

REPORT

## The ecology of tool-use in the woodpecker finch (*Cactospiza pallida*)

Sabine Tebbich,<sup>1,2\*</sup> Michael Taborsky,<sup>1,3</sup> Birgit Fessl<sup>1</sup> and Michael Dvorak<sup>4</sup>

<sup>1</sup>Konrad Lorenz Institute for Comparative Ethology, Savoyenstr. 1a, A-1160 Vienna, Austria.

<sup>2</sup>Max Planck Institute for Behavioural Physiology, D-82319 Seewiesen, Germany.

<sup>3</sup>University of Bern, Zoological Institute, CH-3032

Hinterkappelen, Switzerland.

<sup>4</sup>BirdLife Austria, Museumsplatz 1 / 10 / 8, A-1070 Wien, Austria.

\*Correspondence:

Present address: Sabine Tebbich, University of Cambridge, Department of Experimental Psychology, Downing Street, Cambridge CB2 3EJ, UK  
E-mail: tebbich@ss20.mpi-seewiesen.mpg.de

### Abstract

Insects, mammals and birds are known to use tools, but empirical evidence of the ecological importance of tool-use is scarce. Here, we present the first ecological study of tool-use by a bird species. Woodpecker finches use twigs or cactus spines to pry arthropods out of tree-holes. We compared tool-use during wet and dry seasons in two different vegetation zones: the Arid Zone and the humid *Scalesia* Zone. In the *Scalesia* Zone, where food was abundant and easily accessible, woodpecker finches rarely used tools. In contrast, in the Arid Zone, where food was limited and hard to access, they obtained half of their prey using tools during the dry season. Tool-use enabled the birds to reach particularly large and otherwise inaccessible prey hidden in tree-holes. Our data suggest that tool-use in the woodpecker finch has evolved in response to the dry and unpredictable conditions in the coastal zone of the Galápagos Islands.

### Keywords

Darwin's finches, tool-use, *Cactospiza pallida*.

Ecology Letters (2002) 5: 656–664

### INTRODUCTION

Tool-use is commonly attributed to humans and other primates. However, several bird species are also known to use tools habitually. Egyptian vultures (*Neophron percnopterus*) are famous for dropping stones on ostrich eggs (Van Lawick-Goodall & Van Lawick-Goodall 1966), green-backed herons (*Butorides striatus*) use bait to catch fish (Walsh *et al.* 1985), satin bower birds (*Ptilonorhynchus violaceus*) use bark-wads to paint their bower (Chaffer 1945), and New Caledonian crows (*Corvus moneduloides*) make and use two forms of tools to capture prey (Hunt 1996). The woodpecker finch (*Cactospiza pallida*), one of 15 species of Darwin's Finches, is perhaps the most famous example of a tool-using bird. It uses twigs or cactus spines to pry arthropods from tree-holes and crevices (Eibl-Eibesfeldt 1961; Eibl-Eibesfeldt & Sielman 1962).

The advantage of using tools may seem evident, but empirical evidence is scarce. To date, the costs and benefits of tool-use have been studied only in chimpanzees (Nishida

& Hiraiwa 1982; Yamakoshi 1998). In our study we focused on two, not mutually exclusive, hypotheses.

**1** Tool-use may facilitate or be essential for gaining access to resources. Several authors have suggested that tool-use correlates with the necessity of extracting hidden food (Alcock 1972; Parker & Gibson 1977; Beck 1980). This may be especially important in habitats where food is scarce. Tool-use may compensate for a lack of morphological adaptations and enable animals to colonize habitats that would otherwise be unsuitable (Alcock 1972; Parker & Gibson 1977).

**2** The use of tools may quantitatively or qualitatively improve the diet. For example, by catching ants and termites with tools, chimpanzees gain qualitatively important nutrients such as lipids, essential amino acids and vitamins (e.g. Nishida & Hiraiwa 1982; Yamakoshi 1998).

We examined these hypotheses in the woodpecker finch by comparing different populations and seasons. We

expected that structural and climatic differences impose different necessities and possibilities for tool-use. Firstly, plant communities on the Galápagos Islands vary markedly along an altitudinal gradient. Secondly, the climate is highly seasonal, with a wet period from January to May and a drier period for the rest of the year. We selected two vegetation zones that differ greatly with regard to structure and climate: (i) the Arid Zone near the coast, a semi-desert open-canopy forest and (ii) the evergreen *Scalesia* Zone at higher elevations.

Given that tool-use extends the potential foraging sites of woodpecker finches, we predicted that (i) tool use should give woodpecker finches access to significant amounts of otherwise inaccessible prey. However, if the extraction of hidden prey is costly (e.g. due to handling time or search time) woodpecker finches should use tools only when more profitable prey is lacking or scarce. If tool use is costly we predict that (ii) tools should be used more often in the food-limited Arid Zone than in the prolific *Scalesia* Zone, and (iii) tools should be used more extensively during the dry season, when arthropod abundance is reduced, than during the wet season (Grant & Grant 1980; Boag & Grant 1984; Schluter & Grant 1984; Price 1985).

