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Mobility of *Impatiens capensis* flowers: effect on pollen deposition and hummingbird foraging

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Abstract Flexible pedicels are characteristic of bird-pollinated plants, yet have received little attention in studies of hummingbird-flower interactions. A major implication of flexible pedicels is that flowers may move during pollination. We examined whether such motion affected interactions between ruby-throated hummingbirds (*Archilochus colubris*) and jewelweed (*Impatiens capensis*) by increasing pollen deposition and by altering the effectiveness of nectar removal. For *I. capensis*, flower mobility enhanced pollen deposition: birds had significantly longer contact with anthers and more pollen deposited on their bills and crowns when foraging at mobile flowers than at flowers that had been experimentally immobilized. In contrast, flower mobility imposed a cost on hummingbirds by significantly increasing their handling times and reducing their extraction rates relative to their interactions with immobile flowers. Field observations indicated that the motion observed during hummingbird visits did not occur when bees (*Bombus* spp., *Apis mellifera*) visited *I. capensis* flowers, which suggests that the mobility of *I. capensis* flowers is an adaptation for hummingbird pollination.

Key words Pollination · *Archilochus colubris* · *Impatiens capensis* · Hummingbird · Flower morphology

Introduction

Many flowers pollinated by hummingbirds exhibit the ornithophilous syndrome (Baker 1961; Faegri and van der Pijl 1971; Grant and Grant 1968; Snow and Snow 1980; Stebbins 1989). Some of the documented characteristics of ornithophilous flowers are narrow tubular corollas, red coloration, lack of odor, and thickened tissue around the base of the corolla to protect against nectar thievery. These characteristics apparently make the flow-

ers an attractive food source for hummingbirds by reducing competition with insect foragers.

Another characteristic of ornithophilous flowers is a flexible pedicel (Grant and Grant 1968; Faegri and van der Pijl 1971). Grant and Grant (1968) hypothesized that flexible pedicels prevented flower tissue from being damaged by the probing bill of a hummingbird. Alternative explanations for the role of flexible pedicels, however, have not been developed and tested. This lack of study is surprising, given that a flexible pedicel is diagnostic of ornithophily, and other ornithophilous floral characteristics have been well studied.

A major implication of a flexible pedicel is that the flower may move during the act of pollination. Such motion could affect flower/hummingbird interactions by increasing pollen transfer and by altering the effectiveness of nectar removal. Here, we investigate these hypothetical effects using jewelweed (*Impatiens capensis*) and ruby-throated hummingbirds (*Archilochus colubris*). First, we examine whether floral motion increases pollen transfer. Then, we assess whether floral motion impairs the foraging performance of hummingbirds, and whether hummingbirds prefer flowers that have been experimentally immobilized.

Methods

The hummingbirds

Fourteen ruby-throated hummingbirds were live-trapped in the late summer and early fall of 1993 in Amherst and Shutesbury, Mass. When not being used in the experiments, individual birds were housed in cages of dimensions 0.6 m × 0.6 m × 0.6 m in a temperature- and light-controlled room. Birds were fed *ad libitum* a solution of 11.5% Nektar-Plus commercial hummingbird food (Nekton USA), 1% soy protein and 87.5% distilled water (by volume).

The flowers

Thirty-eight young (~0.6 m tall) plants of *I. capensis* were acquired on 21 December 1993, and 16 adult plants (1.0–1.5 m) were obtained on 23 February 1994 from the laboratories of J. Schmitt at

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Brown University. All plants were from native stock. Plants were maintained in fertilized 20-cm pots in a greenhouse at approximately 22°C on a 0600 to 2000 hours light/dark cycle.

Ruby-throated hummingbirds and several species of bees have been observed to visit *I. capensis* flowers in nature (Rust 1979; Bertin 1982; Laverty and Plowright 1985; personal observation) and enclosure experiments show that both hummingbirds and bees are successful pollinators (Bertin 1982).

