

A Meager Nectar Offering by an Epiphytic Orchid is Better than Nothing¹

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ABSTRACT

When a nectar reward is relatively low in quality and quantity, is it an effective pollinator attractant? In Puerto Rico, *Comparettia falcata*, a hummingbird-pollinated epiphytic orchid, produces an average one-time secretion of 3.3–4.0 μ l of nectar (composed of 12.9–15.1% sugar) per flower. In contrast, nectar sugar concentrations of other hummingbird flowers on Caribbean islands are 17–37 percent, and those of Puerto Rico visited by the *C. falcata* pollinator have standing crops averaging 2.0–6.2 μ l and daily secretion rates of 3.1–10.6 μ l. In 1989 and 1990, we monitored pollinator abundance, effective flower visitation, pollinarium removals (male success), pollinations, and fruit production (female success) at two sites in the Toro Negro Forest Reserve. Reproductive success at the two sites did not differ in either year when adjusted for differences in pollinator activity. In 1991, we clipped the spur tips of all flowers at one site rendering them nectarless. Visitation frequencies and measures of male and female fitness were adjusted for site differences in pollinator activity, and all were significantly lower at the site where flowers were nectarless. In 1992, we abandoned one site and manipulated the other by clipping the floral spurs of a randomly chosen subset of plants so that 25 percent of the flowers in the population were nectarless. Pollinarium removals from intact flowers were significantly different from those with cut spurs and total visits were nearly significant as well. However, the difference in female success was clearly not significant between the two treatments. The number of visits per flower dropped dramatically from previous years despite the highest level of bird activity yet censused. The data are consistent with the hypothesis that the pollinator, *Chlorostilbon manguensis*, perceives the nectar reward despite its small quantity and low sugar content, this to the advantage of *Comparettia falcata*.

RESUMEN

Cuando la recompensa floral en forma de néctar es relativamente baja en calidad y pobre en cantidad, ¿es ésta un atrayente efectivo de polinizadores? En Puerto Rico, *Comparettia falcata*, una orquídea epifítica polinizada por colibríes, produce un promedio de 3.3–4.0 μ l de néctar por flor. Éste néctar no se produce continuamente y tiene una concentración de azúcares de 12.9–15.1 por ciento. En contraste, la concentración de azúcares de los néctares de otras flores polinizadas por colibríes en islas del Caribe varía entre 17 por ciento y 37 por ciento. En Puerto Rico, las flores visitadas por el polinizador de *C. falcata* tienen una disponibilidad de néctar en un momento dado de 2.0–6.2 μ l y una tasa de producción diaria de 3.1–10.6 μ l. En 1989 y 1990, determinamos abundancia de polinizadores, visitación efectiva a flores, frecuencia de remoción de polinarios (éxito reproductivo masculino), polinizaciones y producción de frutos (éxito reproductivo femenino) en dos localidades en la Reserva Forestal de Toro Negro. El éxito reproductivo en las dos localidades no difirió en ninguno de los dos años cuando fue ajustado por diferencias en actividad de los polinizadores. En 1991, cortamos la punta de los espolones de todas las flores en una localidad para que éstas carecieran de néctar. La frecuencia de visitación y estimados de éxito reproductivo masculino y femenino fueron ajustados en cada localidad por diferencias en actividad de los polinizadores y todos fueron significativamente menores en la localidad donde las flores no tenían néctar. En 1992, abandonamos una localidad y cortamos los espolones florales de un grupo de plantas seleccionado al azar en la otra localidad, de manera que el 25 por ciento de las flores de la población careciera de néctar. Las remociones de polinarios a flores intactas y a flores con los espolones cortados fueron significativamente diferentes, mientras que el total de visitas casi lo fue. Sin embargo, las diferencias en el éxito reproductivo femenino entre los dos tratamientos no fueron significativas. El número de visitas por flor para esta localidad se redujo dramáticamente en comparación con años anteriores, a pesar de tener el mayor nivel estimado de actividad de polinizadores. Estos datos son consistentes con la hipótesis de que el polinizador, *Chlorostilbon manguensis*, percibe la recompensa floral de néctar a pesar de su pequeña cantidad y bajo contenido de azúcares, lo cual favorece a *Comparettia falcata*.