## MATERIALS AND METHODS

### Study area and study birds

Data were collected on Santa Cruz Island in the Galápagos archipelago during three field seasons: December 1995 – April 1996, October 1996 – April 1997 and January – February 1998. The climate is unusually dry and seasonal for the tropics, with two main seasons, a warm and wet period from January – May and a dry and cool period for the remainder of the year. Additionally, the onset and amount of rainfall is highly variable between years (Grant & Boag 1980). Total recorded rainfall during our three study periods for the wet season amounted to 118 mm in 1996, 893 mm in 1997, and 1654 mm in 1998 (an ‘El Niño’ event). For the dry seasons rainfall was 68 mm in 1996, 761 mm in 1997 (‘El Niño’) and 98 mm in 1998. Darwin’s finches can experience extreme food shortages during dry years and a superabundance of prey during ‘El Niño’ events.

Rainfall within the archipelago also varies locally and with altitude, thus creating distinct vegetation zones on the higher islands. Our study was conducted in two floristically and structurally very different areas: the Arid Zone extends from just inland of the coast up to an elevation of 80–120 m. It is characterized by a semi-desert forest consisting of deciduous trees (mainly *Bursera graveolens*), shrubs (e.g. *Croton scouleri*) and cacti (*Opuntia* spp. and *Jasminocereus thouarsii*). The so-called *Scalesia* Zone is an evergreen, lush cloud forest on the slopes between 300 and 650 m a.s.l., which is dominated by the tree-like composite

*Scalesia pedunculata*. Tree-trunks and branches are densely covered with epiphytes, mostly mosses. During the wet season, the *Scalesia* forest receives strong rains, and during the dry season in the lowlands, it is almost continually covered by mist. Therefore conditions are wet throughout the year except in marked drought years.

Woodpecker finches occur in all vegetation zones, but the highest densities (about 1.5 territories / ha in our study area) are reached in the *Scalesia* Zone. Woodpecker finches are much rarer in the Arid Zone, reaching densities of only one territory / 5 ha in our study area.

For intensive foraging observations two sites were selected. In the Arid Zone we investigated an area of approximately 70 ha and in the *Scalesia* Zone an area of approximately 110 ha. Observations were taken mainly between 6.30 a.m. and 12.30 p.m.

### Field observations

Woodpecker finches were located visually or by song. Focal observations were conducted with binoculars by continuously recording until the focal bird was lost from sight. Type and duration of foraging techniques, feeding substrates, and prey types obtained were recorded. Total observation times were 845 min in the Arid Zone and 430 min in the *Scalesia* Zone. Data in the Arid Zone were only collected from October 1996 to April 1997, but during three field periods from December 1995 to February 1998 in the *Scalesia* Zone.

Because of the tameness of the birds, most observations were made from distances of less than 10 m, allowing identification of prey items often to the level of order. Prey size was estimated in relation to the size of the beak. For the estimation of the caloric content, first the dry weight of each prey was estimated from its estimated lengths using order-specific allometric equations (Díaz & Díaz 1990), then the caloric content was calculated using data from the literature, again at order level (Singh 1973; Mathavan *et al.* 1976; Anderson 1978; Norberg 1978; Robel *et al.* 1995).

Six different foraging techniques were classified: probe = insertion of the beak into moss or curled leaves, chip off = removal of bark by inserting the beak sideways under the bark and levering the bark forcefully, glean = take prey from the surface of the substrate, peck = forceful, vertical downward movement of head and beak onto bark, bite = bite into petioles of leaves, tool-use = hold a twig or cactus spine in the beak and insert it into an opening in the bark. Observations were recorded with a portable tape recorder and later transferred to a computer using an event recording program (‘THE OBSERVER’, Noldus Laboratories).

In the Arid Zone, four males were colour-banded. Additionally, three pairs were observed in the vicinity of their nests and therefore assumed to be the same individuals at repeated visits. Sex was distinguished by behavioural

differences (song). Age (adult vs. juvenile) was determined from different beak coloration (black vs. pink). Intensive territory mapping from November 1996 to March 1997 enabled us to identify 11 additional territorial males. In total, a minimum of 21 birds was recorded at the study site.

In the *Scalesia* Zone, the birds were not individually recognized. To avoid observation biases, the observation effort was distributed equally over the whole area, and data were not collected at the same location more than once a day. Density estimates revealed that at least 143 territorial males were present at this study site (see below).

### Density estimates

The breeding density in both zones was estimated based on standardized point counts (Buckland *et al.* 1993). From a fixed point the observer recorded direction and distance between himself and a singing bird to the nearest 10 m within an unlimited radius. Each census lasted 5 min. Censuses were carried out during the wet season in January and February 1997, when woodpecker finches were territorial and singing activity was high. In the *Scalesia* Zone, counts were conducted twice at 17 locations and in the Arid Zone once at 21 locations. Results were analysed using the program DISTANCE, V.3.5 (Thomas 1998).

### Data analyses

*Comparison of first foraging observations between seasons and zones*  
Only the first foraging observation (i.e. first feeding technique and first feeding substrate used after the detection of a bird) per day of each focal individual was included in the analyses to avoid data dependency (Wagner 1981). In the *Scalesia* Zone, repeated observations of the same individual on different days cannot be excluded. Pooling data from different years may also result in an overestimation of the degrees of freedom in statistical tests. However, the pooled data set containing first foraging observations did not exceed the total number of birds present in the study area. In the Arid Zone, we used first foraging observations of the identified individuals present in the study area. An  $R \times C$  table, an exact test of contingency (Fung & Lee 1989), was used to test the difference between wet and dry seasons in each zone and the difference between zones in each season.

