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Suction feeding in orchid bees (Apidae: Euglossini)

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Energy flux during nectar feeding is maximized at an intermediate sugar concentration, the value of which depends on the morphology of the feeding apparatus and the modality of fluid feeding. Biomechanical models predict that a shift from capillary-based lapping to suction feeding will lead to a decrease in this optimal sugar concentration. Here, I demonstrate that the four major genera of orchid bees (Apidae: Euglossini) are suction feeders and provide experimental evidence that the feeding optimum for one species, *Euglossa imperialis*, falls below the optimum for bee taxa that lap.

Keywords: foraging ecology; nectar; pollination; orchid bee; *Euglossa imperialis*; Euglossini

1. INTRODUCTION

The match between floral morphology and the mouthparts of specialized pollinators includes the most celebrated and controversial examples of plant–pollinator coevolution (Darwin 1862; Müller 1873; Harder 1985; Nilsson 1988; Temeles & Kress 2003). Bees are ubiquitous nectarivores, but, curiously, the flowers most bees visit are shallow compared with those used by butterflies and moths (Grant & Grant 1965; Barth 1991). Whereas most bees use a short proboscis to consume nectar with lapping motions of their hairy tongue (Snodgrass 1956; Harder 1982*a*,*b*), the long-tongued orchid bees (Apidae: Euglossini) employ a purely suctorial feeding mode to ingest nectar from deep flowers.

One dilemma faced by nectar foragers such as orchid bees is that energy content rises linearly with nectar sugar concentration, but viscosity rises exponentially (Baker 1975). Consequently, the rate of energy intake during feeding will be optimal at an intermediate concentration that is dependent on the geometry of the feeding apparatus and the modality of fluid feeding. Kingsolver & Daniel (1995) examined the effects of viscosity on two feeding modalities: capillary-based lapping and suction feeding. They predicted that a shift from lapping to suction feeding will lead to a greater dependence on fluid viscosity, and that optimal nectar sugar concentrations for suction feeders should fall below those of 'lappers'. In the present study, I show that this type of shift in feeding modality has occurred in orchid bees, and provide a comparative test of these theoretical predictions. This study reveals how biomechanical novelties have influenced plant–pollinator interactions.

2. MATERIAL AND METHODS

(a) *Maintenance and collection of the study organism*

Orchid bees are a diverse and abundant group of insects that inhabit forested areas ranging from Mexico to Argentina. Male bees from 30 species were captured using a hand-net at chemical baits of cineole, methyl salicylate, vanillin, skatole and eugenol (see electronic Appendix A available on The Royal Society's Publications Web site). Following capture, bees were brought back to a screened enclosure where they were held until they readily took artificial nectars. This process took between 30 min and 2 h for most bees. All experiments were conducted between June 2002 and April 2003 at field sites in Panama and Costa Rica.

(b) *General feeding observations*

I observed orchid bees ingesting artificial nectars to determine whether suction feeding was shared by the four major genera of orchid bee (*Eufriesea*, *Euglossa*, *Eulaema* and *Exaerete*). *Aglae*, a monotypic genus from South America, was the only genus of orchid bee not examined in this study. Before feeding trials, bees were encouraged to fly around the enclosure for at least 30 s to ensure a relatively constant state of metabolic activity. The artificial nectar solution, 35% sucrose, was placed in a 200 μl micropipette tip sealed at the small end using a drop of cyanoacrylate. This micropipette tip was inserted into a Styrofoam base, and a piece of laminated cardstock at the large end served as the drinking platform for the bee. A needle was used to extend the proboscis of the experimental animal and place it in the nectar solution. If animals were willing to drink, they extended their proboscis immediately upon contact with the solution, and they were released onto the drinking platform for observation.

(c) *Experimental observations with* Euglossa imperialis

To test the role of the glossa during feeding, I cold-anaesthetized five individuals of *E. imperialis* and excised the glossa at its base by using a pair of dissecting scissors (figure 1). After recovering, bees groomed their tongues and readily ingested nectar. I filmed five control individuals and five treatment individuals feeding from a 100 μl capillary tube and tracked the location of the glossa at 60 frames s^{-1} and the fluid meniscus at 1/2 frames s^{-1} to simultaneously gather data on glossal movements (in control animals) and record the nectar intake rate.

