. However, to minimize the effects of age and season, we also repeated our analyses on a restricted database containing only individuals hatched in the 1997/1998 breeding season. All statistics were performed using JMP 4.0 (SAS Institute 2000).

## RESULTS

### *Test 1: Are Island Populations Generalist?*

The foraging behavior of mainland- and island-dwelling silvereyes are illustrated in Figures 1 and 2, respectively. The average  $J'$  value for the mainland sites was 0.16, whereas the corresponding value for the island sites was 0.43. These

two sets of distributions differ significantly with respect to the extent of foraging site specialization, with the mainland populations showing significantly less diverse foraging ecology than the island populations (Mann Whitney,  $U = 22$ ,  $n = 10$ ,  $P < 0.05$ ).

### *Test 2: Individual Generalists or Specialists?*

The observed and expected distributions of ECB values are shown in Figure 3, for natural and experimental observations and for height and substrate, separately. Kolmogorov-Smirnov tests revealed that in all cases there was a significant difference between the observed and expected distribution, with the observed distributions consistently containing more specialists than expected by chance (Fig. 3A, natural observations with regards to height,  $D_{32} = 0.023$ ,  $P < 0.05$ ; Fig. 3B, natural observations with respect to substrate,  $D_{30} = 0.034$ ,  $P < 0.05$ ; Fig. 3C, experimental observations with respect to height,  $D_{81} = 0.032$ ,  $P < 0.05$ ; Fig. 3D, experimental observations with respect to substrate,  $D_{80} = 0.043$ ,  $P < 0.05$ ).

### *Test 3: Morphological Correlates of Specialization?*

The first principal component was positively associated with all measures of morphology, while the second principal component was positively associated with all measures of bill morphology but negatively associated with all other measurements (Table 1). This was true whether we based the principal component analysis on all individuals for which we had behavioral data or used on those individuals in the 1997/1998 cohort (Table 1). For both principal component analysis we therefore refer PC1 and PC2 as body size and bill size, respectively.

Using multiple regression models based on these principal components we found no evidence of significant associations between variation in body size (PC1) or bill size (PC2) and variation in extent of foraging specialization. This remained true irrespective of whether we based our models on observations of natural foraging behavior (Table 2) or observations of birds foraging on the experimental tree (Table 3). We also obtained the same qualitative pattern when we restricted our database to just the 1997/1998 cohort of birds: natural observations with respect to height (full model:  $F = 1.29$ ,  $df = 2, 19$ ,  $r^2 = 0.06$ ,  $P > 0.25$ ); natural observations with respect to substrate (full model:  $F = 0.71$ ,  $df = 2, 19$ ,  $r^2 = 0.08$ ,  $P > 0.50$ ); experimental observations with respect to height (full model:  $F = 0.86$ ,  $df = 2, 44$ ,  $r^2 = 0.04$ ,  $P > 0.25$ ); experimental observations with respect to substrate (full model:  $F = 0.57$ ,  $df = 2, 46$ ,  $r^2 = 0.03$ ,  $P > 0.50$ ).

## DISCUSSION

Our results provide mixed support for the predictions of the generalist foraging explanation for morphological shifts in island-dwelling passerines. In agreement with the core prediction of the generalist foraging hypothesis, we did find consistent evidence that insular populations show a greater diversity of foraging behaviors than their mainland counterparts when viewed on mass. However, when we observed individual birds within one of these apparently generalist