#### *Analyses of tool-use behaviour*

Continuous focal samples of 21 individually recognized woodpecker finches from the Arid Zone were analysed. Tool-use was compared with other foraging techniques with regard to foraging time and success. Observations were included in the analysis only when the foraging time exceeded 3 min and the animal fed at least twice. The

median number of continuous focal observations per individual was 3 (range: 1–7) and the average observation time was 11.1 min (range: 3.2–32.3 min). If an individual was observed more than once, the mean for these observations was calculated. Nine individuals were observed in both seasons. To avoid pseudo-replication, data from only one season were randomly selected for these individuals. A pair-wise comparison of the nine individuals observed in both seasons yielded qualitatively the same result (not presented here). For the calculation of the energy intake per time period we excluded observations in which less than 50% of the obtained prey was identified to order level. In the remaining observations foraging time for unidentified prey was not included. In the *Scalesia* Zone we estimated foraging success (prey items / min) with conventional feeding techniques by analysing 18 and 20 observations from the dry and wet seasons, respectively, which fulfilled the criteria mentioned above. Energy intake per time was not calculated for the *Scalesia* Zone, because there a larger proportion of food was small, unidentified prey, which could have biased the results.

Two-tailed, nonparametric statistical tests were used throughout this paper and we present mean  $\pm$  standard deviations unless otherwise stated. *U* denotes a Mann–Whitney *U*-test.

### Food abundance

The abundance of insects was measured for the six feeding substrates that seemed to be the most important for woodpecker finches: moss, the bark of dead wood and leaves in the *Scalesia* Zone; the bark of dead wood, lichens and leaves in the Arid Zone. The samples were collected both in the wet and the dry seasons with one exception. In the *Scalesia* Zone, quantitative data for the bark of dead wood are missing in the dry season because of the loss of data. Trees for sampling were randomly selected, by following a compass bearing for 120 s at a steady walk, starting from a counting point (see above, for sample sizes, see Table 1). Substrates were sampled in the following manner.

*Leaves.* With an extendable pole, four leafy branches were first covered with a gauze bag to prevent arthropods from escaping, and then cut with pruning shears fixed to a second pole. Samples were then briefly chilled to immobilize the arthropods. Subsequently, the leaves were placed on a white tray and all arthropods > 1 mm in length were noted. Leaves were assigned to three size categories: small, medium and large. In each category, the length and width of a subsample of 50 leaves were measured and surface areas calculated. We then counted the number of leaves in each category and thus calculated the total leaf area per sample.

**Table 1** Food abundance in  $\text{mg m}^{-2}$  on four substrates in the Arid and the *Scalesia* Zones in the wet and dry seasons

Zone	Season	Substrate	Median	Min.	Max.	Quartiles	<i>n</i>
<i>Scalesia</i>							
	Wet	Bark	70.5	0	779.2	0–261.7	26
	Wet	Moss	0	0	276.8	0–46.0	8
	Wet	Leaves	8.1	3.6	21.3	6.35–13.8	10
	Dry	Moss	90.5	0	222.8	0–202.1	8
	Dry	Leaves	8.1	3.6	21.3	6.3–13.7	10
	Wet	Bark	0	0	425.9	0–0	33
Arid							
	Wet	Lichen	0	0	4358.1	0–0	27
	Wet	Leaves	1.7	0.5	5.2	0.99–4.2	9
	Dry	Bark	55.9	0	824.3	11.1–337.1	16
	Dry	Lichen	0	0	121.1	0–0	17

**Table 2** Frequency of tool-use and other first foraging techniques in the *Scalesia* and the Arid Zone and in the dry and wet seasons

Zone	Season	Percent tool-use	Percent other techniques	<i>n</i>
<i>Scalesia</i>	Wet	2.7	97.3	219
Arid	Wet	4.8	95.2	21
<i>Scalesia</i>	Dry	1.4	98.6	68
Arid	Dry	28.6	71.4	21

**Bark.** Dead branches or trunks were selected randomly and their length and circumference were measured. The bark was carefully removed and all arthropods found underneath the bark, as well as those found in the tree-holes, were collected. Because insect abundance was very low in these substrates, data from tree-holes and bark were combined. The condition of the bark was classified as hard (removable only with a machete) or soft (removable by hand).

**Lichens.** In the Arid Zone, randomly selected branches covered with lichens were cut using the same method as for leaves. The surface area of the branches covered by lichens was measured and all arthropods were collected.

**Moss.** From randomly selected trees in the *Scalesia* Zone, we carefully removed an area of  $20 \times 50$  cm of the moss that covered the trunk. All arthropods in and under the moss were collected.

We identified the arthropods to order and measured their lengths (appendages excluded) to the nearest 0.1 mm under a  $40\times$  dissecting microscope. The dry weight of each individual was estimated from these lengths using

order-specific allometric equations (Díaz & Díaz 1990). Isopods and centipedes were excluded from the data analyses since they were never seen being eaten by woodpecker finches nor were they found in stomach analyses (Bowman 1961). Arthropod abundance is given as  $\text{mg m}^{-2}$  of substrate.

### Abundance of substrates

**Dead wood.** In each zone, 20 sample points were randomly selected (as described above) and the number of standing and lying trunks was counted within a radius of 5 m.

