Foraging ability of rufous hummingbirds on hummingbird flowers and hawkmoth flowers

(*Selasphorus rufus*/*Ipomopsis aggregata*/*Aquilegia*/hummingbird foraging/coadaptation)

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ABSTRACT We examine the suitability of ornithophilous flowers and sphingophilous flowers in *Ipompsis* and *Aquilegia* for nectar foraging by the hummingbird *Selasphorus rufus*. In *S. rufus*, bill length averages 18.9 mm in females and 17.3 mm in males. Maximal tongue extension approximates bill length, suggesting that birds can feed from floral tubes up to 33.5 mm in length. However, their ability to do so is limited by two factors. First, the maximal depth at which *S. rufus* can extract nectar decreases with the width of the floral tube. Second, feeding time is shortest in short floral tubes and progressively increases as the tubes lengthen because of increased time required for tongue extension and retraction. Hence, nectar foraging occurs with optimal efficiency in moderately broad floral tubes with lengths that do not exceed or only slightly exceed the bill length plus ≤5-mm tongue extension. In most ornithophilous taxa of *Ipomopsis* and *Aquilegia*, the floral tubes have lengths and widths in the optimal range for nectar foraging by *S. rufus*, whereas in the sphingophilous taxa, the basal nectar either may be reached but at much higher cost or, more frequently, is beyond reach of bills and tongues. The flower-visiting habits of *S. rufus* and other hummingbirds in nature are generally congruent with these conclusions and support the case for coadaptation between these plants and pollinators.

The ability of hummingbirds to extract nectar from trumpet-shaped hummingbird flowers depends on the possession of a bill (culmen) long enough to probe the floral tube (corolla tube, hypanthium, petal spur). A general correspondence does exist between length of culmen in western American hummingbirds and length of floral tube in hummingbird flowers in the same area. This is one argument in favor of the conclusion that western American hummingbirds and western ornithophilous plants are coadapted. However, western American hummingbirds frequently visit flowers with floral tubes longer or shorter than their culmen. Foraging visits of this sort seem at first sight to weaken the case for coadaptation.

We examine this problem by comparing the suitability of flowers in ornithophilous versus sphingophilous taxa of the *Ipomopsis aggregata* group (Polemoniaceae) and the *Aquilegia formosa*–*Aquilegia caerulea* group (Ranunculaceae) for foraging by one western North American species, the rufous hummingbird (*Selasphorus rufus*). Rufous hummingbirds have been the subject of recent experimental studies of foraging ability that consider not only culmen length but also culmen width, tongue extension, and handling (= feeding) time. We relate the evidence concerning these features to the size and shape of the floral tubes in ornithophilous taxa of the *Ipomopsis* and *Aquilegia* groups. Then we assess the suitability of these ornithophilous flowers for hummingbird foraging by comparing them to the closely related hawkmoth flowers. In each genus, the sphingophilous flowers have much longer and more slender floral tubes than the related ornithophilous flowers. Finally, we discuss the implications

of our results for coevolutionary relationships between hummingbirds and their flowers.

MATERIALS AND METHODS

Hummingbirds. Thirty-two rufous hummingbirds, both females and males, were captured at one location near Port Mellon, British Columbia. Birds were housed in individual cages and were fed commercial hummingbird food and live *Drosophila melanogaster* flies. For each bird, the length and width of the exposed culmen was measured with calipers accurate to the nearest 0.02 mm. Subsamples of birds were used in the feeding tests to determine handling time (the time it takes a bird to insert its bill, extract nectar, and withdraw its bill during a single visit to a real or artificial flower) and maximum extraction depth (how deeply a bird can successfully feed from a flower). Feeders were Plexiglas tubes selected in various lengths and widths to simulate corollas of different sizes. They were filled with 20% sucrose solution by weight and were mounted horizontally to resemble a flower on a stalk.

