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Jack-of-all-trades or master of one? Variation in foraging specialisation across years in Darwin's Tree Finches (*Camarhynchus* spp.)

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Abstract Theory predicts that species should have wider foraging niches during conditions of resource scarcity. However, empirical evidence to date has shown mixed patterns, including studies of Darwin's finches that have found narrower foraging niches during conditions of resource scarcity. Here, we compare foraging behaviour in three species of Darwin's Tree Finches (*Camarhynchus* spp.) in a dry versus wet year on Floreana Island to examine the change in foraging breadth under conditions of resource scarcity. We provide descriptive data on diet, foraging substrate, technique, height, and foraging time across the Small Tree Finch (*C. parvulus*), Medium Tree Finch (*C. pauper*), and Large Tree Finch (*C. psittacula*). During dry versus wet years, we made the following predictions: (1) lower intraspecific niche breadth (that is, a higher level of specialisation), (2) lower interspecific overlap in all foraging parameters, and (3) longer foraging times due to relative resource scarcity. Our findings showed that the Small and Medium Tree Finches were generalist foragers, while the Large Tree Finch was a specialist. Resource specialisation varied across years of differing rainfall: both generalist species were less specialised (higher Shannon diversity index) during the dry year, while the specialist species was more specialised (lower Shannon diversity index).

Keywords Annual variation · Extinction risk · Foraging · Rainfall · Specialisation

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Introduction

Rainfall is one of the key drivers of ecosystem production, and hence ultimately influences foraging behaviour of many organisms. Variation in rainfall at local or global scales is predicted to affect foraging attributes of organisms, with possible consequences for biological fitness (e.g. Grant and Boag 1980). Birds are considered a model system to understand variation in environmental conditions for prey abundance, foraging behaviour, dispersal, and survival, and show a range of foraging behaviour that spans the continuum of specialist to generalist. In general, stable or predictable resource distributions favour resource specialisation and particular morphological phenotypes (Morse 1980; Smith 1987; Benkman and Lindholm 1991). In contrast, behavioural adaptations, such as resource switching, may provide greater flexibility in responding to a variety of resource states or varying environmental conditions (Morse 1980; Tebbich et al. 2004).

Higher levels of resource specialisation are linked with higher risks of extinction (Terborgh and Winter 1980; Bennett and Owens 1997, 2002). This pattern arises in part because generalist species are less dependent on particular resources that may suddenly become limiting than specialist species (Eisenberg and Harris 1989; Laurance 1991). Understanding species-level variation in resource use under different environmental conditions is important in measuring potential current and future threats to populations, particularly in the current context of increasing human disturbance to the environment, including climate change (Dunn 2002; Chambers et al. 2005).

The 14 species of Darwin's Finches that inhabit the Galapagos Islands are a model system to examine variation in environment, morphology, and behaviour (reviewed in

Grant and Grant 2008). In the seed-eating Ground Finches (*Geospiza* spp.), bill depth and size was correlated with seed size and hardness, and hence provided insights into trait utility (Abbott et al. 1977; Schluter 1982; Schluter and Grant 1984). The tool-using Woodpecker Finch (*Cactospiza pallida)* shows behavioural flexibility in foraging and modifies cactus spines or twigs to probe into tree holes and bark for arthropods (Tebbich et al. 2002, 2004). Whereas seed availability selects for bill size attributes in the seed-eating finches, environmental variation in the Woodpecker Finch appears to select for behavioural flexibility (Tebbich et al. 2004). In support of this idea, Tebbich et al. (2002, 2004) found higher levels of tool use under conditions of resource scarcity.

Environmental conditions vary widely on the Galapagos Islands across seasons, years, habitats, islands, and epochs (discussed in Grant and Grant 2008). For this reason, the Galapagos Islands are considered an ideal natural laboratory to examine the influence of extreme climatic variation across different temporal and spatial time scales. In general, optimal foraging theory predicts a wider foraging niche when resources are limited (MacArthur and Pianka 1966; Stephens and Krebs 1986). However, in Darwin's ground finches some species have been shown to narrow their niche breadth when resources are limited (Smith et al. 1978; Schluter 1982; Boag and Grant 1984) and prefer foods that can be handled most efficiently (Smith et al. 1978).