**Tree holes.** On the same trunks sampled for arthropod abundance, tree-holes were counted and their number per  $\text{m}^2$  surface area was calculated.

**Moss.** Moss was abundant in the *Scalesia* Zone but absent from the Arid Zone, whereas the reverse was true for lichens.

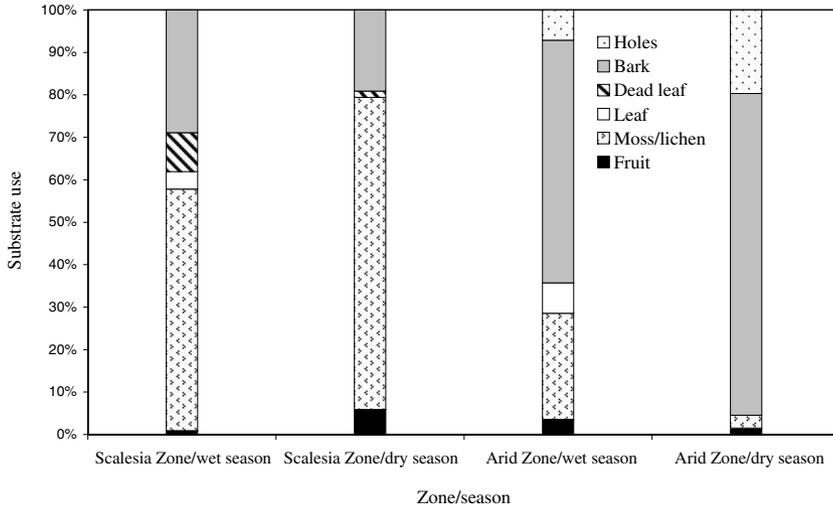
**Leaves.** Leaves were abundant in both seasons in the *Scalesia* Zone, whereas they were absent during the dry season in the Arid Zone.

## RESULTS

### Comparison of foraging substrates between zones and seasons

Woodpecker finches used different foraging substrates between the two zones, as well as between wet and dry seasons in each zone (Fig. 1). Although dead wood was more abundant in the *Scalesia* Zone (median trunks per sample point = 11, range 5–19,  $n = 16$ ) than in the Arid Zone ( $U = 42.5$ , median = 3.5, range 0–11,  $n = 20$ ,  $P < 0.01$ ), woodpecker finches used mainly moss in the *Scalesia* Zone and bark in the Arid Zone. In addition, bark was harder to remove in the Arid Zone (100% could be removed only with the machete,  $n = 36$ ) than in the *Scalesia* Zone (50% could be removed without a machete,  $n = 24$ , Fisher exact test,  $P < 0.001$ ).

In the *Scalesia* Zone during the wet season, the main foraging substrate was moss, followed by bark and leaves. In the dry season, woodpecker finches searched even more in moss (Fig. 1). In the Arid Zone during the wet season, woodpecker finches used mainly bark, but also lichens, leaves, tree-holes and fruits. During the dry season, they used primarily bark, with tree-holes being the second most important source of food (Fig. 1). The latter substrate was very scarce in the *Scalesia* Zone (median tree hole density per  $\text{m}^2 = 0$ , range 0–13.3,  $n = 26$ ) compared with the Arid Zone ( $U = 268.0$ , median = 0, range 0–63.9,  $n = 36$ ,  $P = 0.004$ ).



**Figure 1** Percentages of substrates used in first foraging observations in the *Scalesia* Zone in the dry ( $n = 68$ ) and wet season ( $n = 218$ ) and in the Arid Zone in the dry ( $n = 21$ ) and the wet season ( $n = 21$ ). Woodpecker finches used different foraging substrates in the two zones ( $R \times C$ -test, wet season:  $P < 0.001$ ; dry season:  $P < 0.001$ ) and in each zone during wet and dry seasons (*Scalesia* Zone:  $P < 0.001$ , Arid Zone:  $P = 0.001$ ).

**Food abundance**

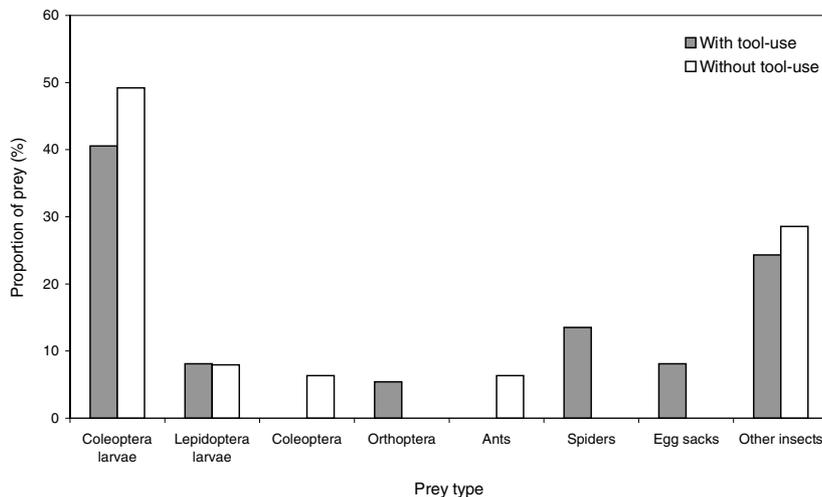
In the *Scalesia* Zone, the abundance of suitable prey items did not differ significantly between substrates in the wet season (Kruskal–Wallis test,  $\chi^2 = 3.190$ , d.f. = 2,  $P = 0.2$ , Table 1) and in the dry season ( $U = 36.0$ ,  $P = 1.0$ ). For the dry season we were not able to include the bark data into the statistical analysis, but arthropods were present and abundant. In the Arid Zone, the abundance of arthropods was very low on all substrates and it differed significantly between substrates in both seasons (Kruskal–Wallis test,  $\chi^2 = 22.788$ ,  $P < 0.001$ , Table 1). In the wet season arthropod abundance was higher under the bark than on leaves and higher in lichens than on leaves (multiple comparisons (Siegel & Castellan 1988),  $P < 0.05$ ). In the dry season arthropod abundance was higher under the bark than in lichens ( $U = 42.0$ ,  $P < 0.001$ ). Comparisons between