Key words: deception; epiphyte; fruit set; hummingbird pollination; nectar reward; orchid; Puerto Rico; reproductive success; tropical forest.

¹ Received 9 December 1992, revision accepted 6 August 1993.

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MOST FLOWERING PLANTS EMPLOY a reward-based pollination system. Pollinators are attracted to flowers by visual or olfactory cues and visitation behavior is reinforced by the presence of collectable and consumable or usable substances such as nectar, pollen, oils, fragrances, waxes, or resins (Simpson & Neff 1983). Some flowering plants present no pollinator reward and visits are based on some form of deception (Little 1983). Such systems are relatively rare except for the Orchidaceae where approximately one-third of the 20,000 species are deceitful (Ackerman 1985).

Several hypotheses have been proposed to account for the evolution of deception pollination, presumably from reward-offering ancestors (Nilsson 1992). Two hypotheses claim an advantage to deception pollination. First, selection for cross-pollination may have favored characteristics that increase pollinator movement among plants (Dressler 1981). A pollinator that visits a flower lacking a reward is less likely to visit an adjacent flower than to move away and visit another plant (Waddington 1980, 1981). Although there is some indication that this may occur in deception-pollinated orchids (Ackerman 1989), it has not been rigorously tested. The second hypothesis suggests that lifetime reproduction of a plant may be resource-limited. Rewards may attract visitors and maintain high levels of pollination, but the cost of reward production or maturing many fruits and seeds may outweigh the benefits. Nectar production can be expensive (Southwick 1984, Pyke 1991), and a cost of sexual reproduction has been demonstrated for several orchids (e.g., Montalvo & Ackerman 1987, Snow & Whigham 1989, Zimmerman & Aide 1989, Ackerman 1989, Ackerman & Montalvo 1990), but Calvo and Horvitz (1990) and Calvo (1993) have demonstrated that lifetime reproductive success remains largely pollination limited.

Two other hypotheses do not require a fitness advantage for the evolution of deception pollination. The fitness bottleneck in orchids may not be pollination or resource constraints. Seed dispersal, germination, and seedling establishment may be the limiting stages in the life history of these plants (Calvo 1990, 1993, Ackerman & Zimmerman, in press). Alternatively, rewards may be rendered ineffective and superfluous if either pollinators or plants are relatively rare and reproductive success is dependent on occasional exploratory visits of naive pollinators (Ackerman 1983, 1986a). Loss of a reward could then be a consequence of genetic drift. Certainly, many orchid species are rare or at least

occur in small, hyperdispersed populations (Ackerman 1986b).

We examine aspects of the latter hypothesis by investigating the relationship between a naturally meager reward, pollinator visits, and plant reproduction for *Compartmentia falcata* Poeppig and Endlicher, a relatively rare, epiphytic orchid pollinated by hummingbirds. The spurs of *C. falcata* contain an average one-time secretion of 3.3–4.0 μ l composed of 12.9–15.1 percent sugar solution (Rodríguez-Robles *et al.* 1992). By contrast, hummingbird pollinated flowers of Caribbean islands average 16.8–36.5 percent sugar solution (Pyke & Waser 1981, Kodric-Brown *et al.* 1984), and those of Puerto Rico, visited by the *C. falcata* pollinator, have standing crops averaging 2.0–6.2 μ l and daily secretion rates of 3.1–10.6 μ l (Kodric-Brown *et al.* 1984). We test the hypothesis that the pollination system of *C. falcata* is functionally deceptive and that the meager reward confers no advantage to the orchid. If this is true, then the system is likely transitional and we may expect that the reward would be lost over evolutionary time.

METHODS

Compartmentia falcata is a twig epiphyte that occurs in moist and wet tropical forests of the Greater Antilles and Mexico to South America. Plants usually produce a single raceme of 1–13 flowers from the base of each new shoot. The red to rose-pink flowers have a slightly curved spur that contains a quantity of visible nectar. The single anther houses one pollinarium composed of two hard, yellow pollinia attached to single stipe and viscidium. Unpollinated flowers remain in anthesis for approximately 14 d. The sole hummingbird and pollinator at our sites is the Puerto Rican Emerald, *Chlorostilbon maugaeus* (Rodríguez-Robles *et al.* 1992), an opportunistic hummingbird that occasionally establishes territories when the resources warrant it (J. Wunderle, pers. comm. 1993).

