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The flowerpiercers' hook: an experimental test of an evolutionary trade-off

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The evolution of features that enhance an organism's performance in one activity can adversely affect its performance in another. We used an experimental approach to document a trade-off associated with the evolution of the long hook at the tip of the bill of birds belonging to the genus *Diglossa* (flowerpiercers). In *Diglossa*, the more derived flower-robbing nectarivorous species have maxillae (upper jaws) that terminate in enlarged curved hooks. The ancestral frugivorous species have maxillae with relatively small hooks. We mimicked bill evolution by clipping the terminal bill hook of nectarivorous Cinnamon-bellied Flowerpiercers (*Diglossa baritula*) to resemble the frugivorous condition. We found that birds with experimentally shortened bills ingested fruit more efficiently, but had a reduced ability to rob flowers. Birds with intact bills, by contrast, were good flower robbers but poor frugivores. The evolution of a hooked bill endowed flowerpiercers with the ability to efficiently pierce flowers and extract nectar, but hindered their efficiency to feed on fruit.

Keywords: adaptation; evolution of diet; evolutionary costs; feeding performance; morphological novelty; nectar robbing

1. INTRODUCTION

The notion that the evolution of new traits is accompanied by trade-offs is central in evolutionary biology (MacArthur 1972; Benkman *et al.* 1984; Stearns 1989; Leigh 1990; Stearns 1992; Zera & Harshman 2001). This view stems from the belief that the evolution of features that enhance an organism's performance in one activity can adversely affect its performance in another (Benkman 1988; Schluter 1995; Benkman & Miller 1996; Temeles *et al.* 2000). Although several studies provide evidence for such a trade-off, few have been experimental and they have been mostly limited to micro-organisms and model organisms such as *Drosphila* (Chippindale *et al.* 1993; Leroi *et al.* 1994; Velicer & Lenski 1999). We used an experimental approach to document a trade-off associated with the evolution of the long hook at the tip of the maxillae (upper jaw) of flowerpiercers.

Flowerpiercers are a diverse group of nectarivorous and frugivorous tanagers (Bledsoe 1988; Burns 1997; Isler & Isler 1999) with notable interspecific differences in bill morphology (Vuilleumier 1969; Bock 1985). The maxilla of nectar-feeding species terminates in a long curved hook, whereas the hook at the tip of the maxilla of fruit-eating species is relatively small (figure 1). Nectarivorous flowerpiercers are specialized nectar robbers of tubular hummingbird-pollinated flowers. They use the long hook at the tip of their bill to hold flowers firmly, while they stab the base of the corolla with their mandible (lower jaw) and extract nectar by inserting their tongues through the slit (Skutch 1954; Vuilleumier 1969). Frugivorous flowerpiercers do not usually perforate flowers (Moynihan 1963, 1979; Snow & Snow 1980; Isler & Isler 1999), and their small hooks seem to represent the ancestral condition in the genus (Vuilleumier 1969; Hackett 1995). The enlarged hooks found in the nectarivorous species appear to be a derived trait (Vuilleumier 1969; Hackett 1995; Isler & Isler 1999) that facilitate robbing the nectar contained in tubular hummingbird-pollinated flowers (Skutch 1954; Vuilleumier 1969).

Here, we consider the hypothesis that the evolution of a hooked bill in nectar-feeding flowerpiercers entailed a trade-off. Although the hook eases the piercing of flowers, we proposed that it hinders the manipulation of fruit. Testing for the existence of a trade-off in the evolution of a morphological novelty requires demonstrating that this novelty increased performance in the new situation, but reduced performance in the ancestral one (Benkman 1988; Benkman & Miller 1996; Schluter 1995; Temeles *et al.* 2000). Here, we describe an experimental test of this hypothesis by mimicking the evolution of the flowerpiercer bill and measuring the effect of beak morphology on feeding ability. As food intake rate is a reliable measurement of performance (Lemon & Barth 1992; Grant & Grant 1996) we used it as an index of the degree of adaptation of bill structure (Bock & Von Wahlert 1965; Bock 1980; Arnold 1983; Schluter 1995; Koehl 1996).

