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Resource Competition, Character Displacement, and the Evolution of Deep Corolla Tubes

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abstract: It is normally thought that deep corolla tubes evolve when the plant's successful reproduction is contingent on having a corolla tube longer than the tongue of the flower's pollinators. Combining optimal foraging theory and quantitative genetics in a spatially explicit, individual-based model, we show that flowers with long corolla tubes can alternatively evolve because they promote resource partitioning among nectar feeders and increase the probability of conspecific pollen transfer. When there is competition for resources, long-tongued flower visitors feed preferentially at deep flowers and short-tongued visitors at shallow flowers. Both plant species thus benefit when the depths of their corollas are so different that each flower visitor specializes on one species. Resource competition can promote the evolution of deep corollas despite the presence of significant amounts of noise, such as deviations from optimal foraging behavior due to perceptual errors or temporal fluctuations in the relative abundance of competing pollinator species. Our results can explain the evolution of long corollas in a number of systems that do not conform to the traditional view.

Keywords: Angraecum sesquipedale, nectar concealment, niche partition, optimal foraging, pollination, *Xanthopan morgani.*

The Malagasy star orchid *Angraecum sesquipedale* is the vortex of a fascinating chapter in the history of evolutionary biology. The flowers of *A. sesquipedale* have corolla tubes that can exceed 40 cm (Wasserthal 1997). Darwin (1862) postulated that *A. sesquipedale* was pollinated by giant moths, at the time unknown, a prediction that was met with skepticism. Four decades later, a candidate pollinator, *Xanthopan morgani praedicta*, was discovered (Rothschild and Jordan 1903). It was immediately assumed to be *A. sesquipedale*'s main pollinator, although it took 90 more years to find evidence of its pollinating role (Wasserthal 1997).

Moth-pollinated orchids in Madagascar and the Neotropics (Haber and Frankie 1989) are the most extravagant examples of a common phenomenon. Long corolla tubes and long tongues have evolved repeatedly and in different habitats. Even within the Acherontiini hawk moths, extremely long tongues have evolved several times (Kitching 2002). Beyond hawk moths, flies with mouthparts of up to 80 mm pollinate deep orchids in South Africa (Johnson and Steiner 1995), and the Andean sword-billed hummingbird *Ensifera ensifera*, the only bird in the world with a bill length that surpasses its body length, pollinates *Passiflora mixta* flowers with corolla tubes of up to 15 cm (Lindberg and Olesen 2001). At a much smaller scale, relationships between bumblebee tongue length and depth of the flowers they visit are well known (Inouye 1980; Harder 1985; Graham and Jones 1996).

According to Darwin (1862, p. 202), the reason why long tongues should select for deep flowers was that plants that "compelled the moths to insert their probosces up to the very base, would be best fertilised." Nilsson (1988) showed that experimental shortening of nectar spurs (hereafter referred to as corolla tubes, regardless of whether they are true corollas) in *Platanthera bifolia* and *Platanthera chlorantha* decreased male and female components of reproductive success. Similar results have been obtained with *Disa draconis* (Johnson and Steiner 1997) and *Gladiolus longicollis* (Alexandersson and Johnson 2002), and Wasserthal (1997) has shown that hawk moths remove with their legs pollinia attached to distal sections of their tongues.

Although these findings seem to support Darwin's hypothesis that flowers are under strong selection to maintain corolla tubes longer than the tongues of their visitors, there

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are reasons to doubt the universality of this scenario. Other than the existence of alternative ways of ensuring pollination, like exsertion of anthers and stigmas that often co-occurs with deep corolla tubes (Thomson et al. 2000), the main objection is that flowers with longer corolla tubes are not always better at exporting or receiving pollen than flowers with short corolla tubes (Herrera 1993; Lindberg and Olesen 2001; Lasso and Naranjo 2003).

An alternative explanation is that long corollas evolved to exclude potential visitors (Heinrich 1979; Laverty 1980; Castellanos et al. 2004). We recently presented game-theoretical models suggesting that long corollas can evolve as a means of nectar concealment (Rodríguez-Gironés and Santamaría 2005). In general, differences in the relative ability of flower visitors to exploit coexisting resources can lead to resource partitioning (Possingham 1992; Rodríguez-Gironés 2006), and resource partitioning can promote the evolution of nectar concealment when the less effective pollinator is most affected by the evolving nectar barriers (Rodríguez-Gironés and Santamaría 2005). This idea can be applied to the evolution of deep corollas, as follows. When short- and long-tongued visitors exploit the nectar of shallow and deep flowers, optimal foraging models predict that there should be an association between a visitor's tongue length and the corolla depth of the flowers it visits (Rodríguez-Gironés and Santamaría 2006). If short-tongued visitors are less effective pollinators of a certain plant species, this species will be under selective pressure to increase the depth of its corolla tube, thus getting rid of its ineffective pollinators.