Our study sites were located on slopes above and below Lago el Guineo in the Toro Negro Forest Reserve of the Cordillera Central, Puerto Rico (18°09'30"N, 66°32'00"W; elevation ca. 1000 m). Most of the reserve lies within the Subtropical Montane Wet Forest life zone (Ewel & Whitmore 1973). *Syzygium jambos* and *Myrica deflexa* are the dominant tree and shrub species, respectively, and the most common phorophytes of *C. falcata* (Rodríguez-Robles *et al.* 1990). Most plants were located on the slopes above the south side of the lake (site A), and the others were both above and below the

TABLE 1. *Four years of flower production, visitation frequencies, and pollinator activity in *Comparettia falcata* at two sites in the Toro Negro Forest Reserve, Puerto Rico.*

Year	Site	Treatment	No. of flowers	Birds/hr	Visitations ^a			Visits/flower	Visits/flower/birds/hr
					Rem	Plln	Both		
1989	A	none	51	3.3	16	12	5	0.65	0.20
	B	none	105	1.3	11	14	10	0.33	0.25
1990	A	none	62	2.2	10	6	8	0.38	0.17
	B	none	73	2.6	18	14	19	0.70	0.27
1991	A	spurs cut	261	2.7	45	23	51	0.46	0.15
	B	none	74	1.0	15	9	13	0.50	0.50
1992	A	none	194	4.1	20	8	22	0.26	0.06
	A	spurs cut	66	4.1	3	2	5	0.15	0.04

^a Effective visitations: Rem = number of flowers with pollinarium removed; Plln = number of flowers pollinated (only); Both = flowers with pollinarium removed and pollinated.

dam on the north side (site B). The two forested sites are separated by at least 300 m, much of it over water and across the cleared slopes of the earthen dam. Plants were scattered throughout the forest understory usually attached to twigs and small branches of host trees and shrubs.

In 1989 and 1990, we monitored pollinator abundance, effective flower visitation, and fruit production at both sites. A random sample of mature plants was tagged at each site. Once a week throughout the flowering season, February through April, we recorded the status of all flowers produced by each of our marked plants. We noted all indications of successful pollinator visitations (pollinarium removals and pollinations), and whether or not fruits were forming. Because of floral morphology, visitors that extract nectar are likely to remove the pollinarium and/or deposit pollinia. During the censuses, we also recorded the number of hummingbirds we had either heard or seen per hour. Final fruit production was determined in the fall, just as fruits were splitting open and dispersing seeds. Further details of these studies are in Rodríguez-Robles *et al.* (1992).

In 1991, we attempted to find and tag all flowering individuals at each site. We repeated observations of previous years but also manipulated flowers at site A by clipping the spur tip of every developing bud we encountered, effectively rendering them nectarless. We compared reproductive success of the nectarless population with that of the unmanipulated site B population. Our measures of reproductive success were pollinarium removals, an estimate of male success, and fruit production. In 1992, we continued our weekly bird and flower censuses. However, we were forced to abandon site B because flowering was asynchronous (unlike all previous years) and many plants were destroyed by

a trail-clearing crew. Consequently, we clipped the spurs of 66 developing buds on 23 randomly selected plants within site A. The remaining 62 plants and their 194 flowers were left intact. We compared the reproductive success of the nectarless and nectar producing plants within this population.

Data among years and sites did not constitute replicates so we did not pool the data for this reason. Instead we looked for consistent patterns among the reproductive data given variation in treatments and pollinator abundances.

RESULTS

PRE-MANIPULATION YEARS.—In 1989, we monitored 30 plants (51 flowers) at site A, and 18 plants (105 flowers) at site B. The number of visits per flower (pollinarium removals + flowers pollinated + flowers with pollinarium removed and pollinated) at site A was double that of site B, but hummingbirds were more commonly encountered at the former site (Table 1). When adjusted for pollinator abundance (frequencies divided by bird/hr), we found no difference in the frequency of pollinarium removals between the two sites (G -tests of independence, all with Williams correction, $G = 0.21$, 1 df, $P = 0.65$), frequency of pollinations ($G = 1.55$, 1 df, $P = 0.21$), nor for fruit production ($G = 1.06$, 1 df, $P = 0.3$). Similarly, we also found no difference in total visitation frequencies when adjusted for hummingbird counts ($G = 0.71$, 1 df, $P = 0.4$).