Experiment 1: pollen transfer and nectar extraction

The first experiment tested the effect of experimental immobilization of flowers on pollen transfer and hummingbird foraging behavior. Experiments were conducted in a temperature- and light-controlled experimental chamber that was approximately 2 m high with a basal area of 3 m². The bird to be tested was placed in the room 1 day prior to the experiment. On the next day, after depriving the bird of food for 45 min, we presented it with *I. capensis* flowers on artificial stalks, and filmed foraging visits using a Nikon VN-720 Hi-8 mm video camera. The artificial stalk was designed either to preserve or restrict the flower's natural mobility. It consisted of a plastic dropper at the end of which was an alligator clip holding a 5-cm piece of Tygon tubing (internal diameter 1.2 mm, external diameter 2.2 mm) into which the flower stem was inserted. To immobilize flowers we looped a piece of plastic-coated wire around the back of the flower (Fig. 1). After mounting flowers in the artificial stalks, a 1- to 2-mm slit was cut in the tip of each flower's spur and the flower's nectar was drained with a 5- μ l Hamilton Microsyringe. The nectar was replaced with 8 μ l of a 20% by weight sucrose solution.

Birds were alternately presented with either one natural ("mobile") or one artificially immobilized ("immobile") flower. After the bird's visit, the flower was removed and the amount of nectar remaining was measured with a 5- μ l or 10- μ l microcapillary pipet. The bird was captured without disturbing the pollen on its bill, and a visual estimate was made of the amount and location of the pollen. Using a disposable plastic syringe filled with water, the pollen was rinsed off the bill into a 1.5-ml microcentrifuge tube. Two drops of methylene blue were added to this suspension to dye the pollen grains, and then the bird was released and presented with the next flower. This was repeated for a total of four mobile and four immobile flowers.

The tubes of pollen suspension were centrifuged at 60 Hz for 30 s, and then decanted, leaving a residual volume of 0.5 ml, which contained a pellet of pollen grains. Tubes were then vortexed for 1 min to resuspend the pollen grains. From each tube, two 5- μ l drops were examined under a microscope at 35 \times magnification. The numbers of pollen grains in each drop were averaged and the average was multiplied by 100 (the ratio of the 0.5 ml of solution to the 5- μ l drop), yielding an estimate of the total amount of pollen retrieved from the bird's bill.

Video recordings were played back on a Panasonic PV-4264 VCR with jog/shuttle remote control, which allowed field by field viewing of the 60 fields that were recorded per second. From these pictures we measured handling times and pollen contact times. We defined handling time as the time between when the tip of the bird's bill entered the opening of the corolla (or bumped into the flower in an attempt to enter) and when the bill-tip was withdrawn. Pollen contact time was defined as the time anthers appeared to be in contact with the bird.

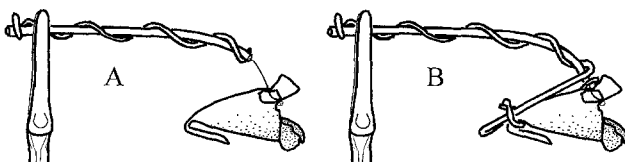


Fig. 1A,B Mounting of *Impatiens capensis* flowers for measurements of pollen transfer and nectar extraction. **A** Mobile flowers. **B** Experimentally immobilized flowers

Experiment 2: patch preference

A patch preference experiment examined whether hummingbirds preferred immobile flowers over mobile flowers. This work was conducted in an experimental chamber measuring 2 m \times 2 m \times 2.1 m high. We placed a perch at the middle of the rear wall and a camera in the middle of the room approximately 60 cm from the front wall. Two "patches" of four flowers each were presented 15 cm from the front wall, 30 cm apart and equidistant to the perch and to the camera. A patch consisted of a row of four flowers filled with sucrose solution and mounted as in the previous experiment, except that the alligator clip rested on the end of a 12.7-cm-long 0.5-cm dowel instead of a plastic dropper. Flowers within a patch were spaced at 1.5-cm intervals.

On the day prior to the experiment, the bird was placed in the experimental room. On the day of the experiment, the bird was deprived of food for 45 min and then presented simultaneously with a patch of mobile flowers and a patch of immobile flowers. Each bird was allowed to visit the two patches for four successive training trials so that it could gain experience feeding at the two flower types. Each trial was terminated when, upon returning to its perch, the bird had visited at least seven of the eight flowers. At the end of each trial, the nectar remaining in each flower was removed, its volume was measured, and the flower was refilled with 8 μ l of 20% by weight sucrose solution.

After these four training trials, an additional set of preference trials was conducted to determine whether birds preferred one flower type over the other. The bird was again presented with the same patches but was only allowed to visit a total of four flowers. Usually this meant the bird would choose one patch and feed at every flower in it; however, occasionally the bird would go back and forth between the two patches. After the bird had visited four flowers, its feeding bout was interrupted. Both patches were removed, and the sucrose solution remaining in the visited flowers was measured. These flowers were then refilled and replaced for a total of ten preference trials. To avoid any spatial preferences a bird might have for one patch site over the other, four birds were presented with the immobile flowers on the right and mobile flowers on the left; the other four were presented with the opposite arrangement.