2. MATERIAL AND METHODS

We imitated the evolution of the flowerpiercer's bill by reconstructing its ancestral hookless condition. We clipped the hook of captive members of a hook-bearing species: the Cinnamon-bellied Flowerpiercer (*Diglossa baritula*). As the hook is mostly keratinous rhamphothecae, it can be removed without harm. Indeed, our clipping procedure is similar to that routinely used to reduce the size of overgrown bills in captive birds. About 30 days after our procedure, the hook regained its former length and we released the birds. Each of our 10 experimental birds had a complete unmanipulated bill that was clipped sequentially to two other lengths: a hook with half the length of an unmodi-

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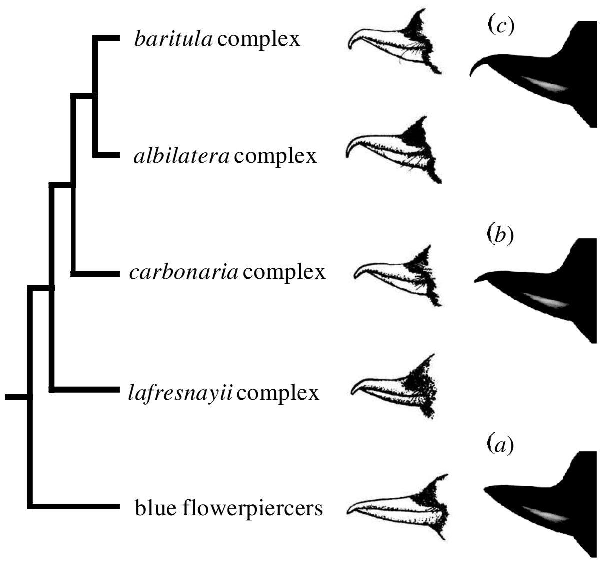

Figure 1. A phylogenetic hypothesis for the relationships of the members of the genus *Diglossa* according to Hackett (1995). We mapped bill morphology onto the phylogeny. Basal members of the genus exhibit maxillas with reduced hooks, whereas derived species have longer hooks. Basal flowerpiercers feed mainly on fruit, whereas derived species with longer bill hooks are predominantly nectarivorous flower robbers. We reconstructed the evolution of the flowerpiercers' bill experimentally by clipping the hook of individuals of *D. baritula* to three sizes: (*a*) no hook, (*b*) half the length of a complete hook, and (*c*) a complete hook. Drawings are modified from Vuilleumier (1969). Bill images to the right were drawn from photographs of individuals of *D. baritula* whose bills were experimentally modified.