In order to obtain analytical results, our earlier model introduced a number of simplifying assumptions. In particular, we assumed (1) that plants are distributed in patches, so pollinators have to choose between visiting patches of one plant species or the other (an implicit assumption of Possingham 1992); (2) that pollinators are omniscient optimal foragers and follow the foraging strategy that maximizes their nectar intake rate; and (3) that all plants with the same phenotype have the same reproductive success, this being a linear function of the rate at which the average flower is visited by pollinators (Rodríguez-Gironés and Santamaría 2005). Furthermore, the model ignored the genetics of the evolving traits, implicitly assuming asexual reproduction, as is standard practice in evolutionary game theory (Maynard Smith 1982). The purpose of this article is to relax these assumptions in a model tailored to study the evolution of deep corolla tubes. To do this, we have developed a series of spatially explicit, individual-based models. The models allow for a random distribution of plants in their environment, forming a community where flower visitors search for nectar using simple foraging strategies. Moths transport pollen grains as they move from flower to flower, thus determining the male and female components of each plant's reproductive success. Notice that in the individual-based models, moths can visit flowers from different species within a foraging bout. It follows that moths can transport pollen grains from one plant species to the other. Pollen loss cannot occur when each pollinator specializes on flowers of a single species, as assumed by Rodríguez-Gironés and Santamaría (2005). The results of the individual-based models show that deep corollas readily evolve when long-tongued nectarivores are more effective pollinators of one plant species and short-tongued visitors are more effective pollinators of the other plant species. Interestingly, deep corollas sometimes evolve even when short- and long-tongued visitors are equally effective at pollinating both plant species.

Model Description

We modeled the evolution of corolla depth in a community formed by two flower-visiting species and two plant species. For narrative simplicity, we refer to the flower visitors as moths, but the model applies equally to any other taxa. Plants grew at the nodes of a 100 × 100 square grid and could belong to species A or B. The simulation started with 5,000 plants of each species randomly distributed on the grid. The parameters reported in this section correspond to the basic model, and most of them were varied systematically to explore their effect.

There were 10 flowers in each plant. At the beginning of the simulation, each flower had a 2-mm column of nectar (assuming that the corolla of the flower was deep enough), and thereafter flowers secreted nectar at a rate of 0.002 mm s^{-1} until the corolla tube filled up, when nectar secretion stopped until a moth consumed some of it. Nectar was consumed by two species of moths, which we refer to as X (short-tongued) and Y (long-tongued) moths. There were equal numbers of X and Y moths, this number being 50 in the basic model. The length of the proboscis was 5 and 15 mm for short- and long-tongued moths, respectively. It took moths 2 s to fly from one plant to its nearest neighbor and 1 s to exploit each flower. Each generation lasted for 10,000 s of continuous foraging activity. At the end of this period, the reproductive success of individual plants and moths was calculated, and a new batch of individuals was produced.

Foraging Strategy of Moths

Because the focus of this model is the evolution of floral traits, no attempt was made to model moth evolution realistically. Model moths were haploid and reproduced asexually. (The only reason for including moth evolution at all was to make sure that moths adjusted their foraging strategy to the changing plant population.)

Moths had to make two foraging decisions: what plants to exploit and when to leave them. On leaving a plant, moths flew in the direction they were flying when they encountered the plant. (There were four possible directions at angles of 0, $\pi/2$, π, or $3\pi/2$ radians with the horizontal axis.) Every time that a moth encountered a new plant, it decided whether to stop and visit it or to go on flying. Moths that continued flying changed flight direction with probability 0.05. Moths could not detect the amount of nectar present in flowers at a distance. If the encountered plant was not being exploited by another moth, the decision of whether to land on it was stochastic: the moth visited the plant with probability $P_{\text{land}}(d)$:

$$P_{\text{land}}(d) = \frac{1}{2}\min\{1 + \tanh[\alpha_0 \times (d - d_0)], \\ 1 - \tanh[\alpha_1 \times (d - d_1)]\}, \qquad (1)$$

where d represents the corolla depth for the plant's flowers and the parameters α_0, α_1, d_0, and d_1 are part of the foraging strategy of an individual moth (see below). With this foraging strategy, moths are likely to land on plants with corolla depths in the range (d_0, d_1) and unlikely to land on plants with corolla depth less than d_0 or greater than d_1. The parameters α_0 and α_1 determine the steepness of the transition from low to high probability around d_0 and from high to low probability around d_1, respectively. By adjusting the values of these parameters, therefore, moths can choose both the range of favored corolla depths, (d_0, d_1), and their selectivity.

Once in a plant, moths chose one of its flowers at random and visited flowers sequentially for as long as the amount of nectar collected in flowers, h, was greater than the product γH, where H represents the "expected" standing crop and was updated after each flower visit according to the algorithm $H = 0.85H + 0.15h$, except for the first visit, where we set $H = h$. The parameter γ is part of the foraging strategy of an individual moth (see below). This part of the foraging strategy allows moths to leave plants that have been recently depleted of nectar.

We implemented periodic boundary conditions. If a moth disappeared from the grid through its right-hand side, it reentered from its left-hand side. Likewise, a moth that had visited the tenth flower of a plant without reaching its departure criterion moved on to the first flower. Moths would collect any nectar within reach in the flowers they visited. (If a moth had a proboscis of length l, it would consume any nectar within a distance l from the corolla opening.)