zones indicate that food abundance was significantly higher in the *Scalesia* Zone than in the Arid Zone on all substrates (bark, wet season:  $U = 241.0$ ,  $P = 0.001$ ; moss vs. lichen wet season:  $U = 77.5$ ,  $P = 0.049$ ; moss vs. lichen, dry season:  $U = 49.0$ ,  $P = 0.039$ ; leaves wet season:  $U = 3.0$ ,  $P < 0.001$ , Table 1).

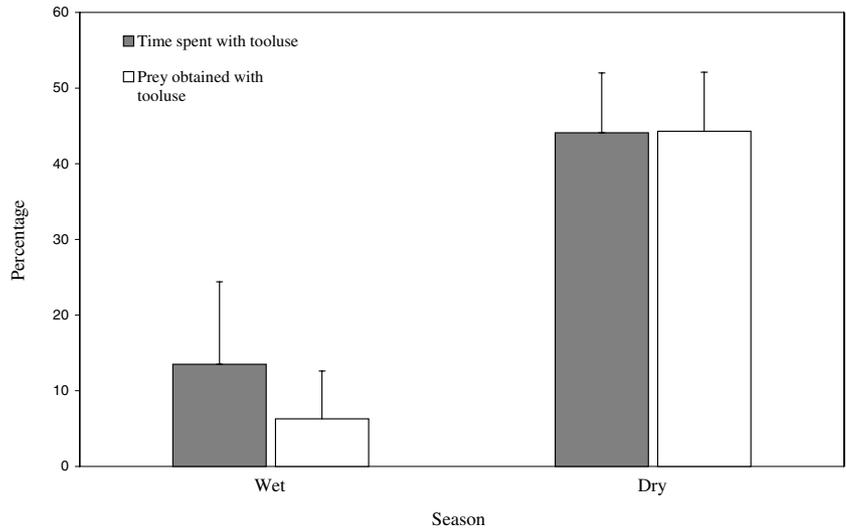
**Ecological correlates of tool-use**

*1st prediction: tool use should give woodpecker finches access to significant amounts of otherwise inaccessible prey*

In the Arid Zone, identified arthropod prey obtained using tools differed from prey types captured using other foraging techniques ( $R \times C$ -test,  $P < 0.001$ , Fig. 2). Three prey types that are particularly rich in proteins and fat (spiders, egg sacks of spiders and Orthoptera) were captured only with the help of tools, whereas ants and adult Coleoptera were



**Figure 2** Percentages of prey types obtained with ( $n = 37$ ) and without tool-use ( $n = 63$ ) during continuous focal observations.



**Figure 3** Percentage of the total foraging time spent with tool-use and of the total prey obtained with tool-use in the wet and dry season in the Arid Zone. Median and percentiles of nine (wet season) and 16 (dry season) individuals are given.

only obtained using other foraging techniques. During the dry season woodpecker finches obtained 50% of their prey with the help of tools (Fig. 3).

*Is tool use more costly than other foraging techniques?*

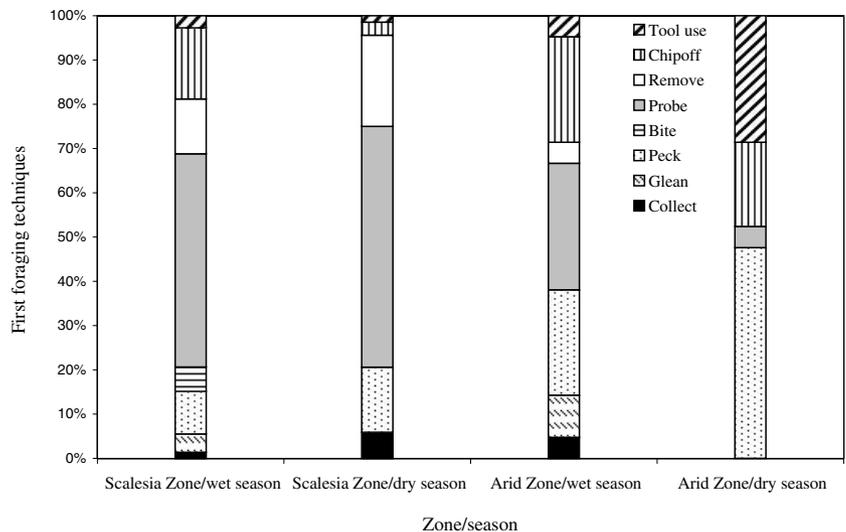
The median duration of prey extraction, excluding search time, was significantly longer when using tools (40 s, range 4–280,  $n = 24$ ) than the equivalent time span using conventional foraging techniques ( $U = 136$ , median = 7 s, range 1–87;  $n = 38$ ,  $P < 0.001$ ). These conventional foraging techniques were performed at a higher rate (median rate per min = 6.9, range 2–18,  $n = 16$ ) than tool-use (Wilcoxon Matched Pairs Signed Ranks Test, median = 0.45, range 0–1.79,  $Z = -4.015$ ,  $n = 16$ ,  $P < 0.001$ ). These data suggest greater foraging costs when using tools, which was a precondition for our 2nd and 3rd predictions.