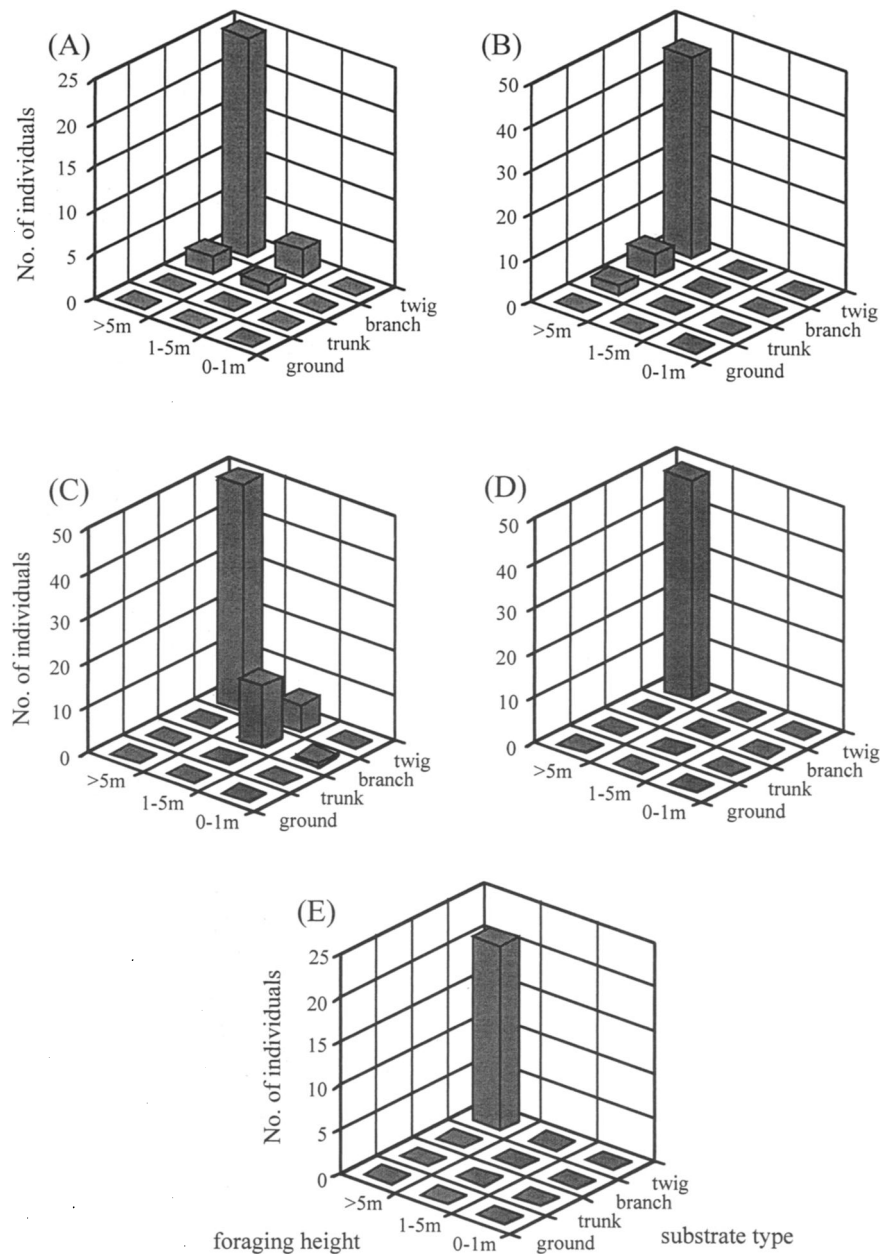


FIG. 1. Foraging behavior of silveryeyes at five mainland sites: (A) Lake Wellington; (B) Mooloolaba; (C) Oxley Creek; (D) Wilson's Promontory; and (E) Lamington National Park. Foraging position is categorized on a three-point scale with respect to height and a four-point scale with respect to substrate. See text for details.

island populations, we found a very different pattern. The Heron Island population of Capricorn silveryeyes contains significantly more foraging specialists than expected by chance alone, with excess specialization occurring with respect to both foraging height and foraging substrate even when we used an experimental tree to control for spatial heterogeneity in foraging site availability. Finally, we were unable to detect significant associations between individual variation in morphology and individual variation in the extent of foraging specialization, whether we based our models on observations of natural foraging behavior or foraging on the experimental tree, and whether we used single or multiple cohorts.