Handling times of 10 birds were measured at corolla tubes having inside diameters of 5 mm and seven different lengths from 5 to 35 mm. Birds were given time to familiarize themselves with these feeders, and then their handling times were clocked by a computer (D.E.C. 11/73) connected to photodarlington photocells on the tube holders. Simultaneously, the birds' visits were observed by means of a television monitor connected to a video camera. More complete details about these methods are given elsewhere (1).

Maximum extraction depths of 12 birds were measured for corolla tubes of four different inside diameters ranging from 1.6 to 6.5 mm and of 90-mm length. Tubes were filled to their opening with sucrose solution, and then birds were allowed to forage ad lib from the tubes. Maximum extraction depth was determined for each bird at each of the four corolla diameters by measuring the distance from the corolla orifice to the meniscus of nectar in the tube at regular intervals until this distance did not increase over three consecutive measurements.

Plants. The *I. aggregata* group (Polemoniaceae) and the *A. formosa*–*A. caerulea* group (Ranunculaceae), though only distantly related, share a number of features. The plants in both groups are diploid perennial herbs with a widespread distribution in western North America. They have showy flowers and an outcrossing breeding system. Each group contains some ornithophilous taxa, which are pollinated primarily by hummingbirds, and some closely related sphingophilous taxa, which are pollinated primarily by hawkmoths.

The ornithophilous and sphingophilous taxa in each species group occur sympatrically in some areas without hybridizing, but hybridize in other areas. Internal sterility barriers

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between the ornithophilous and sphingophilous taxa are known to be weak in both *Ipomopsis* (2) and *Aquilegia* (3–6). Reproductive isolation between nonhybridizing sympatric or parapatric species in nature is therefore determined mainly by external barriers. Ecological isolation is very important in *Ipomopsis* (3, 7, 8) and *Aquilegia* (9–12) and is reinforced by mechanical, ethological, and temporal isolation (refs. 9, 10, 12; V.G., unpublished data).

We are concerned in this paper with the ornithophilous and sphingophilous forms of the *I. aggregata* and *A. formosa–A. caerulea* groups that have not been affected morphologically by hybridization and introgression. The hybrid and introgressive types present a different situation for hummingbird foraging, which will be described elsewhere (V.G., unpublished data).

The significant dimensions for hummingbird foraging are the length of the floral tube, the diameter of the tube orifice, and the diameter of the tube at or near the base. In *Ipomopsis* the floral tube is a corolla tube. Its length is measured from orifice to base. In *Aquilegia* the floral tube is a petal spur. Spur length is usually measured from the lowest edge of the orifice to the spur tip. This measurement includes the approximately 2-mm-long nectary at the tip and is therefore longer than the nectar-containing tube.

We present the normal range of floral tube length for nonintrogressive forms of a subspecies or species in Table 1. Such length measurements for whole taxa are made on pressed specimens, and these are the measurements published in the literature. A test with *Aquilegia canadensis* indicates that floral tubes shrink about 1 mm in length when pressed and dried and that the amount of shrinkage is not correlated with the length of the floral tube ($r^2 = 0$; $F = 0$; $P > 0.90$). To give the ranges for fresh floral tubes in Table 1 we therefore added 1 mm to the published values. As noted above, in *Aquilegia* the nectar-containing spur is about 2 mm shorter than the total spur, and so we give the adjusted (fresh) lengths of both the total spur and the nectar tube proper in Table 1.

As a check on the ranges for whole taxa in Table 1, we examined individual variation in local populations of four taxa, *I. a. formosissima*, *I. a. aggregata*, *I. tenuituba*, and *A. canadensis*. The data are not presented here due to lack of space. Suffice it to say that for each of the four taxa sampled the ranges in floral tube length in the local populations fell within the ranges of their respective subspecies or species.

RESULTS

Length of Mouthparts and Floral Tubes. The length of the total culmen (exposed culmen plus feathered base) in a sample of *S. rufus* from southern California is 18.90 ± 0.72 mm in females and 17.27 ± 0.69 mm in males (14). Measurements of the exposed culmen of two other regional samples of *S. rufus* in Arizona and British Columbia are very similar when adjusted to include the feathered base of the bill, which is about 2 mm long (1, 15). Because hummingbirds use their total culmen to probe into long floral tubes, and because the adjusted length measurements in the three samples are congruent, we will use the figures for the California sample as standard bill lengths.