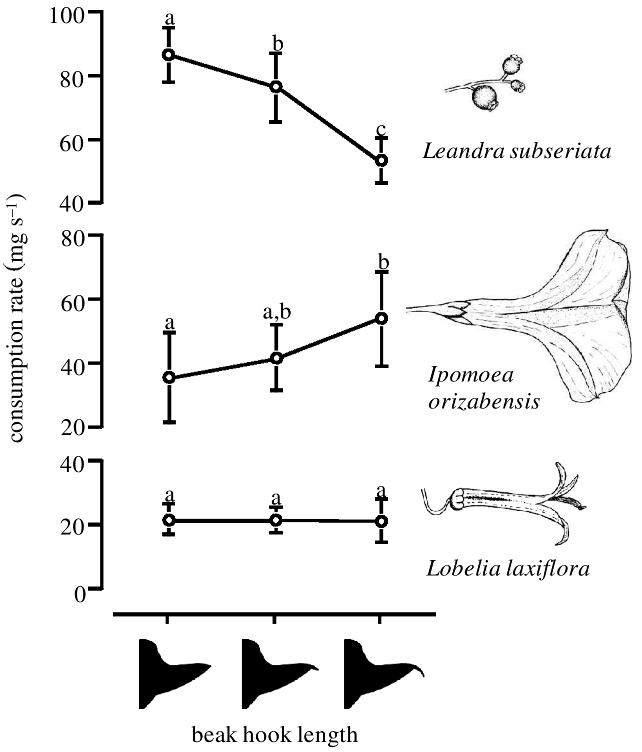

Figure 2. Hook length had a significant effect on consumption rate, and its effect differed with food type. When birds fed on *Lobelia*, they inserted the bill into the spaces between petals and extracted nectar at a rate that was independent of the hook length. To gain access to nectar in the flowers of *Ipomoea*, birds had to pierce the corolla. When birds fed on these flowers, consumption rate increased significantly with increased hook length. By contrast, fruit (*Leandra*) consumption rate decreased significantly with hook length. Points represent mean values ± 95% confidence intervals. Different letters represent groups that are statistically different.

fied hook and no hook (figure 1). To determine half the length of the hook, we measured the complete unmanipulated hook in each bird, divided its length by two and clipped at half its length. At each of these three hook lengths, we measured the rate at which birds consumed fruit (*Leandra subseriata*, Melastomataceae), nectar from a tubular flower whose corolla required piercing (the sympetalous *Ipomoea orizabensis*, Convolvulaceae), and a flower that did not require piercing (*Lobelia laxiflora*, Lobeliaceae, figure 2). These three food items are commonly used by our study species at our field site. In addition to measuring the time used by birds to extract floral nectar or to consume a fruit, we determined the frequency with which birds attempted to feed but failed.

We provided each of our 10 experimental birds with three *Ipomoea* flowers, three *Lobelia* flowers and three *Leandra* fruits at each of their three bill-hook lengths. To prevent the birds from learning how to manipulate each food item, which would affect our measurements of consumption rates, each bird was tested only twice per day (morning and afternoon), and the order in which the food items were presented to them was randomized. To avoid variability in nectar volume and viscosity that could effect handling times, we drained the flowers' natural nectar and then loaded them with 50 µl of artificial nectar (25% sucrose solution per total weight). Each trial was recorded using video, and handling times were obtained from the recordings. Flower handling time was measured from the moment that birds touched the flowers to the moment that they released contact. As birds fed on *Leandra* fruits by biting off pieces of fruit or by swallowing fruits whole, we measured fruit handling time as the time from the moment they touched the fruit to the moment that they swallowed. As birds in the field tend to interact only one time with each flower or fruit they visit, sometimes leaving behind nectar or pulp, we removed the bird after a single handling event was completed and measured the amount of nectar or fruit pulp consumed. Consumption rates were defined as the amount of food ingested (in milligrams) divided by handling time (in seconds). Only successful feeding attempts were considered for this analysis. Data were analysed by conducting one repeated measurement ANOVA for each food type.

To assess the effect of hook length on feeding failure rates, we offered birds fruit or flowers in succession until they fed successfully on three flowers or fruits. We used the number of failures before feeding successfully on three items as a failure rate index. Data were analysed by using a Friedman test.

3. RESULTS AND DISCUSSION

The rate at which birds extracted nectar from flowers that required piercing to access their nectary (*Ipomoea*) increased with hook length (repeated measures ANOVA $F_{2,9} = 5.56$, $p = 0.005$; figure 2). Birds without hooks were able to pierce the corolla tube and extract nectar, but the absence of a hook seemed to hamper their ability to hold the corolla. Even when they pierced the corolla, they could not hold flowers firmly and their intake rate was reduced