These findings are in broad agreement with the detailed

study of the apparently generalist Cocos finches, which were also made up of a diversity of extreme specialists among which there was no detectable association between foraging behavior and morphology (Werner and Sherry 1987). Interestingly, similar overall patterns have been found in the true Darwin's finches of the Galapagos, which are well known to display a staggering range of foraging behaviors at the species and population level but often show specialization at the level of individuals within a particular population at a particular time (Grant 1986; 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

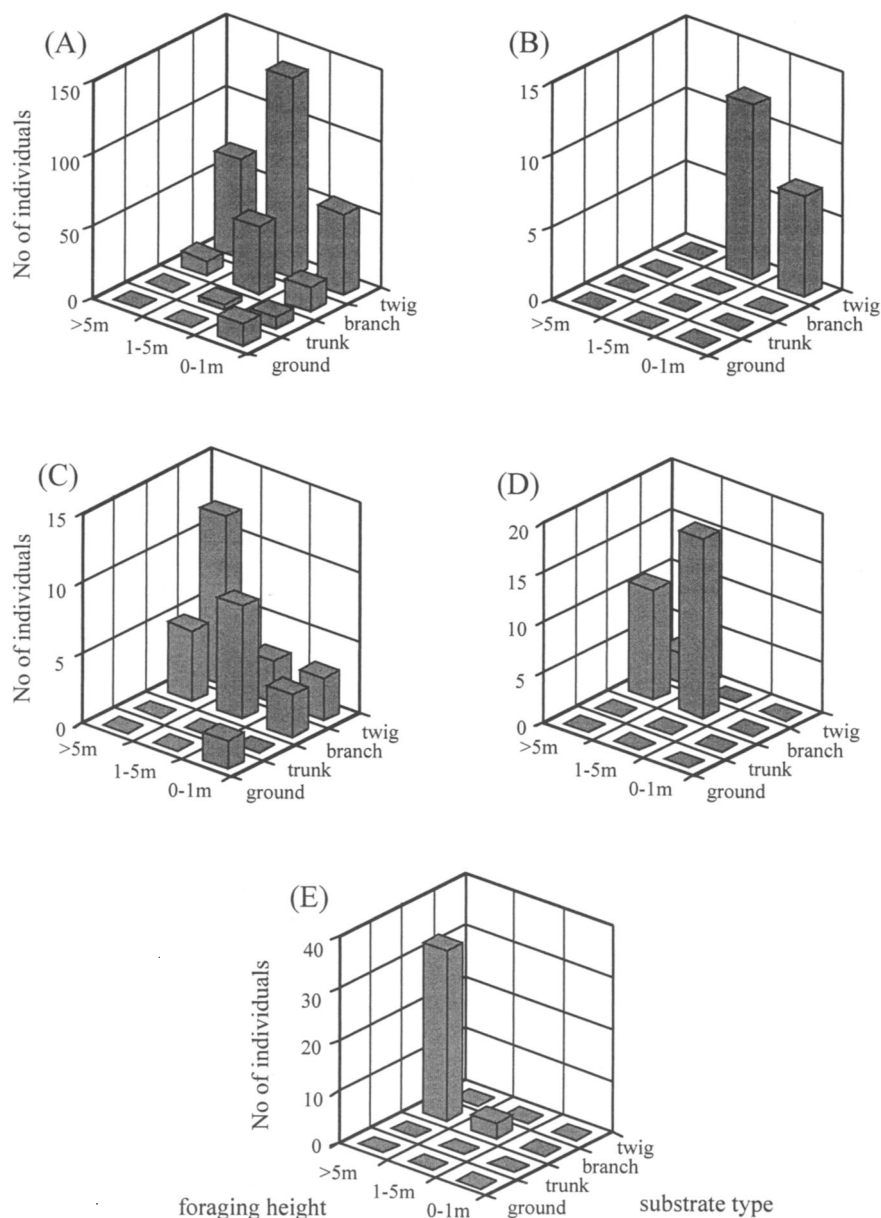


FIG. 2. Foraging behavior of silvereyes at five island sites: (A) Heron Island; (B) Lord Howe Island; (C) Tasmania; (D) Chatham Island; and (E) New Zealand. Foraging position is categorized on a three-point scale with respect to height, and a four-point scale with respect to substrate. See text for details.