Results

Flower motion

Flowers of *I. capensis* hang from a stem that is attached above the mouth of the corolla where one saccate sepal and three petals come together. The corolla narrows from approximately 4–8 mm wide at the mouth to 1–2 mm in diameter toward the back where it forms a recurved tail that is generally full of nectar. The reproductive organs are just under the roof of the corolla mouth. To obtain all of the nectar in a flower, the hummingbird's tongue must negotiate the 180° curve at the base of the spur. Our videos show just this movement: the tongue contacts the back wall of the spur and then curves back 180° toward the nectar at the tip of the spur. With each lick the flower is pushed away, and then the spring-like pedicel brings the flower back toward the bird. This movement often causes the reproductive organs to contact the proximal half of the bird's upper bill.

Effect of flower mobility on pollination

To assess whether restriction of floral mobility affected pollen deposition, we counted the number of pollen

Table 1 Transfer of pollen grains and extraction of nectar at mobile and immobile flow-ers. (Data are means±SD)

	Flower type		n	P*
	mobile	immobile		
Pollen grains per visit	7874±2477	3359±1055	8	<0.01
Anther contact (s) per visit	1.86±0.16	0.94±0.19	7	<0.05
Nectar extracted (µl) per visit	7.91±0.14	7.93±0.16	8	0.9
Handling time (s) per visit	3.54±0.56	2.81±0.30	8	<0.05
Extraction rate (µl/s)	2.68±0.27	3.35±0.28	8	<0.05

* Two-tailed matched pairs randomization test

grains deposited on the bird during each foraging visit. Mobile flowers deposited about two times more pollen on birds than immobile flowers (Table 1, row 1).

The greater quantity of pollen deposited by mobile flowers could have been the result of either or both of two factors: a greater force of contact with the flower's anthers, or a greater duration of contact with the anthers. We lacked the technology to examine force of contact but we used video footage to examine the duration of contact with the anthers during each visit. The mean duration of contact for immobile flowers was about half that for mobile flowers (Table 1, row 2).

Effect of flower mobility on foraging behavior

Qualitative observations

Birds generally had no difficulty entering or foraging at immobile flowers. Once the bill was inside the corolla, a bird could hover almost motionlessly for the duration of nectar extraction. Foraging at mobile flowers required more effort. On the approach, a bird's bill would sometimes graze the side of the corolla mouth, causing the flower to rock back and forth. At this point, the bird would often pull its head back and try to enter again, or it would keep pushing on the side of the corolla, futilely seeking the entrance. Occasionally, the bird would enter the flower from slightly below, so that the bill tip would hit the inside roof of the corolla, pushing the rear of the spur upward and pushing the whole flower back. Even after successful insertion of the bill into mobile flowers, the birds generally readjusted body and bill position to compensate for flower movement. A fraction of a second after the bird succeeded in entering the corolla, the flower typically began moving rhythmically back and forth along and against the bird's bill, as the hummingbird's tongue pushed the back of the curved spur with each lick.

Quantitative observations

Given the difficulty hummingbirds apparently had when feeding at mobile flowers (as determined by visual inspection), we examined the consequences of flower mobility for three measures of foraging performance: the

mean amount of nectar extracted per flower (microliters), the mean handling time per flower (seconds), and the mean nectar extraction rate per flower (microliters per second). Amounts of nectar extracted did not differ significantly for the two flower types (Table 1, row 3). However, mean handling times at mobile flowers were 25% longer than mean handling times at immobile flowers (Table 1, row 4). Consequently, birds had higher nectar extraction rates at immobile flowers than at mobile flowers (Table 1, row 5).