This same pattern of reduced niche breadth during conditions of resource scarcity was also found in Darwin's Tree Finches on Santa Cruz Island. Tebbich et al. (2004) compared Tree Finch foraging behaviour across lowland versus highland habitats that differed by rainfall, and across years. As with some studies of Darwin's Ground Finches—and in contrast to predictions of optimal foraging theory—the Santa Cruz Tree Finches showed no change in niche breadth or an increase in specialisation when resources were limited (Tebbich et al. 2004).

Here, we compare foraging behaviour in three species of Darwin's Tree Finches (*Camarhynchus* spp.) in a dry versus wet year on Floreana Island to test the prediction that birds will increase their foraging breadth under dry conditions to compensate for relative resource scarcity. We provide descriptive data on diet, foraging substrate, height, and foraging time across the Small Tree Finch (*C. parvulus*), Medium Tree Finch (*C. pauper*), and Large Tree Finch (*C. psittacula*). During dry versus wet years we made the following predictions: (1) lower intraspecific niche breadth (that is, a higher level of specialisation), (2) lower interspecific overlap in all foraging parameters, and (3) longer foraging times due to relative resource scarcity.

Methods

Study species and site

The Small, Medium, and Large Tree Finches are socially monogamous passerines that occur preferentially in the moist highland forest of the Galapagos Islands. The species differ in bill size and show minor variation in bill curvature between species (see Lack 1947; Bowman 1961; Grant 1999). We worked on Floreana Island, the only island where the Medium Tree Finch occurs. Our study site was approximately 2 ha in size, and was located in the moist highland forest at the base of Cerro Pajas (1°17S, 90°27W, 250–350 m elevation). The highland forest of Floreana Island is dominated by the endemic trees *Scalesia pedunculata*, *Croton scouleri*, and *Zanthoxylum fagara*, with other dominant plants including *Phoradendron henslowii* (Mistletoe), the shrub *Macraea laricifolia*, and introduced fruit species (*Citrus limetta*, *Passiflora edulis*, *Psidium guajava*).

Foraging observations

Foraging observations were recorded during the breeding seasons of 2005 (2–18 February) and 2006 (3 March–9 April). In 2005, there was no rainfall at our study site during our period of observation and there was little rainfall prior to our arrival (<30 mm during January to March; E. Egas, Galapagos National Park Service, personal communication). In contrast, we recorded consistent rainfall at the study site during our period of observation in 2006, and the area had received rainfall prior to our arrival (ca. 150 mm during January to March; E. Egas, Galapagos National Park Service, personal communication). Hence, we classified 2005 as a dry year and 2006 as a wet year.

We made point observations of foraging behaviour (Boag and Grant 1984; Tebbich et al. 2004; Kleindorfer et al. 2006), recording the details of the first food item ingested for each encountered individual. To reduce the likelihood of recording repeated observations of the same individuals, data were recorded along six 200-m transects throughout the study site. We walked at least one and a maximum four transects each day in a random order. Observations were made between 0630 and 1100 hours when finch activity was greatest. Due to the tame nature of Darwin's finches, the majority of observations were made within 8 m of the focal individual.

For each observation we recorded one of six substrate groups: (1) foliage (live and dead foliage), (2) bark (live and dead bark, branches), (3) flower (live or dead flower, flower bud), (4) moss (moss and lichen), (5) fruit, and (6) other (ground, seed heads). In addition, we recorded the following foraging techniques: (1) glean (removing prey from foliage surface), (2) bite (ingesting part of food item), (3) probe (inserting bill into substrate), (4) pick (removing prey from non-foliage surface), (5) chip off (downward thrust of bill), (6) pry off (using bill to lift substrate), (7) clasp and slide (holding vegetation with foot then sliding through bill), and (8) clasp and bite (holding prey/vegetation with foot then biting with bill). We grouped the foraging techniques (7) clasp and slide and (8) clasp and bite as 'clasp' for our analyses. When possible, we identified the food item ingested and these included four groups: (1) arthropod (insect, larvae, caterpillar, spider), (2) flower (part of flower or bud), (3) fruit (part or whole), and (4) plant (leaf, lichen, bark). Finally, we noted the height (m) at which the individual was foraging, and the time taken to successfully obtain a food item [time to success (s)]. Foraging time was measured using a stop-watch from the moment a bird was first observed until it consumed a food item.