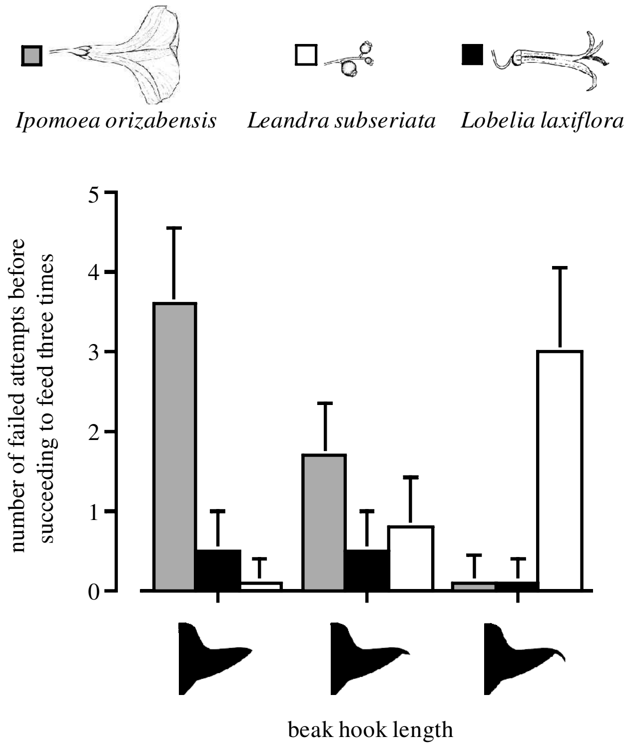

Figure 3. Hook length significantly affected feeding success. We used the number of failures before feeding successfully on three items as a failure rate index. The number of failed attempts while feeding on *Leandra* fruits increased significantly with hook length. By contrast, when birds tried to feed by robbing the nectar of *Ipomoea* flowers, the number of failed attempts decreased with hook length. Hook length had no significant effect on failure rate when birds fed on *Lobelia* flowers that did not require piercing to access nectar. The figure shows the mean values + s.d.

because the tongue and mandible slipped from the perforation (figure 2). Hookless birds also failed more often than birds with intermediate-sized and intact hooks when they attempted to extract nectar from *Ipomoea* flowers (Friedman test $\chi^2_{3,10} = 19.5$, $p < 0.001$; figure 3). The presence of a short hook reduced the number of failed piercing attempts (figure 3) and increased the rate at which flowerpiercers extracted nectar from the flowers (figure 2). Birds with long hooks rarely failed when attempting to rob a flower, and exhibited the highest nectar consumption rates. When flowerpiercers visited flowers that did not require piercing to access their nectar (*Lobelia*), hook length did not affect nectar consumption rate (repeated measures ANOVA $F_{2,9} = 0.036$, $p = 0.96$). Flowerpiercers did not use the hook to hold the corolla when extracting nectar from *Lobelia* flowers; they simply introduced their mandible between the petals and imbibed nectar. Hence, hook length had no significant effect on failure rate (Friedman test $\chi^2_{3,10} = 2.4$, $p = 0.3$; figure 2).

Our experimental manipulation enhanced the ability of nectarivorous flowerpiercers to handle fruit. Hookless flowerpiercers had the highest rates of fruit consumption and the lowest rates of failure (repeated measures ANOVA $F_{2,9} = 31.9$, $p < 0.001$, figures 2 and 3). As hook length increased, consumption rate decreased (figure 2). The presence of the hook caused birds to drop berries or to approach and bite them sideways. This increased the number of unsuccessful feeding attempts (Friedman test $\chi^2_{3,10} = 16.8$, $p < 0.001$), and reduced the amount of pulp ingested by the birds per unit of time. The ability to feed on fruit and the ability to obtain nectar from flowers with fused corollas at each hook length were negatively correlated for each bird (mean $r = -0.94 \pm \text{s.d.} = 0.03$, $t = -82.32$, $p < 0.001$, n(observations) = 10).

Our results provide experimental evidence of a trade-off associated with the evolution of a morphological novelty. Moreover, they indicate that a slight hook might have provided ancestral flowerpiercers with increased efficiency to pierce and extract nectar from hummingbird-pollinated flowers with sympetalous tubular corollas. Subsequent increases in hook length would have provided flowerpiercers further access to a diverse range of floral nectar sources unavailable to legitimate, non-robbing, floral visitors. However, a longer hook that allows more effective robbing entails a cost: flowerpiercers with longer hooks are less efficient frugivores. The differences in hook length among flowerpiercers with its concomitant trade-off and contrasting diets are also associated with broad interspecific differences in aggressive behaviour and habitat use (Moynihan 1963; Isler & Isler 1999), and presumably have enabled flowerpiercer species with and without hooked bills to coexist with each other and with hummingbirds at several Andean locations (Moynihan 1963, 1979; Snow & Snow 1980).

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