*2nd prediction: tools should be used more often in the Arid Zone than in the Scalesia Zone*

Woodpecker finches used different foraging techniques in the two vegetation zones in both seasons ( $R \times C$ -test, wet season  $P < 0.001$ , dry season  $P < 0.001$ , Fig. 4). Probing into soft substrate was the most commonly used feeding technique in the *Scalesia* Zone, whereas pecking on the bark or chipping off soft bark was most common in the Arid Zone.

As predicted, woodpecker finches used tools significantly more often in the Arid Zone than in the *Scalesia* Zone, but significantly so only in the dry season (Fisher exact test, dry season  $P < 0.001$ , wet season  $P = 0.4$ , Table 2).

During 430 min of continuous focal observations in the *Scalesia* Zone (both seasons combined), tool-use was only seen six times. In the Arid Zone, however, we observed



**Figure 4** Percentages of feeding techniques used in first foraging observations in the *Scalesia* and Arid Zone in the dry and wet season (for samples sizes, see Fig. 1: for description of feeding techniques, see Methods).

tool-use 134 times during 845 min. In this habitat, 20 of the 21 individually recognized woodpecker finches used tools.

*3rd prediction: tools should be employed more extensively during the dry than during the wet season*

In the Arid Zone, first foraging observations showed that woodpecker finches used tools more often in the dry season, though not significantly so (Fisher exact test,  $P = 0.09$ , Table 2). However analysis of the continuous focal observations revealed that woodpecker finches spent significantly more time using tools ( $U = 28.5$ ,  $P < 0.05$ , Fig. 3) and obtained a larger proportion of their prey items with the help of tools ( $U = 20$ ,  $P < 0.005$ , Fig. 3) in the dry season than in the wet season. In the *Scalesia* Zone, the frequency of tool-use did not differ between wet and dry seasons (Fisher exact test,  $P = 0.4$ , Table 2).

*Is profitability higher when using tools?*

In the Arid Zone during the dry season, arthropods obtained using tools were significantly larger and contained more energy than those obtained using other feeding techniques (size:  $U = 326$ ,  $P = 0.029$ , estimated caloric value:  $U = 137.5$ ,  $P = 0.008$ , Table 3). Thus, although foraging success measured as prey items per time was similar with tool-use and conventional feeding techniques (Wilcoxon Matched Pairs Signed Ranks Test,  $Z = -1.344$ ,  $P = 0.25$ , Table 3), energy intake per time was higher when using tools ( $Z = -1.60$ ,  $P = 0.05$ , Table 3). During the wet season in the Arid Zone and during both seasons in the *Scalesia* Zone, tool-use was observed too rarely to compare its success with that of conventional feeding techniques. However, we found that in the Arid zone, profitability of using conventional foraging techniques was much higher in the wet season than in the dry season (prey items per time:  $U = 182.0$ ,  $P = 0.004$ , energy intake per time  $U = 4.0$ ,  $P = 0.003$ , Table 3), and it did not differ from the

profitability obtained with tool-use during the dry season. In contrast, in the *Scalesia* Zone foraging success with conventional feeding techniques did not differ between seasons ( $U = 160.0$ ,  $P = 0.57$ , Table 3), and it was higher there than in the Arid Zone during the dry season ( $U = 251.0$ , median both season combined = 0.41 prey items / min, range = 0.07–2.07,  $P < 0.001$ ). Prey obtained with conventional feeding techniques did not differ significantly in size (Kruskal–Wallis Test,  $P = 0.62$ ) and caloric value (Kruskal–Wallis Test,  $P = 0.44$ , Table 3) between zones and seasons.

## DISCUSSION

Tool-use extends the feeding range of woodpecker finches and allows them to collect arthropods from tree-holes that would otherwise be inaccessible. During the dry season in the Arid zone, bark is the main feeding substrate available, since leaves are absent and the food abundance in lichens is extremely low. Woodpecker finches rely almost exclusively on the extraction of food from bark and tree-holes and spend a greater proportion of time using tools and acquire a greater proportion of food with this technique than chimpanzees or any other animal hitherto studied. (Nishida & Hiraiwa 1982; McGrew 1992; Boesch *et al.* 1994; Yamakoshi 1998).

Our data reveal that tool use is costly, as it takes more time to acquire prey with it than with other foraging techniques. However, during the dry season in the Arid Zone, tool use is more profitable than using conventional feeding techniques. Even though the foraging success per minute foraging time was similar with the different feeding techniques, the prey obtained with tools was significantly larger and contained more energy.