in passerines, but perhaps not in exactly the way traditionally envisaged. As predicted by the generalist foraging hypothesis, island populations do often show a remarkable expanded niche, but this generalism is achieved through diverse individual specialization.

Before speculating on plausible alternative explanations for morphological shifts in insular white-eyes, it is important to consider the possible limitations of our study. Could we have investigated the wrong aspects of feeding ecology and morphology to characterize generalist foraging, or could there be insufficient variation in the traits that we studied? While we cannot discount these possibilities entirely, we think they are unlikely explanations for why we have been unable to corroborate the generalist foraging hypothesis.

First, we have been able to show significant divergence between mainland and island populations with respect to the measures of foraging ecology employed in our study, suggesting that these measures do provide an index of ecological divergence. Second, in a parallel study of the pattern of morphological divergence among island-colonizing silvereyes, we demonstrated significant directional divergence with respect to the morphological variables that we have used here (Clegg et al. 2002b). Finally, all the results we have reported here remain qualitatively unchanged even if we use other statistical methods to summarize variation in feeding behavior and morphology, and/or base our analyses on natural foraging behavior rather than that on experimental trees, and/or use information on individuals from different cohorts. It

TABLE 1. Loading factors from principal component analyses on the morphology of Heron Island silvereyes, based on all individuals across cohorts and individuals hatched during the 1997/1998 breeding season alone.

Trait	Individuals from all cohorts		Individuals from 1997/1998 cohort only	
	PC1	PC2	PC1	PC2
Wing length	+0.45	-0.15	+0.46	-0.22
Tail length	+0.44	-0.24	+0.43	-0.43
Tarsus length	+0.35	-0.55	+0.37	-0.34
Culmen length	+0.35	+0.57	+0.30	+0.73
Culmen depth	+0.44	+0.06	+0.40	+0.17
Culmen width	+0.38	+0.51	+0.46	+0.30

seems unlikely, therefore, that our results are simply an artifact of the measures used to quantify foraging ecology and morphology.

A more general limitation of our study is that the detailed behavioral data we report here were collected from a single population in a single season. It is possible, therefore, that in other years and/or other populations there may be an association between morphology and feeding behavior. It would be particularly interesting to observe the foraging ecology of more recently founded island populations, rather than evolutionarily older populations in which ecological and morphological divergence is already well advanced. Comparable data from more individually marked populations of other island races is the only empirical way to tackle this problem, and this is the focus of our ongoing work.

Another general limitation is that, although we have multiple-mainland and multiple-island estimates of population-level specialization, we only have individual-level estimates of foraging specialization from one population, the Capricorn silvereyes of Heron Island. Thus, although we have demonstrated that individual silvereyes within the Heron Island population are more specialized than expected by chance alone, we have not demonstrated that individuals within this population are significantly more specialist than individuals in mainland populations. Nor have we demonstrated that individuals within island populations are, in general, more specialized than individuals within mainland populations. Our study is, therefore, only the first step in exploring the individual basis of generalist island populations.

With the above limitations in mind, we will now speculate on alternative hypotheses on why generalist foraging and niche may not be the full explanation for morphological shifts

in insular passerines. Several plausible alternatives have been suggested, many of which have been reviewed by Case (1978), Alder and Levins (1994), Grant (1998), and Whittaker (1998).