The payoff to a moth was the amount of nectar collected throughout its lifetime. The probability that a certain moth was selected as the mother of a new moth was proportional to its normalized payoff, (payoff − minimum payoff)/(maximum payoff − minimum payoff).

The "genome" of a moth consisted of a single copy of the parameters α_0, α_1, d_0, d_1, and γ. Genes coding for the foraging strategy mutated with probability 0.01 at each reproductive event, and the magnitude of mutations was normally distributed, with mean 0 and standard deviation 0.05.

Pollen Transport

The processes of pollen removal and pollen deposition, as implemented in the simulations, are not unlike those found in orchids. Each flower had two pollinia. Every time a moth visited a flower, and regardless of the length of its tongue, it removed one pollinium (if the flower had any pollinia left). Removed pollinia were immediately lost with probability 2/3 and otherwise remained attached to the body of the moth until they were deposited on a new flower.

If a pollen-loaded moth of species j (j = X or Y) visited a flower of species i (i = A or B), it transferred a pollinium from its body with probability P_{ij}. For most simulations, the probability of pollen transfer depended on the combination of plant and moth species ($P_{\text{AX}} = 0.4$, $P_{\text{AY}} = 0.1$, $P_{\text{BX}} = 0.1$, and $P_{\text{BY}} = 0.4$). This probability was always independent of the relationship between corolla depth and proboscis length. This is not to say that, in real situations, the probability of pollen transfer is independent of the relationship between corolla depth and proboscis length. But if we want to show that alternative mechanisms can induce the evolution of deep corollas, we must test these mechanisms on their own. (If the probability of pollen transfer increased when the corolla depth was deeper than the proboscis of the flower visitor, and if flowers with deep corollas evolved in the simulations, we would be hard put to decide whether character displacement had played any role.)

When pollen transfer took place, we assumed that the pollinia that had been collected more recently had a greater probability of being transferred. Thus, if a moth had N pollinia on its body, ordered in such a way that pollinium number 1 was the most recently collected and pollinium number N had been on the moth's body for the longest time, the probability that pollinium number j was transferred was proportional to $e^{-0.2 \times j}$.

Pollination and Seed Set

Each flower had six ovules that could be converted into seeds. For each ovule, a pollinium was chosen among those present on the stigma to contribute the pollen grain that fertilized the ovule. Pollinia that had arrived earlier to the stigma had higher probabilities of fertilizing ovules. The probability that the pollen grain was contributed by the ith pollinium ($i = 1$ for the first arrival) was proportional to w/i, where $w = 1$ if the pollinium and the ovule belonged to the same species and $w = 0.25$ otherwise (representing clogging of stigma by heterospecific pollen grains). Ovules "fertilized" by pollen grains of different species produced no seed.

Plant Genetics

Each plant was endowed with two sets of genes. At each locus, two alleles could occur: we will refer to them as alleles 0 and 1. The first set consisted of 10 loci that determined the depth of corolla tubes in the flowers of the plant, the depth being equal to the number of 1 loci. (Corolla depth could therefore take any integer value between 0 and 20.) The second set of genes consisted of 15 loci that determined viability (seedling competitive ability), as explained below. Genes segregated independently from each other. (Essentially, each "gene" was carried on a different "chromosome.") Genes coding for corolla depth mutated with probability 0.01, and viability genes mutated with probability 0.001.

Seed Dispersal and Seedling Competition

Seeds dispersed to random grid nodes. The probability that a seed dispersed to a site decreased exponentially with the distance between the site and the plant that produced the seed. Average dispersal distance was 10.

Once all seeds had dispersed, one seed was selected at each node to produce the new plant. (If no seeds had arrived at a particular site, the plant that had grown there the previous generation reproduced asexually.) The probability that seed n originated the plant eventually growing at a site was

$$P_{\mathrm{germ}}(n) = \frac{(1 - f_n) \times e^{-0.5 \times s_n}}{\sum_m (1 - f_m) \times e^{-0.5 \times s_m}}, \tag{2}$$

where f_n is the proportion of plants in the previous generation belonging to the same species as the nth seed and s_n, the genetic load of the seedling, is the number of loci (of the 15 determining competitive ability) where the nth seedling is homozygotous for allele 1. The exponential term implements inbreeding depression. In the denominator, the sum is carried over all seeds present at the node. The frequency-dependent factor makes sure that the two species coexist even if one of them has a higher reproductive success than the other. While this term might look artificial, it should be remembered that most plant species coexist for reasons having little or nothing to do with their ability to attract pollinators. Essentially, we are assuming that the population size of each species varies little in time and that competition for reproductive sites occurs within and not between species. Factors that can favor coexistence of two plant species and that might be implicitly represented in the frequency-dependent factor are habitat heterogeneity, herbivores and pathogens, or resistance to stress.

Results

Spatial Analysis

Modeled variables (corolla length and plant species distribution) showed no spatial autocorrelation over the complete range of scales included in the grid, indicating that the randomness of their initial distribution was maintained across the 50,000 generations simulated. For this reason, we report only the average values of the traits, ignoring their spatial distribution.