Hummingbirds extend their tongues varying distances when feeding. To obtain a preliminary standard estimate of mouthpart length for easy nectar extraction, we first assumed a tongue extension of 5 mm and added that to the total culmen length. The average length of the mouthparts of rufous hummingbirds is then 23.9 mm in females and 22.3 mm in males.

The normal range of floral tube lengths in several taxa of *Ipomopsis* and *Aquilegia* is shown in Table 1. The nectar level in these tubes rises when production exceeds consumption and falls during periods of heavy feeding. Rufous hummingbirds with mouthparts 23.9 mm long (♀ ♀) or 22.3 mm long (♂ ♂) will clearly be able to reach the nectar at the base of the floral tubes in the ornithophilous taxa. However, mouthparts of the same size fall short of the basal nectar in the shortest floral tubes of the sphingophilous taxa of *Ipomopsis* and *Aquilegia* and far short of the midrange and longest floral tubes (Table 1).

Although the longest floral tubes of some ornithophilous taxa of *Ipomopsis* (*I. a. bridgesii* and *I. a. collina*) are as long as or longer than the shortest tubes of sphingophilous *Ipomopsis*, the midranges of the two classes of taxa differ significantly ($P = 0.0036$, $t = 11.72$, one-tailed t test).

Nectar Extraction with Long Tongue Extensions. The previous conclusions regarding hummingbird bills and flower tube lengths are based on the assumption that hummingbirds extend their tongues about 5 mm for easy nectar extraction, whereas they actually can extend their tongues to varying distances beyond the bill tip (1, 16–18). For the 12 rufous hummingbirds studied here, maximum tongue extension beyond the bill tip ranges from 11.88 to 15.10 mm (Table 2). The extended part of the tongue ranges from 5.5 mm shorter than

Table 1. Length of floral tube in some ornithophilous and sphingophilous taxa of *Ipomopsis* and *Aquilegia*

Ornithophilous taxa			Sphingophilous taxa		
Taxon	Tube length, mm	Ref.	Taxon	Tube length, mm	Ref.
I. aggregata formosissima	16–24	7	*I. aggregata candida*	29–41	7
I. a. aggregata, widespread mid-elevation race	17–26	2	*I. tenuituba*	30–46	7
I. a. bridgesii	21–31	7	*I. macrosiphon*	31–41	V.G., unpublished data
I. a. collina	21–31	8			
I. arizonica	12–16	7			
A. formosa truncata		13	*A. pubescens*		9, 13
Total spur	11–21		Total spur	30–41	
Tube only	9–19		Tube only	28–39	
A. triternata		13	*A. chrysantha*		13
Total spur	19–23		Total spur	41–71	
Tube only	17–21		Tube only	39–69	
A. canadensis, central and eastern North America		13	*A. longissima*		13
Total spur	21–26		Total spur	91–151	
Tube only	19–24		Tube only	89–149	

The figures given are the normal ranges for nonintrogressive forms in each taxon. Published figures have been adjusted to provide estimates of length of nectar-containing tube in live flowers. See *Materials and Methods* for further explanation.

Table 2.   Maximum nectar extraction depths in artificial corolla tubes and maximum tongue extension beyond bill tip of *S. rufus*

Sex	Bill length of individual bird, mm	Maximum extraction depth, mm, in tubes of different width				Estimated maximum tongue extension beyond bill tip, mm
		6.5 mm	5.0 mm	3.0 mm	1.6 mm	
♀	16.05	41.93	40.25	36.57	28.26	12.21
	16.30	42.21	40.62	37.10	28.18	11.88
	16.75	42.57	40.92	38.29	29.57	12.82
	17.00	43.00	42.30	38.51	31.49	14.49
	17.38	43.44	42.56	38.72	29.28	11.90
	17.60	44.11	43.42	39.12	30.79	13.19
♂	14.64	38.41	37.14	34.45	29.03	14.39
	14.95	38.50	37.31	34.71	30.05	15.10
	15.26	38.81	37.83	35.40	28.33	13.04
	15.40	39.28	37.90	36.02	29.99	14.59
	15.90	40.05	38.35	36.43	29.30	13.40
	16.00	41.42	38.89	36.62	28.78	12.78