As expected, in the Arid zone woodpecker finches spent less time using tools in the wet season than in the dry season. Foraging success with conventional feeding tech-

**Table 3** Comparison of tool use vs. conventional foraging techniques in Arid and *Scalesia* zone during the wet and dry seasons. Parameters shown are prey size, energy content of prey obtained, foraging success and energy intake. Medians and ranges are given

Zone	Season	Foraging technique	Prey size (mm)	Energy content (Cal / mg)	Foraging success (prey / min)	Energy intake (Cal / min)
Arid	Dry	Tool-use	12 (4–36) $n = 33$	134 (6–1004) $n = 19$	0.3 (0–1.1) $n = 16$	53 (0–281) $n = 10$
		Convent.	7 (4–30) $n = 29$	29 (5–181) $n = 27$	0.1 (0–1.0) $n = 16$	2 (0–23) $n = 10$
Arid	Wet	Convent.	15 (3–30) $n = 27$	43 (2–134) $n = 27$	0.4 (0.1–1.4) $n = 10$	31 (6–50) $n = 6$
<i>Scalesia</i>	Dry	Convent.	12 (3–31) $n = 13$	29 (2–668) $n = 13$	0.4 (0.1–2.1) $n = 18$	
<i>Scalesia</i>	Wet	Convent.	20 (12–24) $n = 7$	68 (29–378) $n = 7$	0.5 (0.2–0.9) $n = 20$	

niques was much higher during the wet season, probably because woodpecker finches found prey also on leaves and in lichens. The higher foraging success seems to outweigh the advantage of finding larger prey with tools, since the estimated energy gains per time were similar with both feeding techniques in the wet season.

In the *Scalesia* Zone woodpecker finches hardly ever used tools. Two factors may account for this: (i) as in the Arid Zone during the wet season, the abundance of surface prey or prey in soft substrate is sufficient and therefore foraging success / time with conventional feeding techniques is high; (ii) tree-hole density is significantly lower in the *Scalesia* than in the Arid Zone. This relative scarcity could increase search time for tree holes, thereby making tool-use less profitable.

In general, our comparison of feeding techniques between habitats and seasons indicates that tools are only employed when and where foraging profitability is higher than that attained with alternative foraging techniques. It is unlikely that local differences in tool-use frequency are a consequence of variable cultural tradition, as shown in chimpanzees (e.g. Whiten *et al.* 1999), since social learning is not an important mechanism in the acquisition of tool-use in the woodpecker finch (Tebich *et al.* 2001).

There are two shortcomings with our data set. Firstly, because of the very low frequency of tool use, our data set did not suffice to allow for a direct comparison of profitability between tool use and other foraging techniques in the Arid Zone during the wet season, and in the *Scalesia* Zone. Secondly, data in the Arid Zone were only collected during one field season as opposed to three field seasons for the *Scalesia* Zone. Thus, the high frequency of tool-use in the Arid Zone might have been the consequence of an exceptional year. However, this is not very likely as rainfall was average in 1996 (Grant 1986), and we observed frequent tool use during occasional checks in the Arid Zone also in another year (October / November 2001).

The Arid Zone is a suboptimal habitat for woodpecker finches, as is reflected by their low population density with only 0.2 singing males per ha as opposed to 1.5 males in the *Scalesia* Zone. On islands where dispersal possibilities are limited, special feeding skills may be selected for as they may allow the colonization of poor habitats and survival during food shortages. Grant & Grant (1989) showed that cactus finches (*Geospiza scandens*) that developed dry-season feeding skills (bark stripping, cactus-pad ripping) survived better in times of food shortage than individuals without these abilities. Since 18 of 19 repeatedly observed woodpecker finches in the Arid Zone used tools, we could not quantify the adaptive value of this feeding technique. However, woodpecker finches in this zone caught half of their prey with the help of tool-use during the dry season, and therefore, this feeding technique contributed significantly to their dietary subsistence.

Irregular, severe droughts occur frequently on the Galápagos Islands and are a strong selective force acting on Darwin's finches (Grant 1986). This may explain why Darwin's finches are a group with an exceptionally high rate of unusual feeding techniques (Grant 1986). Our study suggests that tool-use in the woodpecker finch is a special adaptation to harsh conditions in suboptimal habitats, specifically the unpredictable and food-limited environment in the arid coastal areas of the Galápagos Islands.

## ACKNOWLEDGEMENTS

We thank the Galápagos National Park Service, the Charles Darwin Research Station, TAME and especially W. Wickler for enabling this study; L. Vivanco for data collection and D. Blomqvist, B. McGrew, B. Kempnaers for advice on the manuscript. We also thank two anonymous referees and the editor for their constructive comments. The project was financed by the MPI Seewiesen and KLIVV.