Analyses

To assess niche breadth of each species across seasons, we calculated the Shannon diversity index (H) from the proportions of used substrates, techniques, and food groups (Hutcheson 1970; Colwell and Futuyma 1971; Tebbich et al. 2004). Chi-square tests were used to compare differences in foraging behaviour across species and years. After log-transforming time to success to meet assumptions of normality, we used analysis of variance to compare both time to success and height of foraging across species and seasons. We also calculated percent overlap in substrate use, technique, and food group use between each species pair using the following formula: $100\left(1 - {}^{1}\!/_{2}\sum_i \left|P_{xi} - P_{yi}\right|\right)$ (Schoener 1970; Colwell and Futuyma 1971). Here, p_{xi} and p_{yi} are the proportion of observations in category i (i.e. substrate, technique, or food group category) for species x and y, respectively.

Results

Foraging behaviour across years

The relative use of substrates, techniques, and food groups by each species in each year are presented in Tables 1, 2 and 3. There was a significant difference in the use of substrates across years in the Small Tree Finch ($\chi^2 = 18.54$, $df = 5$, $P = 0.002$), with an increase in moss use during the dry year and flower use during the wet year (Table 1). Technique use did not vary across years in the Small Tree Finch ($\chi^2 = 6.82$, $df = 6$, $P = 0.34$; Table 2) but food group did, with an increase in the consumption of flower parts during the wet year ($\chi^2 = 15.08$, $df = 4$, $P = 0.005$; Table 3).

The relative use of food groups did not vary across years in the Medium Tree Finch ($\chi^2 = 5.76$, $df = 4$, $P = 0.22$; Table 3); however, its use of both substrate and technique did (substrate: $\chi^2 = 17.53$, $df = 5$, $P = 0.004$; technique: $\chi^2 = 12.46$, $df = 6$, $P = 0.05$). Bark and moss were used relatively more during the dry year, while flower and fruit (as substrates) were favoured during the wet year (Table 1). The relative use of gleaning by the Medium Tree Finch also increased during the wet year (Table 2).

Table 1 Relative use of substrates (% cases observed) across 2 years in the Small Tree Finch (*Camarhynchus parvulus*), Medium Tree Finch (*C. pauper*), and Large Tree Finch (*C. psittacula*) on Floreana Island

Species	Year	Frequency of use (%)						H	n
		Foliage	Bark	Flower	Moss	Fruit	Other[a]		
Small Tree Finch	Dry	54.5	4.6	13.6	13.6	9.1	4.6	1.37	88
	Wet	57.1	3.2	33.3	0.0	6.4	0.0	0.97	63
	Difference*	2.6	−1.4	**19.7**	**−13.6**	−2.7	−4.6	−0.40	
Medium Tree Finch	Dry	28.9	20.0	8.9	28.9	11.1	2.2	1.58	45
	Wet	31.1	6.6	24.6	9.8	27.9	0.0	1.47	61
	Difference*	2.2	**−13.4**	**15.7**	**−19.1**	**16.8**	−2.2	−0.11	
Large Tree Finch	Dry	0.0	80.0	0.0	20.0	0.0	0.0	0.50	20
	Wet	9.1	63.6	0.0	27.3	0.0	0.0	0.86	11
	Difference	9.1	**−16.4**	0	7.3	0	0	0.36	

The change in substrate use from the dry to wet year are given (*Difference*), changes greater than 10% are highlighted in bold. H is the Shannon diversity index; higher values indicate a greater diversity of substrates used. The change in Shannon diversity indices from the dry to wet year are given. Positive values represent an increase in diversity of substrates used from dry to wet conditions. Full statistics reported in text

* Statistically significant difference in substrate across years for the species

[a] Other includes the substrates ground and seed heads

Table 2 Relative use of techniques (% cases observed) across 2 years in the Small, Medium, and Large Tree Finch on Floreana Island

Species	Year	Frequency of use (%)							*H*	*n*
		Glean	Bite	Probe	Pick	Chip off	Pry off	Clasp		
Small Tree Finch	Dry	39.8	28.4	23.9	2.3	1.1	1.1	3.4	1.37	88
	Wet	47.6	19.1	20.6	1.6	0.0	0.0	11.1	1.31	63
	Difference	7.8	−9.3	−3.3	−0.7	−1.1	−1.1	7.7	−0.06	
Medium Tree Finch	Dry	8.9	31.1	33.3	0.0	8.9	8.9	8.9	1.59	45
	Wet	21.3	44.3	23.0	1.7	0.0	3.3	6.6	1.39	61
	Difference*	**12.4**	**13.2**	**−10.3**	1.7	−8.9	−5.6	−2.3	−0.20	
Large Tree Finch	Dry	0.0	0.0	10.0	0.0	55.0	35.0	0.0	0.93	20
	Wet	0.0	9.1	36.4	9.1	0.0	45.4	0.0	1.16	11
	Difference*	0.0	9.1	**26.4**	9.1	**−55.0**	**10.4**	0.0	0.23	