One important, but often overlooked, alternative hypothesis is that the phenotypic differences between island and mainland forms may be due to environmental, rather than genetic, sources of variation (see Gotthard and Nylin 1995). Like all adaptationist explanations, the generalist foraging hypothesis implicitly assumes that shifts in morphology between island and mainland forms are largely genetic in origin, but it is possible that environmental factors may play an important role. For instance, island birds may be larger simply because there is more food available on islands and therefore they can grow larger while in the nest. Or island birds may be larger because islands tend to be warmer than mainland and therefore allow chicks to devote more energy to growth rather than thermoregulation.

To test these sorts of hypotheses it is necessary to either translocate individuals between populations, bring individuals from different populations together in a common environment, or experimentally hybridize parents from different populations (Mousseau 2000). In birds, rather few of these types of experiments have been performed, but those that have been carried out suggest that morphological differences between populations are determined largely by genetic factors (review by Merilä and Sheldon 2001). A classic example involving insular differentiation comes from the study of interspecific competition among Fennoscandinavian tits, where Alatalo and Gustafsson (1988) transplanted coal tits between the Swedish mainland and the island of Gotland to show a substantial genetic component for a range of morphological traits that are known to both differ between island and mainland populations of this species (Gustafsson 1988). In the case of white-eyes we already have data to show that there is a substantial additive genetic component to variation in morphology within populations (unpublished data), but it remains to be tested whether this is also true for differences between populations. Hence, the hypothesis that morphological divergence in insular white-eyes is a product of environmentally determined variation remains plausible, although, according to the studies reviewed by Merilä and Sheldon (2001), environmental determination of morphological divergence between populations would be rather unusual for birds.

Other alternative hypotheses on insular shifts in morphol-

TABLE 2. Results of multiple regression models to test for associations between morphology and foraging behavior specialization under natural foraging conditions, with respect to foraging height and foraging substrate.

Component	Coefficient	( $\pm$ SE)	F-ratio	P-value
Foraging height				
PC1 (body size)	-0.07	0.04	2.40	>0.10
PC2 (bill size)	+0.13	0.09	2.12	>0.10
Full model: $F = 2.51$ , $df = 2, 28$ , $r^2 = 0.09$ , $P > 0.10$				
Foraging substrate				
PC1 (body size)	-0.01	0.03	0.10	>0.75
PC2 (bill size)	+0.02	0.07	0.05	>0.75
Full model: $F = 0.08$ , $df = 2, 28$ , $r^2 = 0.07$ , $P > 0.90$				