In 1990, we monitored 18 plants (62 flowers) at site A and 11 plants (73 flowers) at site B. Again, visitation frequencies and fruit production differed between sites, but this time site B had the greater number of pollinarium removals, fruit production, and also hummingbird activity (Table 1). When we adjusted visitation frequencies and fruit produc-

TABLE 2. *Final fruit production of Comparettia falcata over four years at two sites in the Toro Negro Forest Reserve, Puerto Rico.*

Year	Site	Treatment	No. of flowers	No. of pollinations	% Abortions	No. of fruits	% Fruit set	Fr set/birds/hr
1989	A	none	51	17	24	13	25.5	7.7
	B	none	105	24	25	18	17.1	13.1
1990	A	none	62	14	14	12	19.3	8.8
	B	none	73	33	33	22	30.1	11.6
1991	A	spurs cut	261	74	53	35	13.4	5.0
	B	none	74	22	59	9	12.1	12.1
1992	A	none	194	30	23	23	11.8	3.1
	A	spurs cut	66	7	0	7	10.6	2.6

tion by our estimate of pollinator abundances, we again found that no differences occurred between the two sites (total visits: $G = 1.76$, 1 df, $P = 0.18$; pollinarium removals: $G = 0.93$, 1 df, $P = 0.33$; pollinations: $G = 1.40$, 1 df, $P = 0.24$; fruit production: $G = 0.30$, 1 df, $P = 0.58$). These data suggest that differences between the two sites in the reproductive success of unmanipulated *C. falcata* were a consequence of variation in pollinator abundances.

MANIPULATION YEARS.—In 1991, we cut the spurs of all flowers at site A (261 flowers on 95 plants) and left site B plants unmanipulated (17 plants and 74 flowers). Visitation frequencies, pollinarium removals, and fruit production per flower were similar for both sites, but we censused more hummingbirds at site A (Table 1). When these data were adjusted for differences in pollinator abundances, the nectarless plants at site A had significantly fewer total effective visits, pollinarium removals, pollinations, and fruits than the nectar-containing flowers of site B (total visits: $G = 34.6$, 1 df, $P < 0.00001$;

pollinarium removals: $G = 19.32$, 1 df, $P < 0.00001$; pollinations: $G = 7.27$, 1 df, $P = 0.007$; fruit production: $G = 3.96$, 1 df, $P = 0.047$).

In 1992, our observations were limited to site A. Here, pollinator abundance was the highest in 4 yr by about 25 percent, yet the number of visits per flower decreased substantially for both the nectarless and intact flowers, and fruit production was among the lowest on record (Table 2). Effective pollinator visits and pollinarium removals of intact flowers were almost significantly higher than that of nectarless flowers (total visitation: $G = 3.3$, 1 df, $P = 0.07$; pollinarium removals: $G = 3.73$, 1 df, $P = 0.05$), but the frequency of pollinations and the resultant fruit set were clearly not significant (pollinations: $G = 0.98$, 1 df, $P = 0.33$; fruit set: $G = 0.24$, 1 df, $P = 0.62$; Table 2). Because the manipulated plants were randomly scattered among the controls, no adjustment for bird activity was necessary.

If an inflorescence is visited once, will a second visit depend on the presence of a nectar reward? We analyzed the frequency of hummingbird visits (pol-

TABLE 3. *Single and multiple visits to inflorescences with two or more flowers. A visit is defined as a pollinarium removal, pollination, or both. Data combine 1991 and 1992 results. Statistics are G-tests of independence with Williams' correction and two-tailed Fisher's exact test of independence (Sokal & Rohlf 1981).*