Patch preference

Given that birds had higher nectar extraction rates at immobile flowers than at mobile ones in the first experiment, we predicted that they should prefer patches of immobile flowers to patches of mobile flowers. When presented with a choice, six out of eight birds visited immobile flowers more frequently than mobile flowers (ran-

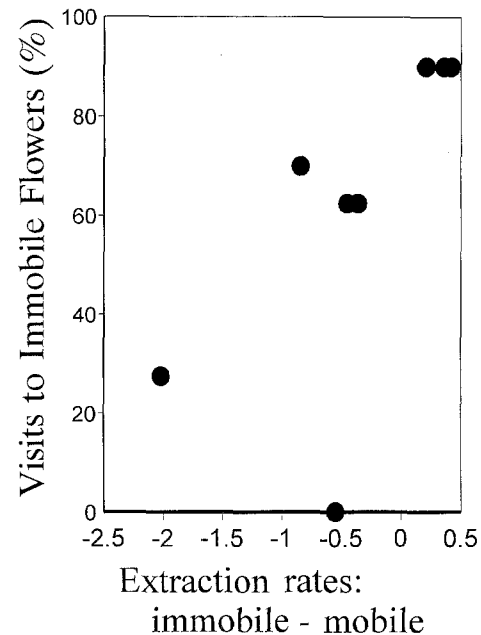


Fig. 2 Relative frequency of visits to immobile flowers during preference trials as a function of the differences between nectar extraction rates at mobile and immobile flowers during training trials

domization test, two-tailed, $P = 0.26$). One explanation for the lack of a significant preference for immobile flowers is that extraction rates for some birds may not have been much greater at immobile flowers than at mobile flowers. To investigate this possibility, we examined the relationship between the difference in their extraction rates at immobile and mobile flowers during the training trials and their degree of preference for immobile flowers during the preference trials. The more quickly birds extracted nectar at immobile flowers compared with mobile ones (i.e., the greater the difference), the more frequently they visited immobile flowers (Spearman rank, $r_s = 0.86$, $P < 0.01$, $n = 8$), which supports this explanation. This association was particularly evident for the three birds that fed most efficiently at immobile flowers and visited immobile flowers 90% of the time (Fig. 2).

Figure 2 shows that five of the eight birds had lower nectar extraction rates at immobile flowers than at mobile flowers during the training trials. These results contrast with the measurements of extraction rates from individual flowers obtained in Experiment 1. However, during the preference trials, all birds had greater nectar extraction rates at immobile flowers than at mobile flowers (mean difference = $1.6 \mu\text{l/s} \pm 0.5 \mu\text{l/s SE}$, range 0.1–3.6 $\mu\text{l/s}$). These findings suggest that extraction rates at the two flower types changed with experience. For all birds, extraction rates increased disproportionately at immobile flowers, their mean increase being $2.0 \mu\text{l/s}$ ($\pm 0.7 \mu\text{l/s SE}$, range 0.1–5.2 $\mu\text{l/s}$).

Discussion

The results indicate that floral mobility does play a role in the interaction between ruby-throated hummingbirds and *I. capensis* flowers. When foraging at mobile flowers, birds had significantly greater contact with anthers and had more pollen deposited on their bills and crowns than when foraging at immobile flowers. For *I. capensis*, then, flower mobility appears to facilitate pollination.

Our data indicate that flower mobility imposes a cost on the bird, both in terms of increased handling times and reduced nectar extraction rates. Field and laboratory studies have demonstrated that hummingbirds distinguish between high and low quality food sources, and that they preferentially visit sources (flowers or feeders) that yield greater energy extraction rates (Pulliam 1974; Gass and Montgomerie 1981; Gass and Sutherland 1985). Our results suggest that the higher feeding costs at mobile flowers may sometimes be great enough to make individual birds preferentially visit immobile flowers.

Impatiens capensis is pollinated by both hummingbirds and bees (Rust 1979; Bertin 1982; Lavery and Plowright 1985). The few studies on the relative importance of these two kinds of pollinators suggest that birds may be responsible for a relatively small proportion of the

pollination (Rust 1979; Bertin 1982). On this basis one might question whether the effects of mobility described in this study are adaptations for hummingbird pollination; however, even a low visitation by hummingbirds may be sufficient to generate finely tuned adaptations for hummingbird pollination if such adaptations have little or no negative effect on bee pollination. When bees (*Apis* and *Bombus* spp.) and wasps (*Vespula* spp.) visit *I. capensis* flowers, mobile mechanisms of pollen deposition do not occur (personal observation). This difference indicates that the mobility of *I. capensis* is not an adaptation for bee pollination and causes little if any interference with pollination by bees. Other morphological characteristics of *I. capensis* flowers, such as a wide opening, may be more strongly related to bee pollination. Our results therefore draw attention to a possibility that needs to be more generally assessed in pollination biology: a generalist flower may have one structure evolving as a specific adaptation for one kind of pollinator and another structure for another kind of pollinator.

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