I determined the optimal nectar concentration for *E. imperialis* by timing bees as they drank from 5, 15, 25, 35, 45, 55, 65 and 75% sucrose solutions. I measured the mass consumed from the difference in the bee's mass before and after feeding trials (±1 mg), and I calculated the rate of sucrose consumption by multiplying mass intake rate by sucrose concentration. A total of 71 individuals were used in these trials and no individuals were used more than once.

(d) *Nectar collection in nature*

Nectar stored in a bee's crop is not diluted or modified in any way, and is thus representative of nectars actually collected during foraging (Roubik *et al.* 1995). I extracted nectar into 25 μl capillary tubes by gently squeezing the abdomens of individuals of *E. imperialis* that arrived at the chemical baits. Equivalent sucrose concentrations were determined using a temperature-corrected pocket refractometer (0–62%; samples greater than 62% were diluted). Owing to the presence of amino acids in floral nectars, these readings are likely to be several per cent higher than true sugar concentrations (Inouye *et al.* 1980).

3. RESULTS

Suction feeding is shared by the four major genera of orchid bees (*Eufriesea*, *Euglossa*, *Eulaema* and *Exaerete*), a conclusion based on over 735 feeding observations with individuals of 30 species (see electronic Appendix A). Even when offered low nectar volumes (less than 10 μl), orchid bees were never observed lapping nectar.

During ingestion, the glossa of *E. imperialis* was always fully extended and stationary, reaching *ca.* 6 mm beyond the apical end of the feeding tube formed by the galeae and the labial palps (see figure 1). In fact, not only could *E. imperialis* feed after surgical removal of the glossa, but this treatment had no effect on the rate of nectar intake ($t_9 = 0.333$, $p = 0.7469$), indicating that the glossa is not an essential component of nectar transport in these bees under these experimental conditions.

In drinking trials with *E. imperialis*, the rate of sucrose intake was significantly different among sucrose concentration

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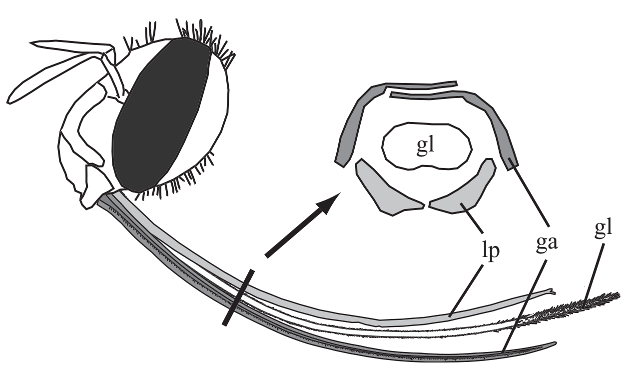

Figure 1. Lateral view of the head and proboscis of *E. imperialis* and a cross-section of the proboscis indicating the glossa (gl), galea (ga), and labial palps (lp). The symmetrical elements are excluded in the lateral view. Orchid bees suck nectar through the tube formed by the galeae and labial palps.