Bill length is the length of the exposed culmen. Widths given for corolla tubes are inside diameters. The estimates of tongue extension beyond bill tip are derived from the maximum extraction depth in the 1.6-mm-diameter tube minus bill length.

the bill in one female to about the same length as the bill in one male. Some of the variation in maximum extraction depths may be explained by corolla tube width, because greater widths allow more of a bird's head to enter the tube, thereby increasing extraction depth (Table 2). Together with previous measurements of maximum extraction depths (1), the data in Table 2 indicate that maximum tongue extension of rufous hummingbirds beyond the bill tip is approximately equal to bill length.

It can be argued that a rufous hummingbird with a long tongue extension could reach the basal nectar in long-tubed hawkmoth flowers. However, this conclusion is subject to three qualifications. First, some hawkmoth flowers—e.g., *Aquilegia longissima* (Table 1)—are too long for the bill and extended tongue combined. A second factor to be discussed in the next section is floral tube width.

Here we consider a third factor, the relationship between tongue extension and rate of nectar uptake. Studies of this relationship in rufous and other hummingbirds at artificial feeders and artificial corollas show that as tongue extension increases, the time required to obtain nectar also increases (1, 16–18).

In *S. rufus*, handling time—the time spent on a single feeding visit—goes up gradually as the artificial corolla length increases from 5 to 25 mm, and it rises sharply for corollas 30 and 35 mm long (1). Montgomerie (18) obtained similar results with *Archilochus colubris* and *Amazilia rutila*. In *Calypte anna* the duration of each tongue lick increases as tongue extension beyond the bill tip increases; the tongue extensions and lick durations are as follows (17):

1- to 2-mm tongue, 0.04–0.07 sec per lick
3-mm tongue, 0.07 sec per lick
4-mm tongue, 0.08–0.09 sec per lick
8- to 9-mm tongue, 0.10–0.11 sec per lick.

The general finding from these studies is that as corolla length exceeds bill length, handling time increases exponentially with increasing corolla length (Fig. 1A). Specifically, at corollas in excess of bill length, the bird must extend its tongue to reach the nectar supply, and tongue transit times increase with an increase in the length of tongue extension (17). Thus, the ability of rufous and other hummingbirds to extract a given amount of nectar per second progressively decreases with an increase in floral tube length (1, 18).
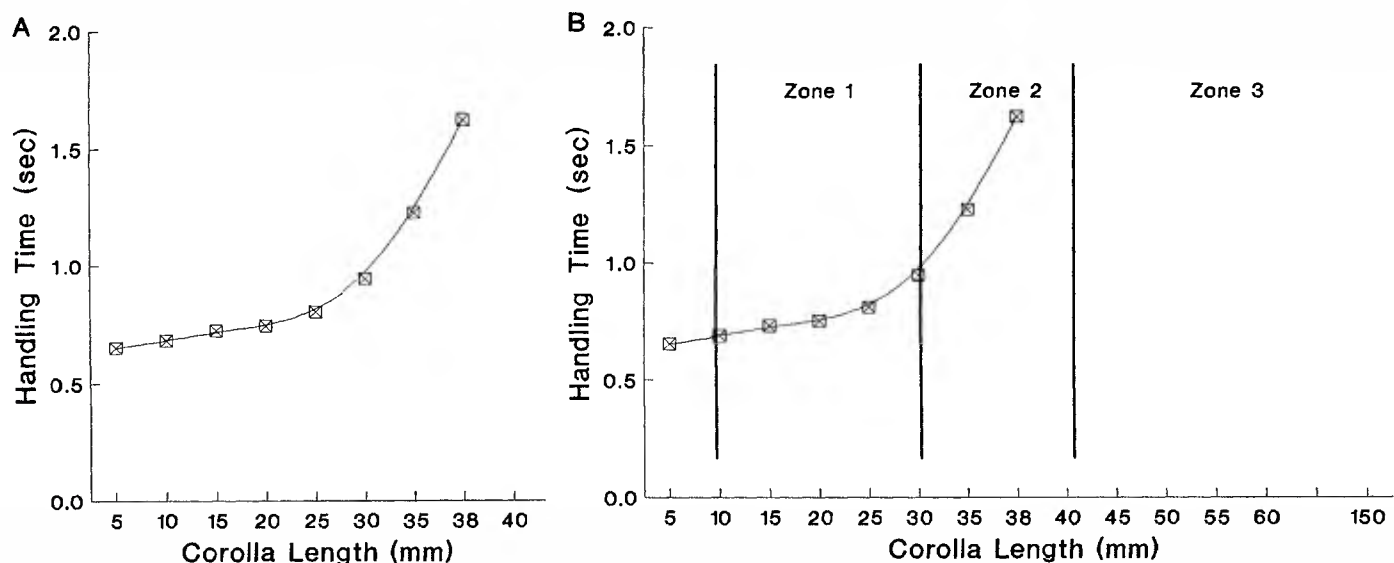