Foraging Strategies of Moths

Competition for nectar resulted in resource partitioning (fig. 1). Short-tongued moths, species X, specialized on shallow flowers, avoiding flowers with corollas deeper than 10 mm and exploiting fewer flowers per plant when flowers had deep corollas than when flowers had short corolla tubes. Long-tongued moths, species Y, were less specialized. They visited all but the shallowest flowers they encountered, and although they exploited more flowers per plant in plants with deep flowers than in plants with shallow flowers, the difference was not as pronounced as for short-tongued moths (fig. 1).

Evolution of Deep Corollas

Resource partition results in rapid elongation of corolla tubes in plant species B, which were best pollinated by long-tongued moths (fig. 2). Following 50,000 generations, there was virtually no corolla depth overlap between the flowers of the two species. The B flowers with short corolla tubes were penalized because, being visited predominantly by short-tongued moths, they received mainly pollen from A flowers (producing very little seed set), and most of their pollen was correspondingly lost to A flowers. The reverse penalty was exacted from A flowers with deep corollas (fig. 3).

Deep corollas evolve even when short- and long-tongued moths are equally effective at pollinating A and

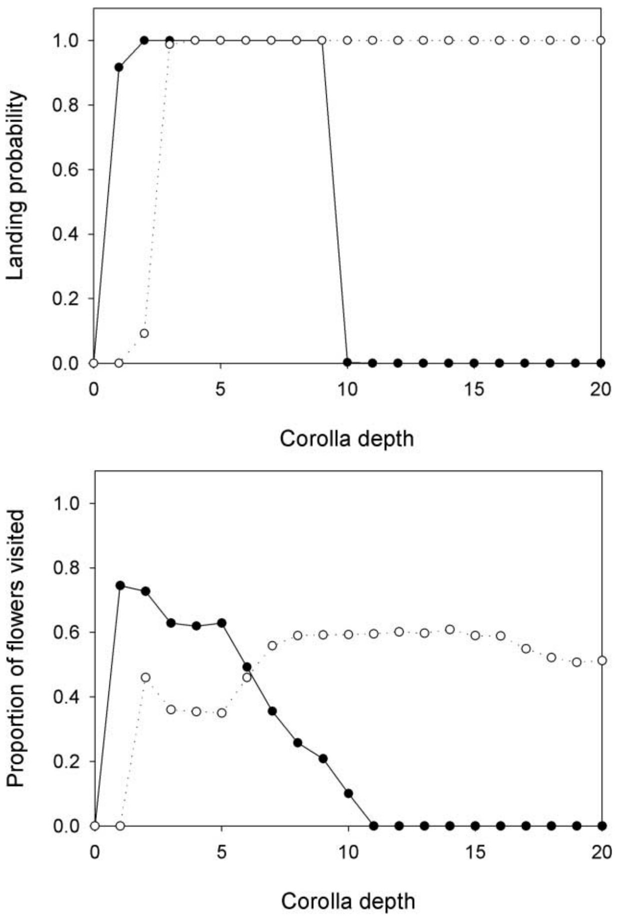

Figure 1: Foraging strategy for short-tongued (*solid line, filled symbols*) and long-tongued (*dotted line, open symbols*) moths following 50,000 generations. *Top*, probability of landing on a plant versus the depth of its flowers' corolla tubes. Both short- and long-tongued moths leave plants when the amount of nectar they collect at a flower is less than half the expected amount of nectar harvested ($\gamma = 0.46$ and 0.59 for short- and long-tongued moths, respectively). *Bottom*, proportion of flowers exploited at visited plants.

B flowers, and the asymmetry in pollination effectiveness does not affect average corolla depths following 10,000 generations (fig. 4*A*). Out of 10 simulation runs when the probability of pollen transfer was 0.25 for all plant-moth combinations, eight runs resulted in A and B flowers with different corolla depths. In these cases, A and B plants were equally likely to evolve deep corollas, and the resulting corolla depths were similar to those observed in figure 2: short corollas 4.6 ± 0.1 mm ($N = 8$), long corollas 12.3 ± 0.1 mm ($N = 8$). This result can be explained as follows. Long-tongued moths preferentially visit deep flowers, and short-tongued moths preferentially visit shallow flowers. This is because long-tongued moths (Y) can reach more nectar from the plants with longer tubes even when they have recently been visited by a short-tongued (X) moth that drained them to the extent possible. As long as the distribution of corolla depths in the two plant species is identical, this behavioral preference does not result in disruptive selection, because the fitness of plants is independent of their corolla depth. (Shallow flowers preferentially export pollen to shallow flowers, but shallow flowers are equally likely to belong to one species or another, so there is no advantage in reducing the depth of the corolla tube.) In a finite population, however, random sampling produces fluctuations in the distributions of corolla depth. At any given time, the corolla tubes of one species will be, on average, deeper than those of the other species. And if the difference is large enough, shallow flowers of the species with shorter corolla tubes will have higher reproductive success than deep flowers of the same species, while the reverse will be true for the species with deeper corollas. The system enters a positive feedback loop, leading to segregation of corolla depths between the two species.