The change in technique use from the dry to wet year are given (*Difference*), changes greater than 10% are highlighted in bold. *H* is the Shannon diversity index; higher values indicate a greater diversity of techniques used. The change in Shannon diversity indices from the dry to wet year are given. Positive values represent an increase in diversity of substrates used from dry to wet conditions. Full statistics reported in text

* Statistically significant difference in substrate across years for the species

Table 3 Relative use of food groups (% cases observed) across 2 years in the Small, Medium, and Large Tree Finch on Floreana Island

Species	Year	Frequency of use (%)					*H*	*n*
		Arthropod	Flower	Fruit	Plant	Unknown		
Small Tree Finch	Dry	50.0	12.5	10.2	11.4	15.9	1.38	88
	Wet	34.9	28.6	6.3	1.6	28.6	1.32	63
	Difference*	**−15.1**	**16.1**	−3.9	−9.8	**12.7**	−0.06	
Medium Tree Finch	Dry	40.0	17.8	13.3	8.9	20.0	1.48	45
	Wet	23.0	24.6	26.2	4.9	21.3	1.51	61
	Difference	**−17.0**	6.8	**12.9**	−4.0	1.3	0.03	
Large Tree Finch	Dry	65.0	0.0	0.0	0.0	35.0	0.65	20
	Wet	54.5	0.0	0.0	0.0	45.5	0.69	11
	Difference	**−10.5**	0.0	0.0	0.0	**10.5**	0.04	

The change in food groups from the dry to wet year are given (*Difference*), changes greater than 10% are highlighted in bold. *H* is the Shannon diversity index; higher values indicate a greater diversity of techniques used. The change in Shannon diversity indices from the dry to wet year are given. Positive values represent an increase in diversity of substrates used from dry to wet conditions. Full statistics reported in text

* Statistically significant difference in substrate across years for the species

There were no significant differences in the use of substrates or food groups across years in the Large Tree Finch (substrate: $\chi^2 = 2.24$, $df = 2$, $P = 0.33$; food group: $\chi^2 = 0.33$, $df = 1$, $P = 0.57$; Tables 1 and 3). However, there was a significant difference in technique ($\chi^2 = 12.44$, $df = 4$, $P = 0.014$): chip off and pry off were the dominant techniques during the dry year, while pry off and probe were dominant during the wet year (Table 2).

After controlling for the effect of species, foraging height did not vary across years (year: $F_{1,288} = 0.72$, $P = 0.40$; species × year: $F_{2,288} = 0.57$, $P = 0.57$; Fig. 1). Time to success was significantly longer for all species during the dry year, and this effect was most pronounced for the Large Tree Finch (year: $F_{1,276} = 36.72$, $P < 0.001$; species × year: $F_{2,276} = 4.84$, $P = 0.009$; Fig. 2).

Specialisation in resource use

In both years, the Large Tree Finch showed less diversity in resource use (i.e. greater specialisation) than both the Small and Medium Tree Finches, as indicated by consistently lower Shannon diversity indices (Tables 1, 2, 3). The difference in the Shannon diversity index across years showed greater specialisation in use of substrate and technique in Small and Medium Tree Finches during the wet rather than

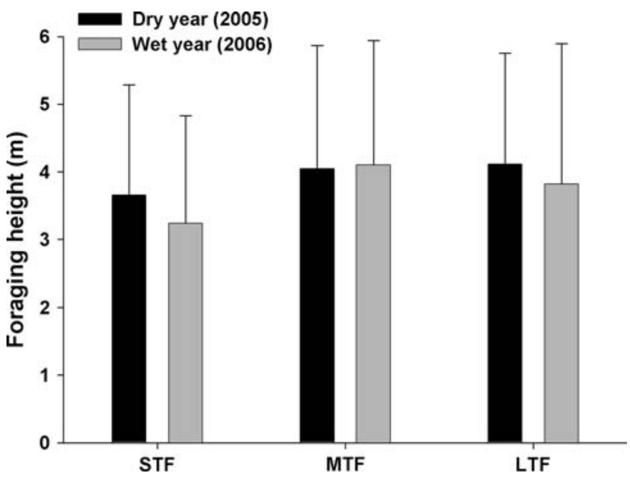

Fig. 1 Mean foraging height (m) of the Small Tree Finch (*Camarhynchus parvulus*) (*STF*), Medium Tree Finch (*C. pauper*) (*MTF*), and Large Tree Finch (*C. psittacula*) (*LTF*) on Floreana Island across 2 years of varying rainfall. Due to significantly reduced levels of rainfall (none between January and March 2005), we classified 2005 as a dry year and 2006 as a wet year (see "Methods")