FIG. 1.   Relationship between handling time (means of five female *S. rufus*) and nectar tube length. (*A*) Handling times in Plexiglas tubes, slightly modified from ref. 1. (*B*) The same curve drawn in relation to lengths of floral tubes in ornithophilous and sphingophilous flowers of *Ipomopsis* and *Aquilegia*. Zone 1 is the range in most ornithophilous taxa; zone 2 is the range in sphingophilous flowers with accessible basal nectar; and zone 3 is the range in sphingophilous flowers with inaccessible basal nectar. Further explanation is in *Discussion*.

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The rate at which rufous and other hummingbirds can extract nectar is a measure of their foraging efficiency, and this decreases at longer floral tube lengths as just noted. Floral tubes of hawkmoth flowers in *Ipomopsis* and *Aquilegia* that are within the reach of *S. rufus* mouthparts have lengths in a range where handling times are expected to be quite high, and foraging efficiency reduced, as compared with related hummingbird flowers (Table 1, Fig. 1).

Role of Floral Tube Width. The corolla tube is broader in ornithophilous taxa of the *I. aggregata* group than in related sphingophilous taxa. The diameter of the orifice is 3–5 mm (or more) in *I. a. formosissima* and 3–4 mm in *I. a. aggregata*, and the tube at the base is 1.5 mm or more wide. In the sphingophilous taxa of this species group the orifice diameter is 2–3 mm (*I. tenuituba*) or 2–4 mm (*I. a. candida*), and the tube becomes narrower toward the base. In *Aquilegia* the petal spurs are ≈5 mm wide at the orifice in both the ornithophilous and sphingophilous taxa. But the spurs remain relatively broad at the base (≈2 mm wide) in the ornithophilous *A. formosa truncata*, whereas in the sphingophilous aquilegias they taper down to very slender tubes in the distal region and are ≈1 mm wide at the tube base.

The bills of 12 rufous hummingbirds used in experimental feeding tests ranged in width from 1.70 to 1.95 mm in females and 1.45 to 1.60 mm in males. These figures refer to closed bills. Birds when feeding must open the bill tip slightly to retract a nectar-laden tongue without wringing out the nectar (17). The effective width of the bill for feeding is thus greater by a slight but unknown factor than that of the closed bill. Now bills as wide as or slightly wider than 1.45–1.95 mm can probe with ease in the broad floral tubes of ornithophilous taxa of *Ipomopsis* and *Aquilegia*. But they would make a tight fit in the sphingophilous floral tubes of *Ipomopsis* and are too wide for the very slender distal region of the spurs of sphingophilous aquilegias.