A difference of 2 mm in the proboscis length of the pollinators results in a difference of 6 mm in the corolla depth of the flowers, but increasing the difference in proboscis length beyond 4 mm had little effect on corolla depths (fig. 4*B*). Except for very low moth densities, when the corolla depths of both plant species were relatively similar, corolla depth was essentially independent of moth density (fig. 4*C*). The relationship between traveling time

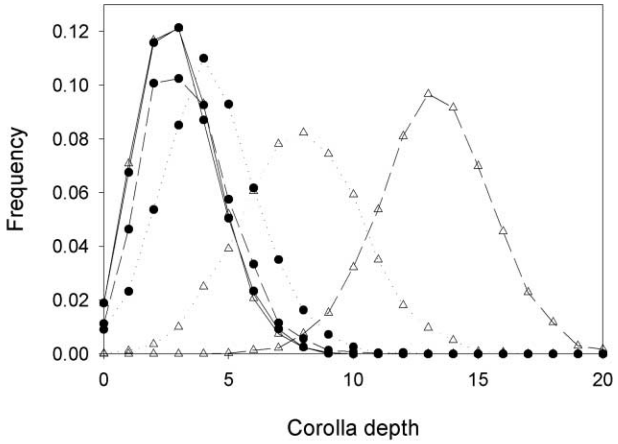

Figure 2: Character displacement. The figure shows, for the basic model, the change through time of the frequency distribution of corolla depths for plant species A (*filled circles*) and B (*open triangles*). Points linked by solid lines represent the frequency distribution at the beginning of the simulation. Points linked by dotted lines represent the distribution following 20 generations, and points linked by dashed lines represent the asymptotic distribution (50,000 generations). The initial segregation of corolla depths is very rapid, and it is almost complete following 50 generations.

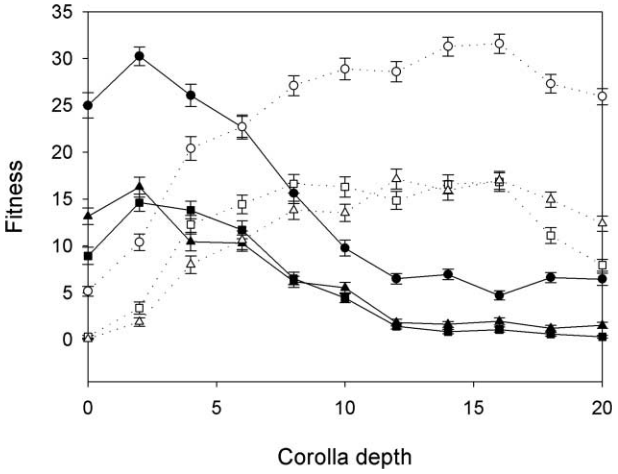

Figure 3: Relationship between corolla depth of flowers and expected fitness for A (*filled symbols, solid lines*) and B (*open symbols, dotted lines*) plants following 50,000 generations. Circles represent total seed set, squares represent the number of outcrossed seeds produced, and triangles represent the number of outcrossed seeds sired (male fitness).

and handling time of flowers had little impact on the evolution of deep corollas. In the basic model, handling time was independent of nectar availability, and travel time was twice as long as handling time. A fivefold increase in the duration of travel time and assuming that handling time increased linearly with the amount of nectar that a moth collected did not hamper the evolution of deep corollas.

Resource partitioning is a prerequisite for the differentiation of corolla length between A and B flowers. When moths visit every plant they encounter, leaving it with constant probability ($P = .7$) after every visited flower, there is no difference in the corolla depth of A and B flowers after 50,000 generations.

Perceptual Errors and Evolution of Deep Corollas

The basic model, although acknowledging that pollinators are not optimal foragers, assumes that they can assess without errors the depth of the corolla tubes and that they behave accordingly. In practice, pollinators may be unable to assess accurately the depth of the corolla tubes. At first sight, it might appear that the inability of pollinators to discriminate corolla depth should preclude the evolution of deep corolla tubes. This, however, need not be so: moths visiting plants irrespective of their floral traits could nevertheless leave sooner those plants where they are unable to collect nectar. For this reason, when studying the effect of perceptual errors on the evolution of deep corolla tubes, we must consider the interaction of two factors: the num-