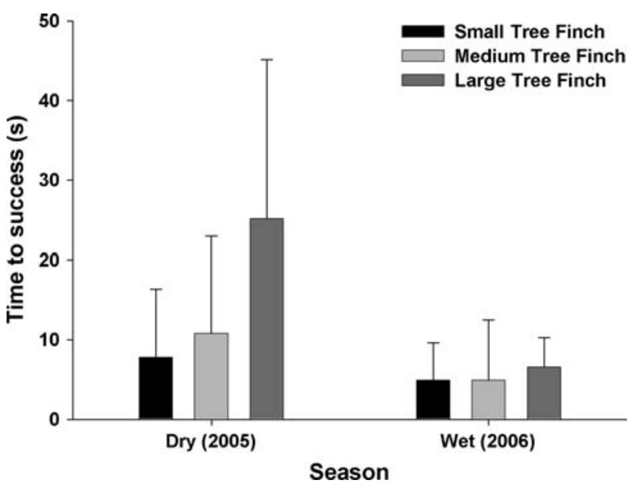

Fig. 2 Mean foraging time [Time to success (s)] of the Small Tree Finch, Medium Tree Finch, and Large Tree Finch on Floreana Island across 2 years of varying rainfall. Due to significantly reduced levels of rainfall (none between January and March 2005), we classified 2005 as a dry year and 2006 as a wet year (see "Methods")

the dry year, but an opposite pattern in the Large Tree Finch (Tables 1, 2). There was little variation in the diversity of food group across years in any species (Table 3).

Foraging behaviour across species

In both years, we found a significant difference across species in substrate use (dry: $\chi^2 = 73.13$, $df = 10$, $P < 0.001$; wet: $\chi^2 = 72.02$, $df = 8$, $P < 0.001$; Table 1) and technique (dry: $\chi^2 = 99.83$, $df = 12$, $P < 0.001$; wet: $\chi^2 = 62.31$, $df = 10$, $P < 0.001$; Table 2). The Small Tree Finch (STF) primarily gleaned on foliage, the Medium Tree Finch (MTF) used a range of substrates and primarily bit and probed, while the Large Tree Finch (LTF) mainly foraged on bark where it probed, chipped, and pried off (Tables 1, 2). Use of food groups was significantly different across species during the wet but not the dry year (dry: $\chi^2 = 13.22$, $df = 8$, $P = 0.11$; wet: $\chi^2 = 20.43$, $df = 8$, $P = 0.009$; Table 3). All species were primarily insectivorous; however, during the wet year, the Small Tree Finch consumed more flower parts and the Medium Tree Finch consumed more flower parts and fruit (Table 3).

There was a significant difference in foraging height between species that was not influenced by year (mean ± SD: STF = 3.48 ± 1.63, MTF = 4.08 ± 1.83, LTF = 4.01 ± 1.78; species: $F_{2,288} = 4.33$, $P = 0.014$; species × season: $F_{2,288} = 0.57$, $P = 0.57$; Fig. 1). Tukey post hoc analysis showed that there was a significant difference in foraging height between the Small and Medium Tree Finches ($P = 0.018$, Fig. 1), but no significant differences between the Large Tree Finch and the Small or Medium Tree Finches (LTF and STF: $P = 0.26$; LTF and MTF: $P = 0.98$).

After controlling for the effect of year, we found a significant difference in time to success across species (mean ± SD: STF = 6.56 ± 7.28, MTF = 7.23 ± 9.99, LTF = 18.10 ± 18.22; species: $F_{2,276} = 13.18$, $P < 0.001$; species × year: $F_{2,276} = 4.84$, $P = 0.009$; Fig. 2). Tukey post hoc tests showed that the Large Tree Finch had consistently longer time to success than either the Small ($P < 0.001$) or Medium Tree Finch ($P < 0.001$) while there was no significant difference between the Small and Medium Tree Finches ($P = 0.76$; Fig. 2).

