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Reply to Williamson and Black's Comment

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## REPLY TO WILLIAMSON AND BLACK'S COMMENT<sup>1</sup>

James H. Brown and Astrid Kodric-Brown<sup>2</sup>

We reported a population of *Lobelia cardinalis* which differs from most red, tubular, temperate-zone flowers (including some conspecific populations in other areas) by not secreting floral nectar (Brown and Kodric-Brown 1979). We hypothesized that these plants act as Batesian mimics, i.e., they attract hummingbird pollinators through resemblance to other flowers which secrete nectar; by previous experience with rewarding models, birds are conditioned to visit and pollinate effective mimics.

Williamson and Black (1981) claim that three alternative hypotheses are more parsimonious than our mimicry hypothesis. We consider these in order, and suggest that none of them adequately and realistically account for all the facts:

1) Pollination by selfing: We have not conducted bagging experiments to exclude this possibility unequivocally. However, if these *L. cardinalis* were autogamous, we might expect a general reduction in floral attractants, but nectar secretion is the only floral trait which appears to be reduced or absent. Furthermore, we have observed hummingbirds visiting the flowers, we have found pollen of other hummingbird-pollinated flower species on the stigmas, and we have collected *L. cardinalis* pollen from birds captured in the area. These observations indicate that the birds are capable of pollinating the flowers and providing any benefits that would accrue from outcrossing.

2) Pollination by insects: In the absence of nectar secretion, insects might be attracted to forage for pollen. We saw many hummingbirds and a very few insects (e.g., swallowtail butterflies) apparently probing the flowers for nectar, but no insects collecting pollen. Although hummingbirds appear to be the primary pollinators, the mimicry could also be effective on insects with previous experience with rewarding models.

3) Pollination by naive hummingbirds: This does not seem to differ substantively from our mimicry hypothesis. We suggested (Brown and Kodric-Brown 1979:1034) that mimicry would be an effective strategy "... only for rare flowers which occur where there are sufficient inexperienced pollinators and nectar-producing model flowers." The birds probably are indeed naive in that they have not had extensive ex-

perience with these unrewarding flowers. All that is necessary for effective mimicry is that the birds have sufficient experience with rewarding flowers and that they sample enough individuals to effect pollination before learning that the mimic flowers are unrewarding. Considerable sampling of new flowers is probably necessary in order for the birds to assess the rewards accurately, because even flowers which secrete nectar may be empty temporarily because of recent foraging. This is not inconsistent with any generally accepted definition of Batesian mimicry, including that used by Williamson and Black. There are two kinds of signal transmitters, flowers of *L. cardinalis* which secrete no nectar (mimics) and red, tubular flowers of other species which secrete nectar (models). The transmitters are sufficiently similar that the mimics are able to take advantage of the regular response of another species (the operator) to signals of model. Neither this definition nor the effectiveness of the mimicry requires that the operator have extensive experience with the mimics. In fact the mimicry will often be most effective if the operator is relatively naive about mimics; with extensive experience the operator might learn to distinguish model from mimic, and the deceptive advantage of the similarity would be lost or diminished.

We also reply to Williamson and Black's criticisms of the evidence we advanced to support our mimicry hypothesis:

1) "It is rare." Williamson and Black claim that alternating experiences of operators (i.e., pollinators) with models and mimics are necessary for effective mimicry. However, as they subsequently admit when discussing automimicry, all that is really required is prior experience of the pollinator with a rewarding model, so that the mimic is subsequently mistaken for the model, visited, and pollinated. Effectiveness of the mimicry is enhanced if the mimic is rare, because otherwise the hummingbirds might learn to avoid it before pollinating many flowers.

2) "It closely resembles *I. aggregata* and *P. barbatus*." Flowers of these species resemble those of *L. cardinalis* and bloom abundantly in the immediate vicinity. Rewarding experiences with nectar-secreting models would enhance the effectiveness of the mimicry until the birds visit sufficient flowers to learn to avoid unrewarding mimics. It is not at all inconsistent that a rare flower might benefit by being an unrewarding Batesian mimic, whereas common ones would be selected to converge in appearance and nectar rewards to act as Mullerian mimics.

3) "*L. cardinalis* blooms in late August and September when most of the hummingbirds present are juvenile migrant *Selasphorus rufus*." Such young migrant birds not only have no experience with the local

flowers, but also they probably have been conditioned to forage from similar red, tubular flowers on the basis of previous experience with such models. In this sense, as the Grants (Grant 1966, Grant and Grant 1968) implied and as we argued more explicitly, all of the red, tubular flowers pollinated by the migrant hummingbirds in western North America can be regarded as part of the same mimicry complex, with most species secreting nectar and acting as Mullerian mimics.

4) "*Lobelia cardinalis* has a very large stigmatic surface . . ." We only wished to suggest that this attribute, like the late blooming time, might be a pre-adaptation which makes mimicry by a rare plant more effective.

Given their other criticisms, we find that Williamson and Black's comments on automimicry are inconsistent. We agree that the mimicry appears to depend on stationary flowers being sampled by mobile birds inexperienced with the reward structure of local plants. The question is: what previous experience conditions the birds to forage on flowers of *L. cardinalis*? It is unlikely that even migrant individuals have had previous experience with nectar-producing flowers of this species. Although *L. cardinalis* has a very wide geographic range, it almost always occurs in small, isolated populations because of its restrictive geographic requirements. It is likely, however, that any hummingbird visiting the mimetic population will previously have obtained nectar from several flower species which are sufficiently similar to *L. cardinalis* to serve as effective models.

Williamson and Black (1981) assert that Batesian flower mimicry should be rare in plants, because plants are sessile and clumped. We cannot understand their logic. Since pollinators are attracted to flowers largely by long-distance visual and olfactory signals, some flower species which do not provide

any reward may evolve to attract animal pollinators by mimicking signals associated with rewards provided by other species. Such mimics will be particularly effective if they are rare, because the pollinator will have limited opportunity to learn that it is being deceived. It is not even necessary that the mimics always resemble other flowers. One of the great "oh my" stories of biology (but perhaps it should still be regarded as an hypothesis) concerns the orchids which mimic female insects and are pollinated by males attempting copulation (van der Pijl and Dodson 1967).

We agree with Williamson and Black that ad hoc explanations should be treated as hypotheses until they can be evaluated rigorously with additional observations and experiments. Williamson and Black have not done such empirical work, so the possible explanations for lack of nectar secretion in *L. cardinalis* must be evaluated on the basis of the data at hand. We still believe that the Batesian mimicry hypothesis best accounts for our observations, but we would encourage further work on this interesting system.

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