Inflorescence size	Treatment	1 visit	2 or more visits	Statistics	
				Test	P
2-flowered	control	9	7	$G = 0.71$ Fisher	$=0.40$ $=0.67$
	cut spurs	3	5		
3-flowered	control	4	9	$G = 0.58$ Fisher	$=0.45$ $=0.62$
	cut spurs	3	3		
2 or more	control	18	27	$G = 0.92$ Fisher	$=0.34$ $=0.36$
	cut spurs	11	26		

linarium removals + pollinations + both) to multiflowered inflorescences and discovered that they were similar for manipulated and unmanipulated flowers (Table 3). The data for the two treatment years were pooled only after we determined that inflorescence sizes were similar among control and treatment groups for 1991, 1992 and the two years combined (Mann-Whitney *U*-tests, single-flowered inflorescences excluded; 1991: $T = 1.44$, $P > 0.05$; 1992: $T = 1.58$, $P > 0.05$; combined years: $T = 1.65$, $P > 0.05$). Return visits were therefore not linked to the presence of a pollinator reward.

DISCUSSION

Considerable annual variation in reproductive effort and success may occur in tropical orchids (Ackerman & Montalvo 1990) and *C. falcata* is no exception. At a given site the number of pollinarium removals or total visits per flower and percent fruit set varied as much as two-fold or more (Tables 1, 2). However, much of this variation may be attributed to variation in pollinator abundance. During those years when sites were unmanipulated, visitation frequencies fluctuated with changes in our estimates of hummingbird activity.

Similarly, substantial variation in these parameters also occurred among the two sites. Visitations per flower, pollinarium removals, percent fruit set, and bird abundances were higher at site A than at site B in 1989, but they were reversed in all three categories for 1990 (Table 1). Thus, plant reproductive success shifted in response to hummingbird activity in a consistent manner among years and sites, despite substantial variation.

These relationships changed when flowers were rendered nectarless. In 1991, nectarless flowers at site A were visited much less frequently and suffered reduced male and female reproductive success, even though hummingbird activity was higher than at site B (Table 1). The loss of nectar reward, however meager, did make a difference.

For the 1989 and 1990 seasons natural variation in nectar availability was not a good predictor of visitation frequencies to individual plants (Rodríguez-Robles *et al.* 1992). In 1992, when the choice was something or nothing within the same site, hummingbirds still did not show clear preference for rewarding plants within a site. Visits per flower

were lower for nectarless plants, but the results were not quite significant, perhaps a consequence of the overall infrequency of pollinator visits (Table 1).

The 1992 season had the highest number of hummingbirds recorded per hour, but the number of effective visits per flower was lower than in previous years. From other studies and our 1989 and 1990 data, we had expected pollination frequencies to increase with greater pollinator abundances (Waser 1979; Ackerman 1981, 1983; but see Zimmerman *et al.* 1989). By rendering approximately 25 percent of the flowers nectarless at this site, we imposed a degree of uncertainty which may have affected hummingbird foraging choices. Consequently, nectar depletion may have resulted in a decrease in visits. For bees, wasps, and birds, variable nectar resources are avoided in favor of predictable rewards (Real 1981, Wunderle & O'Brien 1986, Real & Caraco 1986).

The meager nectar offering by *C. falcata* is perceived by its hummingbird pollinators and is thus an effective reward. When an entire population or a portion of it is rendered nectarless, effective visits decrease and either male fitness or both male and female fitness drops. If a nectarless mutant existed, it would not likely spread under the conditions we observed at our two populations.

The presence or absence of the reward had little effect on the probability that a plant would be effectively visited more than once (Table 3), but what would happen if the reward were richer? Would it result in more frequent visits? Would inbreeding increase via geitonogamous pollinations? Is there a cost associated with self-pollinations? Hypotheses pertaining to these and other questions associated with understanding the evolution of reward and deception pollination systems remain to be tested.

ACKNOWLEDGMENTS

We thank José Meléndez, Raquel Ortega and Carmen Ortiz for field assistance, and the Department of Natural Resources for permission to use the site. Critiques by Jess Zimmerman, Robert Klips, and an anonymous reviewer substantially improved the manuscript. This work was supported by grants from Sigma Xi, The Scientific Research Society to (JAR); from Fondo Institucional para la Investigación, University of Puerto Rico (to JDA and Manuel Vélez); and from the National Science Foundation (RII-8903827) to the University of Puerto Rico.

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