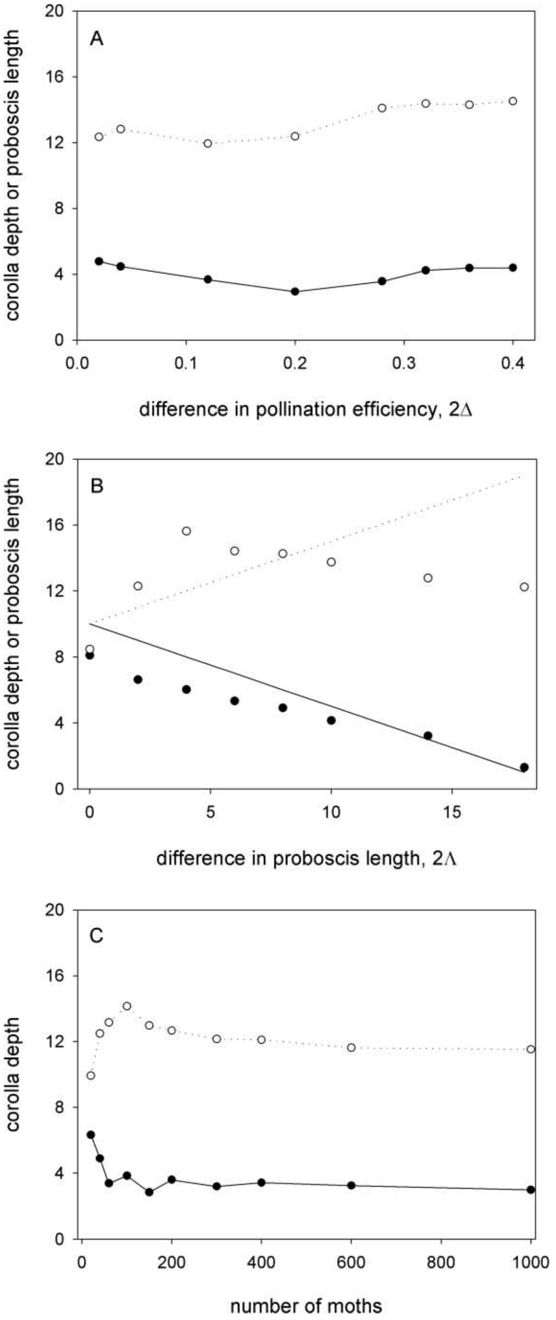

Figure 4: Effect of parameter values on the mean corolla depth of plant species A (*filled circles*) and B (*open circles*) after 10,000 generations. *A*, Mean corolla depth versus the asymmetry in pollinator effectiveness. The probability that a moth transfers pollen to the stigma of the flower is $P_{AX} = 0.25 + \Delta$, $P_{AY} = 0.25 - \Delta$, $P_{BX} = 0.25 - \Delta$, and $P_{BY} = 0.25 + \Delta$. *B*, Mean corolla depth versus the difference between the proboscis length of long-tongued (length $= 10 + \Lambda$) and short-tongued (length $= 10 - \Lambda$) pollinators. Straight lines represent the tongue lengths of short-tongued (*solid lines*) and long-tongued (*dotted lines*) moths. *C*, Mean corolla depth versus the total number of moths. All other parameters as in the basic model.

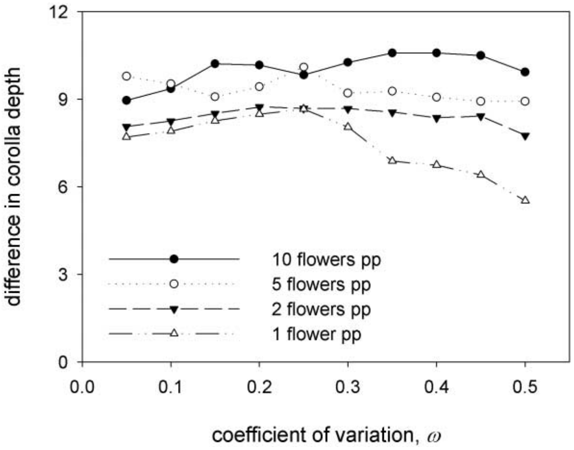

Figure 5: Effect of increasing the magnitude of perceptual errors (the coefficient of variation, ω) on the average difference between corolla depth of A and B plants for different numbers of flowers per plant after 10,000 generations.

ber of flowers per plant and the accuracy with which moths can assess corolla depth.

We assume that a flower with corolla depth d is perceived by moths as having corolla depth $\delta = d + \varepsilon$, where ε is a random deviate, normally distributed, with mean 0 and standard deviation ωd. The magnitude of the perceptual error is therefore assumed proportional to the size of the stimulus, in agreement with psychophysical findings (Stevens 1960). The coefficient of variation of the error term, ω, is typically of the order of 0.2 (Stevens 1960). Because moths do not have access to the real depth of the corolla tubes, they must decide whether to land on a plant using the perceived depth, δ, in equation (1). (Note that in order to maximize intake rate, the parameters in eq. [1] must change with ω.)

As figure 5 shows, deep corollas evolve even when moths make very rough assessments of corolla depths ($\omega = 0.5$) and there are very few flowers per plant. Indeed, it is only when plants have a single flower and perceptual error is high ($\omega > 0.3$) that the effect of perceptual errors on corolla elongation becomes noticeable. (Note that with a single flower per plant and a maximum of six seeds per flower, plants did not produce enough seeds to replace the population. We therefore increased to 12 the maximum number of seeds per flower in this case.)

Temporal Heterogeneity in Population Sizes

It is often assumed that evolutionary processes require a high degree of temporal and spatial constancy and that fluctuations in community composition can interfere with the evolution of complex traits. To address this problem, we have studied the evolution of long corollas in environments where the number of short- and long-tongued moths changed from year to year. Specifically, we assumed that the total number of moths in the community remained equal to 100 but that the proportion of short- and long-tongued moths changed from year to year. In a given year, the proportion of short-tongued moths was a random variate, uniformly distributed in the range ($0.5 - \Omega$, $0.5 + \Omega$). This could interfere with the evolution of deep corollas because the optimal strategy of the pollinators will change from year to year: a corolla depth that is mainly exploited by short-tongued moths one year may be visited by only long-tongue moths the following year (Rodríguez-Gironés and Santamaría 2006). As figure 6 shows, however, increasing Ω did not hamper the evolution of deep corolla tubes.