Niche overlap

Percentage overlap in use of substrate, technique, and food group for each species pair in each year are shown in Table 4. All species had relatively high overlap in use of food groups during both years (Table 4). The Small and Medium Tree Finches had high overlap in substrate and technique in both years (65–69%), while the Large Tree Finch had the least overlap with either species (12–40%) (Table 4). During the dry year, the Small and Large Tree Finches had less overlap in technique, while the Small and Medium Tree Finches had more overlap in food group (Table 4). The Medium and Large Tree Finches had less overlap in technique, but more overlap in substrate and food group during the dry year (Table 4).

Table 4 Percentage overlap in use of substrates, techniques, and food groups between the Small (*STF*), Medium (*MTF*), and Large Tree Finch (*LTF*) on Floreana Island

Species pair	Year	Niche overlap (%)			Δ Overlap		
		Substrate	Technique	Food group	Substrate	Technique	Food group
STF × MTF	Dry	67	67	88	−2	2	−11
	Wet	65	69	77			
STF × LTF	Dry	18	12	66	−6	19	−2
	Wet	12	31	64			
MTF × LTF	Dry	40	28	60	−14	9	−16
	Wet	26	37	44			

The change in overlap from dry to wet years is shown (Δ *Overlap*), positive values indicate an increase in niche overlap from dry to wet year

Discussion

Selection for optimal foraging behaviour can lead to a continuum of different strategies for successful resource use. The extreme positions of this continuum can be thought of as the jack-of-all-trades (the ultimate generalist) and the master-of-one (the ultimate specialist) (Morse 1980). The most efficient level of resource specialisation for an organism may change in relation to varying environmental conditions (Morse 1980). We found evidence of both generalist and specialist foraging across the Small, Medium, and Large Tree Finches on Floreana Island. According to our quantification of niche breadth, the Small and Medium Tree Finches were generalist foragers and the Large Tree Finch a specialist (discussed below). Resource specialisation varied across years of differing rainfall: both generalist species were less specialised (higher Shannon diversity index) during the dry year, while the specialist species was more specialised (lower Shannon diversity index). Our findings provide insight into the response of species to varying environmental conditions, according to their patterns of resource use. By demonstrating varying changes in resource use to changes in rainfall across species, this study also contributes to discussion about the impact of variation in climatic conditions for avian population response to resource availability (Forchhammer et al.1998; Visser et al. 1998; Sætre et al. 1999; Walther et al. 2002).

Foraging specialisation across species and years

The Small and Medium Tree Finches showed the highest levels of generalist foraging. The Shannon diversity indices for substrate, technique, and food group in these two species are relatively high, and are similar to those calculated for the Small Tree Finch on Santa Cruz Island (Tebbich et al. 2004). The diversity of substrate and technique in the Small and Medium Tree Finches (as indicated by the Shannon diversity index) is also comparable to the diversity of substrate and technique recorded in other insectivorous passerines described as generalists, such as the Pied Flycatcher (*Ficedula hypoleuca*) [H(substrate) = 1.51, H(technique) = 1.32; Salewski et al. 2002]. In contrast, the Large Tree Finch showed the highest levels of foraging specialisation in this study. The range of substrates, techniques, and food groups used by the Large Tree Finch was clearly narrower than the ranges used by the Small and Medium Tree Finches (Tables 1, 2, 3). Accordingly, the Large Tree Finch had smaller Shannon diversity indices, which indicated a similar diversity of resource use to that recorded for other specialist passerine insectivores, such as the Green-backed Eremomela (*Eremomela pusilla*) [H(substrate) = 0.51, H(technique) = 0.35; Salewski et al. 2003].

In comparison to specialist species, generalist foragers are predicted to experience fewer negative impacts of changing environmental conditions because they are less likely to depend on a specific resource that may become limiting (Eisenberg and Harris 1989; Laurance 1991; Bennett and Owens 2002). Our findings are consistent with this prediction, given that we found evidence of opportunistic resource use in both of the generalist species in our study. The Small and Medium Tree Finches increased their use of flowers and fruits in the wet year, which was most likely an opportunistic response to the increased availability of these substrates and foods during the wet conditions.