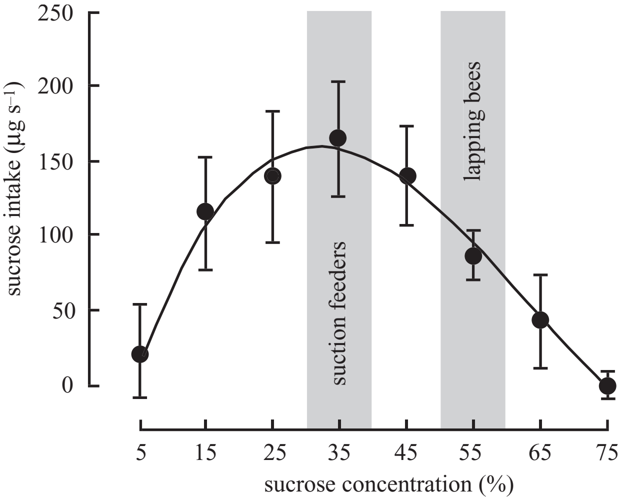

Figure 2. Sucrose intake rate is optimal between 30 and 40% sucrose for *Euglossa imperialis* feeding on artificial flowers at 29.8 ± 9.2 °C (range of 27.6–31.6). Error bars show 95% CIs for treatment means. The fitted least-squares regression line is $y = 17.0x - 0.387x^2 + 0.002x^3 - 49.109$. The grey rectangles depict the energy intake optima derived from other studies for suction feeders and lapping bees (see § 4 for references).

treatments (ANOVA: $F_{7,63} = 13.0$, $p < 0.0001$), with the 35% solution giving the highest rate of sucrose intake (figure 2). The mean nectar sugar concentration collected by *E. imperialis* in Costa Rica, 38.3 ± 1.59% (mean ± 95% CI, $n = 108$), closely matched the optimum derived from drinking trials.

4. DISCUSSION

The present study demonstrates that a shift from capillary-based lapping to suction feeding in orchid bees has led to a decrease in the nectar sugar concentration that maximizes the rate of energy intake. Orchid bees maximize their rate of energy intake by feeding on nectars with sugar concentrations between 30 and 40%. This optimal concentration coincides with the optima found for suction-feeding butterflies (May 1985; Pivnick & McNeil 1985; Boggs 1988), hawkmoths (Josens & Farina 2001) and flies (Kingsolver & Daniel 1995), whereas the optima for bees that lap lie between 50 and 60% sucrose (Roubik & Buchmann 1984; Harder 1986). The field portion of this study confirms that *E. imperialis* harvests nectars matching this feeding optimum. Previously, Roubik *et al.* (1995) showed that *E. imperialis* and 12 other species of orchid bees collect more dilute nectars than sympatric, lapping bees.

In contrast to the short flowers frequented by most bees (Barth 1991), many orchid bees visit deep flowers in the families Bignoniaceae, Costaceae and Marantaceae (Ackerman 1985). Harder (1985) and Ranta & Lundberg (1980) found that although bumble-bee species with long tongues can access deep flowers, they also frequently visit shorter flowers. In fact, such asymmetric specialization also occurs in long-tongued guilds of hawkmoths (Nilsson *et al.* 1987; Haber & Frankie 1989), nemestrinid flies (Manning & Goldblatt 1997) and orchid bees (Ackerman 1985). Because insects with long tongues have a wide selection of flowers from which to choose, but the deepest flowers often depend on a single pollinator, these flowers are expected to evolve nectars at optimal sugar concentrations for their primary pollinator. Indeed, *E. imperialis* visits a wide variety of flowering plants, but the understorey herbs, *Costus laevis* and *Costus allenii*, are entirely dependent on female *E. imperialis* for their pollination (Schemske 1981; Ackerman 1985). Not only do the nectar spurs of *C. laevis* and *C. allenii* match the 30 mm tongues of their exclusive visitors, but these plants provide nectars with sugar concentrations between 30 and 40% (Schemske 1981).

Orchid bees possess a derived feeding mode, as outgroups in both short-tongued and long-tongued bee families lap nectar (Harder 1982*a*). One probable evolutionary scenario is that as proboscis length evolved in concert with floral morphologies, anatomical constraints on glossal reciprocation would have rendered nectar transport via lapping less effective than suction feeding. This type of functional shift in feeding modality appears to have occurred independently in orchid bees, butterflies (Krenn & Kristensen 2000), pollen wasps (Krenn *et al.* 2002) and long-tongued bee-flies (Szucsich & Krenn 2002), representing a general trend among nectarivorous insects that use deep flowers. Nectarivorous insects first appear in the fossil record as early as the Late Jurassic, but suction feeding from deep, funnel-shaped flowers is more likely to be post-Cretaceous in origin (Labandeira 1997). The present study adds a biomechanical perspective to the evolutionary history of these interactions: deeper flowers exerted selection for longer tongues, and insects with longer tongues selected for more dilute nectars.

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