Table 2 shows the maximum extraction depth of rufous hummingbirds in artificial corolla tubes of different inside diameters. The extraction depth decreases as the tube becomes narrower, and drops off sharply from a 3.0-mm-wide tube to a 1.6-mm-wide tube. The 3.0-mm artificial tube is comparable to many ornithophilous floral tubes, and the 1.6-mm tube, to many sphingophilous floral tubes. The probing depth of rufous hummingbirds is diminished in very slender tubes.

The maximum extraction depths of rufous hummingbirds in 1.6-mm tubes is 31.5 mm for females and 30.05 mm for males (Table 2). This foraging depth is adequate for the longest ornithophilous floral tubes—e.g., *I. a. bridgesii* and *I. a. collina*, with tubes up to 31 mm long (Table 1). It is adequate for the shortest floral tubes of some sphingophilous taxa (Table 1). But it is inadequate for reaching nectar from sphingophilous floral tubes in the middle or upper part of their range in length (Table 1).

The relationship between tube width and extraction depth is apparently affected by several factors. The bird can insert the feathered base of the bill and front of the head in wide tubes. In addition, because some nectar is carried on the surface of the tongue, very narrow tubes probably hamper nectar uptake (17), as noted earlier.

DISCUSSION

Mouthpart length and floral tube length do not appear to have any particular narrow optimum for efficient nectar foraging by rufous hummingbirds. The evidence points to a moderately broad optimum with upper limits (Fig. 1*B*). At the upper end the optimum zone grades into a second zone where nectar is accessible but is taken up with reduced efficiency. In this second zone the rate of nectar uptake decreases as floral tube length and nectar depth become greater. The

upper end of the second zone is followed by a third zone, where the nectar is beyond the reach of both bill and tongue in legitimate probes.

We assumed earlier a tongue extension of 5 mm, which produces mouthparts with average lengths of 23.9 mm in females and 22.3 mm in males. These lengths lie in the optimum zone for nectar foraging but approach the second zone. Most of the ornithophilous flowers of *Ipomopsis* and *Aquilegia*, with floral tubes ranging up to 26 mm long (Table 1), also lie within the optimum range for foraging by both sexes of *S. rufus*, or, at the upper extreme, by female birds.

In some ornithophilous taxa of *Ipomopsis*—e.g., *I. a. bridgesii* and *I. a. collina* (Table 1)—the floral tubes range up to 31 mm long. The basal nectar is deeper than would be expected for optimal foraging in these long-tubed individuals. This apparent anomaly is not well understood at present and warrants further investigation.

Rufous hummingbird bills, even with a long tongue extension, are not well suited for extracting nectar from the long slender floral tubes of sphingophilous taxa in *Ipomopsis* and *Aquilegia*. The sphingophilous floral tubes are often too long to be probed by bill and tongue combined; the narrow diameter of the tubes reduces the effective probing depth; and even if the long extended tongue can reach the nectar its nectar-gathering ability is diminished. The shorter sphingophilous flowers lie in the accessible but inefficient zone and the longer flowers in the inaccessible zone.

Field observations are in agreement with the foregoing conclusions. Hummingbirds make exploratory visits to different species of flowers in a locality and quickly learn which ones are satisfactory nectar sources and which are not.

S. rufus is a frequent and regular visitor to the flowers of *I. a. formosissima* (15, 19, 20), *I. a. aggregata* (19–21), *I. a. collina* (22), and *A. formosa truncata* (11, 20). Other widespread western species such as *Selasphorus platycercus* and *Stellula calliope* are also common foragers on these taxa (15, 19–24).

On the other hand, widespread western species of hummingbirds are not frequent visitors to the flowers of nonintrogressive forms of the sphingophilous taxa listed in Table 1. Observations of *A. chrysantha* in three mountain ranges in Arizona will illustrate the point. In the Santa Catalina Mountains, *A. chrysantha* flowers were visited by the hawkmoth *Hyles lineata* but not approached by any hummingbirds during 2 days of observation in September 1951 (ref. 9; V.G., unpublished data). In the Huachuca Mountains, *Archilochus alexandri* was in the vicinity of *A. chrysantha* but ignored its flowers (ref. 25; E.J.T., unpublished data). At several sites in the Chiricahua Mountains, Miller (12) observed four species of hawkmoths, as well as bees, butterflies, and skippers, on *A. chrysantha*, but no visits by any widespread western species of hummingbird. The Mexican and extreme southwestern hummingbird species *Lampornis clemenciae* and *Heliodoxa fulgens*, with longer bills than those of the widespread western species, do visit flowers of *A. chrysantha* infrequently (12) or regularly (25). *A. chrysantha* spurs seems to be marginal sources of nectar for the two long-billed southwestern species but beyond the probing depth of *Archilochus alexandri*.