Pollen Harvesting

In all the simulations that we have shown so far, there were only two types of flower visitors: short- and long-tongued moths. Although the range of corolla depths that each species visits will depend on the value of parameters such as moth density and nectar secretion rate, it will always be the case that short-tongued moths show a preference for flowers with shallow corolla tubes and long-tongued moths prefer flowers with deep corollas. In this section, we introduce a third flower-visiting species: pollen-collecting bees. We assume that these bees visit every flower they encounter, irrespective of their phenotype and species. As a result, they are as likely to transfer pollen

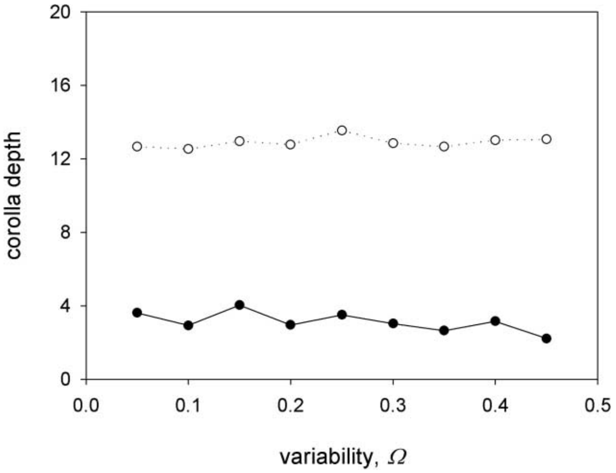

Figure 6: Temporal heterogeneity in the number of short- and long-tongued moths (as measured by Ω) had no effect on the average corolla depth of A (*filled circles*) and B (*open circles*) flowers. Results correspond to 10,000 generations. Tongue lengths were 5 and 15 units.

between plants of the same or different species of similar or dissimilar phenotypes, and they will interfere with the evolution of deep corolla tubes. In this section, we assumed that there were 200 flower visitors. Of these, N were pollen-collecting bees, and among the remaining $200 - N$, there were equal numbers of short- and long-tongued moths. Figure 7 shows the average corolla depth for the two plant species following 25,000 generations; it is only when the number of pollen-collecting bees in the community exceeds 80% that the evolution of deep corolla tubes is precluded.

Discussion

Before our models, at least three hypotheses had been proposed to explain the evolution of flowers with deep corollas. Deep corollas will have a selective advantage if the probability of pollen transfer decreases when their corolla tube becomes shorter than the proboscis of their pollinators (Darwin 1862; Nilsson 1988), if they promote flower constancy (Laverty 1994) or if they exclude ineffective generalist pollinators (Heinrich 1979; Laverty 1980). The first of these hypotheses has received most attention in the literature, and while data support its assumptions (Nilsson 1988; Johnson and Steiner 1997; Alexandersson and Johnson 2002), it cannot be regarded as a universal explanation of the phenomenon (Herrera 1993; Lindberg and Olesen 2001; Lasso and Naranjo 2003).

The second hypothesis poses that complex floral structures can promote flower constancy if pollinators are unable to learn several flower exploitation skills simultaneously (Darwin 1876). Although some studies have found that flower-handling performance decreases with increasing flower diversity (Lewis 1986; Gegear and Laverty 2005), switching among flowers of varying morphology may also have a negligible cost (Woodward and Laverty 1992), and in particular, a long corolla tube does not really increase the time required to learn how to handle flowers efficiently (Laverty 1994). It therefore follows that, if enhancing flower constancy plays a role in the evolution of deep corolla tubes, this role is not mediated by learning.

As for the third hypothesis, the exclusion of ineffective generalist pollinators, its main limitation was that, while it was clear that deep corollas prevent short-tongued pollinators from exploiting the nectar they contain, it was less clear what selective pressures drove the evolution of deep corollas in a community where there are minor differences in corolla depth. Thus, because of the effects of gene flow and competition, Jones (2001) finds it unlikely that partitioning among pollinator taxa would be important for initiating divergence within a population experiencing disruptive selection. Our model, however, suggests an ecological mechanism that can explain how evolutionary divergence can be initiated. It also shows how flower constancy can be enhanced in the absence of cognitive constraints. The mechanism is based on the idea that foraging decisions will lead to resource partitioning when flower visitors differ in the length of their proboscis (Peleg and Shmida 1992; Rodríguez-Gironés and Santamaría 2006), as it has repeatedly been observed (Heinrich 1976; Inouye 1980; Pyke 1982; Harder 1985; Haber and Frankie 1989; Graham and Jones 1996; Irwin 2000; Borrell 2005; Stang et al. 2006). This mechanism is not incompatible with Darwin's (1862) original idea, and both mechanisms can work in synergy.