Overall, the two generalist species in our study decreased their level of specialisation during the dry year. This change was opposite to the specialist species in our study, which increased its level of specialisation during the dry year. Previous studies of Darwin's Ground Finches have recorded similar patterns of resource specialisation across seasons and years in generalist and specialist foragers. For example, the Medium Ground Finch (*G. fortis*), described as a generalist forager, broadened its foraging niche as food abundance decreased during a drought (Boag and Grant 1984). This was in contrast to the more specialised Cactus Finch (*G. scandens*) which narrowed its foraging niche during the same drought (Boag and Grant 1984).

Specialisation in resource use is often associated with morphological adaptation or specialisation, for example Darwin's Cactus Finch has a highly elongated bill suitable for probing in cactus flowers (Grant 1999). There are similar patterns of morphological and foraging specialisation in the Floreana Tree Finches. The Large Tree Finch was the most specialised forager, and also had the most pronounced bill morphology (curvature and size) (Christensen and Kleindorfer, in review; Kleindorfer, in preparation). Bill size itself does not necessarily predict resource specialisation in Darwin's Finches, as the Large Ground Finch (*G. magnirostris*) is not the most specialised of the ground finches despite clearly having the largest bill (Abbott et al. 1977). Hence, further study of Large Tree Finch bill morphology in relation to resource use and trait utility would be useful in better understanding the link between morphological specialisation and resource specialisation in this species.

Comparison with Santa Cruz Island

Floreana and Santa Cruz Islands are home to differing compositions of Tree Finch species. The Small and Large Tree Finches are found on both islands, while the Medium Tree Finch is only found on Floreana. Santa Cruz is home to the Warbler and Woodpecker Finch. Here, we discuss foraging differences in the Small and Large Tree Finches between Floreana and Santa Cruz Island in light of these differences in species composition across islands. While the Large Tree Finch consumes primarily arthropods on both islands, the dominant foraging techniques used by Large Tree Finches in our study (probe, pry off, chip off) were hardly used by Large Tree Finches on Santa Cruz Island (Tebbich et al. 2004). However, these techniques were used by the Woodpecker Finch, which had a longer and more elongated bill than the Large Tree Finch. As in our study, on Santa Cruz Island the Small Tree Finch exploited a range of substrates and foods with a range of techniques (Tebbich et al. 2004). However, the dominant Small Tree Finch behaviour observed in our study (gleaning on foliage) was not a prominent component of Small Tree Finch foraging on Santa Cruz Island. Instead, gleaning on foliage was the dominant behaviour recorded for the Warbler Finch on Santa Cruz Island (Tebbich et al. 2004).

The Woodpecker Finch is not known to have ever occurred on Floreana Island, and the Warbler Finch is considered locally extinct on the island since 2004 (Grant 1999; Grant et al. 2005). Perhaps a lack of competition from these species has provided the opportunity for the Small and Large Tree Finches on Floreana Island to exploit different niches. Bill morphology of the Small and Large Tree Finches also varies across islands (Christensen et al. 2006; Christensen and Kleindorfer 2007; Christensen and Kleindorfer, in review; Kleindorfer, in preparation), which may be a result of adaptation to different niches on each island.

Conservation implications of foraging behaviour

Resource specialists are predicted to be more susceptible to both natural fluctuations in environmental conditions, and human-induced changes (Eisenberg and Harris 1989; Laurance 1991; Bennett and Owens 1997). Our findings are consistent with this prediction, given that the Large Tree Finch (a specialist) experienced longer foraging times than either the Small or Medium Tree Finches (generalists) (Fig. 2). In addition, while all species required significantly longer foraging time during the dry year (when resources were assumed to be more scarce), this effect was far greater for the Large Tree Finch (Fig. 2).

Floreana Island has the longest history of permanent human habitation of any Galapagos Island, and was the first island to experience a series of noteworthy extinctions within years of Charles Darwin's first visit (Lack 1947; Sulloway 1982; Schofield 1989). Introduced organisms are currently considered the biggest threat to the biota of the Galapagos system (reviewed in Causton et al. 2006). Both purposeful introduction and accidental escape of plant species has altered the highland habitat where the Tree Finches occur (Schofield 1989). We recorded both the Small and Medium Tree Finches frequently foraging on introduced fruit species, suggesting that they are able to adapt to and potentially benefit from this change in the environment. In contrast, we have not observed any species of Tree Finch nesting in an introduced plant species (R Christensen, personal observation; J O'Connor, personal communication).