How general are the results obtained with *S. rufus*, *Ipomopsis*, and *Aquilegia*? The bills of other widespread western hummingbird species are similar in shape and length to the bill of *S. rufus* (14, 15, 26). The mean length of the exposed culmen in seven widespread western species ranges from 15.6 to 20.6 mm in females and from 14.3 to 19.2 mm in males, according to data of Johnsgard (26). The seven species are *Calypte anna*, *Calypte costae*, *Archilochus alexandri*, *Stellula calliope*, *Selasphorus sasin sasin*, *S. platycercus*, and *S. rufus*. *S. rufus* is in the middle part of these ranges (average

length of exposed culmen 18.0 mm in females and 16.5 mm in males) (26).

The reduction in rate of nectar uptake with increase in tongue extension has been found not only in *S. rufus* but also in five other North or Central American species (*Archilochus colubris, Archilochus alexandri, Calypte anna, Cynanthus latirostris*, and *Amazilia rutila*) (16–18).

The ornithophilous flowers in *Ipomopis* and *Aquilegia* are representative of a large contingent of hummingbird-pollinated flowers in the western American flora (15, 23, 27). The sphingophilous flowers of *Ipomopsis* and *Aquilegia* are also representative of a large array of hawkmoth flowers in the temperate North American flora (28, 29). The conclusions regarding hummingbird foraging ability on sphingophilous taxa of *Ipomopsis* and *Aquilegia* can reasonably be extended to many other plant groups.

Rufous and other western hummingbirds can take up nectar readily from short artificial corollas or feeders (1, 17). This raises the question, why aren't western ornithophilous floral tubes short? In fact, relatively short-tubed flowers do occur in some ornithophilous species—e.g., *A. formosa* (Table 1). But such cases are uncommon and medium-long tubes are the norm.

This question brings another factor into the picture. The nectar in short-tubed flowers is accessible to bees, wasps, flies, beetles, skippers, butterflies, house finches, etc. as well as to hummingbirds. Medium-long tubes in ornithophilous flowers exclude short-tongued insects and short-billed birds to a large extent, and reserve the nectar supply mainly for their hummingbird visitors and pollinators, to the mutual benefit of both partners (23).

This study deals with the relative costs of hummingbird foraging on two classes of flowers as expressed in handling time and maximum extraction depth. The relative benefits— the quantity and quality of the nectar in the two types of flowers—can and should be quantified in future studies. The relevant question is whether the sphingophilous flowers offer any benefits that can outweigh their greater costs for hummingbirds. First, there is no benefit at all where the nectar is inaccessible (Fig. 1*B*). Second, although the nectar of entomophilous flowers generally has a higher sugar concentration than that of hummingbird flowers (30, 31), the nectar of hummingbird flowers is produced in greater quantity (23, 30, 32, 33), and the differences are offsetting. Finally, the handling time increases exponentially at very long floral tube lengths (1). Handling times at floral tube lengths typical of hawkmoth flowers may be two to three times greater than those at lengths typical of hummingbird flowers (Fig. 1*B*).

Our hypotheses concerning mechanisms for hummingbird–flower coevolution have been drawn from both existing experimental evidence and field observations, and they can be tested in new experiments by offering hummingbirds artificial corollas that simulate either ornithophilous or sphin-gophilous flowers with respect to corolla length and width and nectar depth, concentration, and volume. Foraging efficiency and behavior can then be determined for birds at these alternative flower types to better understand hummingbird–flower relationships.

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