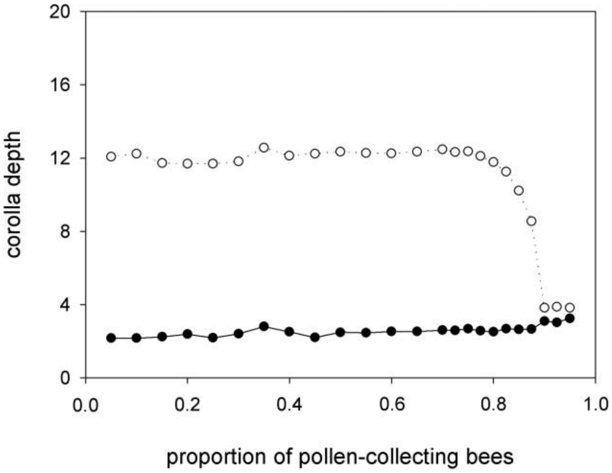

Figure 7: Effect of the proportion of pollen-collecting bees on the average corolla depths of A (*filled circles*) and B (*open circles*) flowers. Pollen-collecting bees disrupt the evolution of deep corollas only if they constitute more than 80% of the flower visitors. Results correspond to 10,000 generations. Tongue lengths were 5 and 15 units.

In the absence of selective flower choice by the pollinators, the mutation regime of our simulations does not lead to the differentiation of corolla depth of A and B flowers. We observe this when short- and long-tongued moths exploited all flowers irrespective of their corolla depth, either because we fixed their foraging strategy because they had the same proboscis length (fig. 4*B*) or because moth density was very low (fig. 4*C*; when moths are present at very low densities and there is a random spatial distribution of corolla depths, moths maximize their intake rate exploiting every flower they encounter [Rodríguez-Gironés and Santamaría 2006]).

Resource competition between pollinators foraging for nectar allows the differentiation of corolla depth in A and B flowers. At evolutionary equilibrium, the corollas of one species are deeper, and those of the other species shallower, than they would be in the absence of selection (figs. 2, 4). The evolutionary force separating corolla depths in both species is character displacement (Brown and Wilson 1956): as long as the corolla depths of the two species overlap, flowers with extreme corolla depths (either very deep or very shallow) are more efficient at exporting pollen to conspecifics and more likely to be cross-fertilized. The mechanism behind character displacement is the foraging behavior of flower visitors, since variability in the length of the pollinators' proboscis leads to their specialization on flowers with different corolla depths. The effect of resource partitioning on the reproductive success of plants is not unlike the pollinator interactions discussed by Aigner (2001), but the two models are difficult to compare because frequency-dependent selection is a key ingredient in our reasoning, while the model developed by Aigner (2001) is frequency independent.

Previous models of floral evolution have been criticized because they assume almost-perfect flower constancy (Grant 1994). It is therefore important to stress that, unlike previous results (Rodríguez-Gironés and Santamaría 2005), this model does not assume that flower visitors are optimal foragers. Indeed, the foraging strategy implemented in the modeled moths, although inspired in optimal foraging models (Rodríguez-Gironés and Santamaría 2006), was a very simple rule of thumb. Studies of resource partitioning by nectarivores based on proboscis length show that the degree of foraging specialization obtained in our simulations is not unrealistic (Heinrich 1976; Inouye 1980; Pyke 1982; Harder 1985; Haber and Frankie 1989; Graham and Jones 1996; Irwin 2000; Borrell 2005; Stang et al. 2006).

One of the most important features of our results is their resilience to perturbations and environmental noise. Differentiation of corolla length persists when moths can only poorly assess the corolla depth of the flowers they visit, when the proportion of short- and long-tongued moths changes from year to year, and when the community of flower visitors includes species that forage indiscriminately at one flower type or another. The evolution of long corolla tubes does not require the consistent selection that has often been assumed (Ollerton 1996). The evolution of long corolla tubes in the presence of pollen-collecting bees is particularly noteworthy. Pollen-collecting bees visited every flower they encountered (there was no flower constancy, not even at the individual level, and because the spatial distribution of plants was random, it follows that bees visited plants of both species in random order), transporting pollen from flower to flower regardless of their phenotype or species. The presence of bees introduced a component of random mating, and yet deep corolla tubes evolved unless the percentage of bees in the population was >80% of all the flower-visiting individuals. (Moreover, because in our simulations bees wasted less time flying than more choosy moths, they performed more than 80% of the visits.)

We originally assumed that deep corollas and other nectar concealment traits evolved to discourage parasites from visiting flowers (Rodríguez-Gironés and Santamaría 2005). In these simulations, we observed differentiation of corolla depth even when short- and long-tongued moths were equally good pollen vectors of A and B flowers. This result stresses the fact that the foraging strategy of flower visitors is as important as their mechanical fit in determining whether they act as effective pollinators or conditional parasites and in driving the evolution of floral morphology through this effect.

While our simulations assume the existence of two reproductively isolated plant species from the beginning, many studies suggest that pollinator behavior can promote floral divergence within a single plant population, leading ultimately to speciation (Hodges and Arnold 1995). To study sympatric speciation, the model must include at least two additional components: disruptive selection on traits other than the length of the corolla tube and a mechanism cementing reproductive isolation after the initial divergence of corolla tube length. We are currently working on such an extension of the model.

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