## REFERENCES

- Alcock, J. (1972). The evolution of the use of tools by feeding animals. *Evolution*, 26, 464–773.
- Anderson, J.F. (1978). Energy content of spider eggs. *Oecologia*, 37, 41–57.
- Beck, B. (1980). *Animal Tool Behavior: The Use and Manufacture of Tools by Animals*. Garland STPM Press, New York.
- Boag, P.T. & Grant, P.R. (1984). Darwin's finches (*Geospiza*) on Isla Daphne Major, Galapagos: breeding and feeding ecology in a climatically variable environment. *Ecol. Monogr.*, 54, 463–489.
- Boesch, C., Marchesi, P., Marchesi, N., Fruth, B. & Joulian, F. (1994). Is nut cracking in wild chimpanzees a cultural behaviour? *J. Hum. Evol.*, 26, 325–338.
- Bowman, R.I. (1961). Morphological differentiation and adaptation in the Galápagos finches. *Univ. Calif. Publ. Zool.*, 58, 1–302.
- Buckland, S.T., Anderson, D.R., Burnham, K.P. & Laake, J.L. (1993). *Estimating Abundance of Biological Populations*. Chapman & Hall, London.
- Chaffer, N. (1945). The Spotted and Satin Bower-birds: A comparison. *Emu*, XLIV, 161–181.
- Díaz, J.A. & Díaz, M. (1990). Estimaciones de tamaños y biomásas de artrópodos aplicables al estudio de la alimentación de vertebrados insectívoros. *Donana, Acta Vertebrata*, 17, 67–74.
- Eibl-Eibesfeldt, I. (1961). Über den Werkzeuggebrauch des Spechtfinke *Camarhynchus pallidus* (Scalper und Salvin). *Z. f. Tierpsychol.*, 18, 343–346.
- Eibl-Eibesfeldt, I. & Sielman, H. (1962). Beobachtungen am Spechtfinke *Cactospiza pallida* (Scalper und Salvin). *J. Orn.*, 103, 92–101.
- Fung, K.P. & Lee, J. (1989). Extensions of Fisher Exact Test to 2-by-K Contingency Tables — A Computer Program in Basic. *Biomedicine*, 28, 195–196.
- Grant, P.R. (1986). *Ecology and Evolution of Darwin's Finches*. Princeton University Press, Princeton, NJ.
- Grant, P.R. & Boag, P.T. (1980). Rainfall on the Galápagos and the demography of Darwin's finches. *Auk*, 97, 227–244.

- Grant, P.R. & Grant, R.B. (1980). The breeding and feeding characteristics of Darwin's finches on Isla Genovesa, Galápagos. *Ecol. Monogr.*, 50, 381–410.
- Grant, R.B. & Grant, P.R. (1989). *Evolutionary Dynamics of a Natural Population*. University of Chicago Press, Chicago, IL.
- Hunt, G.R. (1996). Manufacture and use of hook-tools by Caledonian crows. *Nature*, 379, 249–251.
- Mathavan, T.J., Pandian, M. & Jaya, M. (1976). Use of feeding rate as an indicator of caloric value in some Lepidopterous larvae. *Oecologia*, 24, 91–94.
- McGrew, W.C. (1992). *Chimpanzee Material Culture: Implications for Human Evolution*. Cambridge University Press, Cambridge.
- Nishida, T. & Hiraiwa, M. (1982). Natural history of a tool-using behavior by wild chimpanzees in feeding upon wood-boring ants. *J. Hum. Evol.*, 11, 73–99.
- Norberg, A.R. (1978). Energy content of some spiders and insects on branches of spruce (*Picea abies*) in winter; prey of certain passerine birds. *Oikos*, 31, 222–229.
- Parker, S.T. & Gibson, K.R. (1977). Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in cebus monkeys and great apes. *J. Hum. Evol.*, 6, 623–641.
- Price, T. (1985). Reproductive responses to varying food supply in a population of Darwin's finches: Clutch size, growth rates and hatching synchrony. *Oecologia*, 66, 411–416.
- Robel, J.R., Press, B.M., Blake, H.L. & Johnson, K.W. (1995). Nutrient and energetic characteristics of sweepnet-collected invertebrates. *J. Field Ornithol.*, 66, 44–55.
- Schluter, D. & Grant, P.R. (1984). Ecological correlates of morphological evolution in a Darwin's finch, *Geospiza difficilis*. *Evolution*, 38, 856–869.
- Siegel, S. & Castellan, J. (1988). *Nonparametric Statistics for the Behavioural Sciences*, 2nd edn. McGraw-Hill, New York.
- Singh, J.S. & Yadva, P.S. (1973). Caloric values of plant and insect species of a tropical grassland. *Oikos*, 24, 186–194.
- Tebbich, S., Taborsky, M., Fessl, B. & Blomqvist, D. (2001). Do woodpecker finches acquire tool-use by social learning? *Proc. Royal Soc. Lond. B*, 268, 2189–2193.
- Thomas, L. (1998). *Distance*. Research Unit for Wildlife Population Assessment, University of St. Andrews, St. Andrews, U.K.
- Van Lawick-Goodall, J. & Van Lawick-Goodall, H. (1966). Use of tools by the Egyptian vulture, *Neophron percnopterus*. *Nature*, 212, 1468–1469.
- Wagner, J.L. (1981). Visibility and bias in avian foraging data. *Condor*, 83, 263–264.
- Walsh, J.F., Grunewald, J. & Grunewald, B. (1985). Green-backed Herons (*Butorides striatus*) possibly using a lure and using apparent bait. *J. Ornithol.*, 126, 439–442.
- Whiten, A., Goodall, J., McGrew, W.C., Nishida, T. & Reynolds, V. (1999). Culture in chimpanzees. *Nature*, 399, 682–685.
- Yamakoshi, G. (1998). Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: possible implications for ecological importance of tool use. *Am. J. Phys. Anthropol.*, 106, 283–295.

Editor, N. Perrin

Manuscript received 24 April 2002

First decision made 29 May 2002

Manuscript accepted 4 July 2002