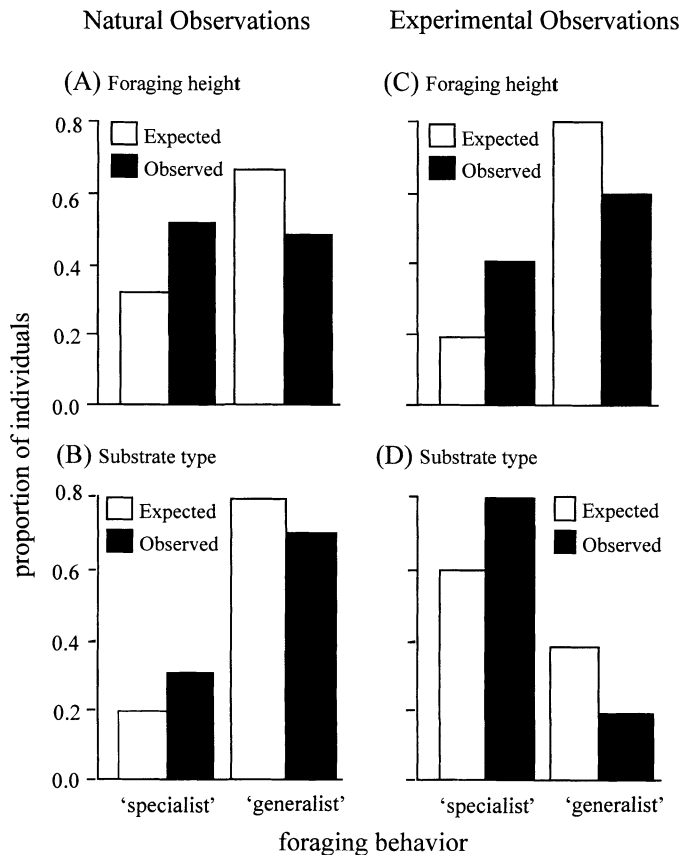


FIG. 3. Comparisons between the observed and expected frequency distributions of feeding specialization for island-dwelling silvereyes foraging under both natural and experimental conditions. Graphs show specialization with respect to (A) foraging height under natural foraging conditions; (B) foraging substrate under natural foraging conditions; (C) foraging height under experimental foraging conditions; (D) foraging substrate under experimental foraging conditions. Observed distributions are from observations of the foraging behavior of silvereyes on Heron Island. Expected distributions are from Monte Carlo simulations based on random distribution of foraging behaviors among individuals. For illustrative purposes, in this diagram foraging behavior is categorized as specialist or generalist, which refer to ECB values of below 1.5 and 1.5 or above, respectively. Throughout the rest of this study, however, statistical tests were performed on the continuous distribution of ECB values, not on these generalist and specialist categories.

ogy tend to be based on the action of natural selection and assume that phenotypic differences between mainland and island forms are largely genetic. Typically, these adaptive hypotheses have dealt with shifts in body size, rather than bill size. Many workers have suggested, for instance, that morphological shifts occur in insular populations because, in the absence of other ecological factors, lineages evolve toward some physiologically optimal body size (e.g., Case 1978; Huey and Hertz 1984; Brown and Maurer 1986; Nee et al. 1991; Brown et al. 1993; McNab 1994, 1999, 2000, 2002). The exact physiological mechanism invoked in these studies are diverse, but the fundamental idea is that among small-bodied animals selection will favor increased body size to maximize energy acquisition, while among large-bodied animals selection may favor reduced size to minimize energy requirements. In the case of mammals, for instance, Damuth (1993) has estimated that the energetically optimal size is around 1 kg, hence the shift toward gigantism in insular rodents and dwarfism in insular elephants (e.g., Lister 1989, 1993). Following the same sort of logic, the optimum size for birds would be about an order of magnitude smaller—approximately 100 g—which fits in well with the trend toward large size in passerines and small-size in large-bodied nonpasserines (Clegg and Owens 2002). Alternatively, large size in small-bodied forms may be the result of reduced risk of predation (Lomolino 1985), reduced need for dispersal (Alder and Levins 1994; Roff 1994), or increased intraspecific competition in high-density insular populations (MacArthur 1961; Kikkawa 1976, 1980; Wright 1980; Blondel et al. 1988; Robinson-Wolrath and Owens 2003). All of these explanations are plausible and, for many, there is at least some supporting evidence. The ongoing challenge is to determine whether some of them are of more general importance than the others.

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TABLE 3. Results of multiple regression models to test for associations between morphology and foraging behavior specialization under experimental foraging conditions, with respect to foraging height and foraging substrate.

Component	Coefficient	(± SE)	F-ratio	P-value
<b>Foraging height</b>				
PC1 (body size)	+0.02	0.03	0.77	>0.25
PC2 (bill size)	+0.04	0.04	0.99	>0.25
Full model: $F = 0.86$ , $df = 2, 70$ , $r^2 = 0.03$ , $P > 0.25$				
<b>Foraging substrate</b>				
PC1 (body size)	-0.01	0.02	0.26	>0.50
PC2 (bill size)	+0.03	0.04	0.99	>0.25
Full model: $F = 0.62$ , $df = 2, 70$ , $r^2 = 0.02$ , $P > 0.50$				



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