Introduced animals to Floreana Island include goats (*Capra hircus*), donkeys (*Equus asinus*), fire-ants (*Solenopsis invicta*), rats (*Rattus rattus*), and cats (*Felis catus*). These animals have had a range of impacts on the island including significant alteration to the habitat and predation of endemic species (Schofield 1989; Grant et al. 2005; Grant and Grant 2008). Significant effects of introduced parasites, such as the parasitic fly (*Philornis downsi*) and avian poxvirus, have also been recorded for Darwin's Finches in particular (Fessl and Tebbich 2002; Dudaniec et al. 2006, 2007; Kleindorfer and Dudaniec 2006). Such impacts have been linked with the extinction of at least four bird species on Floreana Island: the Large Ground Finch, Sharp-beaked Ground Finch (*G. difficilis*), Floreana Mockingbird (*Nesomimus trifasciatus*) and, most recently, the Warbler Finch (Grant et al. 2005). Other species on

Floreana Island are considered to be rare and possibly in decline, including the Large Tree Finch, which was never attracted to a playback during repeated survey attempts (Grant et al. 2005). Previous studies on Floreana Island have either failed to record the presence of Large Tree Finches (e.g. Snodgrass and Heller 1904; Steadman 1986) or have noted them at very low densities (e.g. Swarth 1931; Lack 1947). We have undertaken mist netting and colour banding on Floreana Island across 3 years. Of all Tree Finches caught during this time ($n = 176$, with equal banding effort across species) only 14 were Large Tree Finches in comparison to 125 Small Tree Finches and 37 Medium Tree Finches (Christensen and Kleindorfer, in review). The Large Tree Finch may naturally occur at lower densities, but this smaller population size makes it more susceptible to extinction (Terborgh and Winter 1980; Pimm et al. 1988; Bennett and Owens 1997). In relation to other closely related and ecologically similar species on Floreana Island, the Large Tree Finch has the largest body size (Christensen and Kleindorfer, in review; Kleindorfer, in preparation) a feature also associated with greater extinction risk (Terborgh and Winter 1980; Gaston and Blackburn 1995; Bennett and Owens 1997). Thus, the Large Tree Finch displays three hallmark features of species with higher than normal risk of extinction: small population size, larger body size, and high degree of resource specialisation (Bennett and Owens 2002). We thus conclude that the Large Tree Finch warrants closer monitoring, especially given significantly increasing levels of human activity on Floreana Island (J O'Connor, personal communication).

Zusammenfassung

Alleskönner oder Meister seines Faches? Jahresabhängige Variation der Nahrungssuchspezialisierung bei Darwin's Baumfinken (*Camarhynchus* spp.)

Nach theoretischen Vorhersagen haben Arten unter Resourcenlimitierung eine breitere Nahrunsgsnische. Empirische Beobachtungen unterstützen diese Vorhersage nur teilweise: Untersuchungen an Darwin's Bodenfinken weisen auf eine engere Nahrungsnische unter Resourcenlimitierung hin. Wir verglichen das Nahrungssucheverhalten von drei Darwin Baumfinkarten (*Camarhynchus* spp.) auf der Insel Floreana in Jahren mit viel oder wenig Regen, um Veränderungen in der Breite der Nahrungsnische bei Resourcenknappheit zu untersuchen. Wir präsentieren deskriptive Information über Diät und Nahrungssuche in Bezug auf Substrat, Technik, Höhe, und Dauer in Darwin's Kleiner Baumfink (*Camarhynchus parvulus*), Mittlerer Baumfink (*C. pauper*), und Großer Baumfink (*C. psittacula*). Wir testen folgende Vorhersagen zwischen Jahren mit viel oder wenig Regenfall: (1) geringere intraspezifische Nischenbreite (höhere Spezialisation), (2) geringere interspezifische Überlappung in allen Nahrungssuche Parametern, (3) längere Dauer der Nahrungssuche wegen relativer Resourcenknappheit. Die Ergebnisse zeigen, dass der Kleine und Mittlere Baumfink als Nahrungsgeneralisten, und der Große Baumfink als Nahrungsspezialist einzustufen sind. Die Resourcenspezialisierung varierte zwischen den Jahren in Abhängigkeit vom Niederschlag. Beide Nahrungsgeneralisten zeigten erhöhten Generalismus (höheren Shannon Diversitätsindex) im trockenen Jahr, wohingegen der Nahrungsspezialist erhöhte Spezialisation zeigte (geringeren Shannon Diversitätsindex).

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