fraorbital ridge and 1 cm medial to a line bisecting the pupil in central gaze. The other electrode was placed just above the eyebrow and 1 cm lateral to a line bisecting the pupil in central gaze.
9. The skin under each electrode was abraded and was punctured with a sterile needle at Fz, Cz, Pz, and the right mastoid. Electrode impedences were never greater than 2000 ohms for Fz, Cz, and Pz and 5000 ohms for the upper and lower eye leads.
10. In each stimulus category, only an average of 4 and 12 percent of trials were excluded for these reasons for adult and children's groups, respectively.
11. The ERP wave forms were measured either peak to peak or baseline to peak with 250 msec of the average prestimulus EEG tracing serving as baseline.
12. The mean N1-P2 amplitudes at Cz in children were 25.2 μv for targets, 21.2 μv for background slides, 18.5 μv for novel slides, and 19.9 μv for dim slides. The mean N1-P2 amplitudes at Cz in adults were 21.1 μv for targets, 16.1 μv for background slides, 13.7 μv for novel slides, and 22.2 μv for dim slides. The mean N1 and P2 latencies at Cz in children were 144 and 259 msec for targets, 148 and 238 msec for background slides, 173 and 243 msec for novel slides, and 155 and 266 msec for dim slides. The mean N1 and P2 latencies at Cz in adults were 150 and 240 msec for targets, 152 and 243 msec for background slides, 133 and 209 msec for novel slides, and 158 and 246 msec for dim slides.
13. The mean amplitudes of Nc waves in children for novel slides were 11.6 μv at the lower eye (LoE), 22.3 μv at the upper eye (UpE), 33.4 μv at Fz, 29.9 μv at Cz, and 19.0 μv at Pz; the mean amplitudes of Nc waves in children for dim slides were 12.5 μv at LoE, 14.0 μv at UpE, 27.8 μv at Fz, 23.0 μv at Cz, and 15.1 μv at Pz. The mean amplitudes of Pc waves in children for novel slides were 11.6 μv at LoE, 31.5 μv at UpE, 26.2 μv at Fz, 25.6 μv at Cz, and 14.4 μv at Pz; the mean amplitudes of Pc waves in children for dim slides were 13.0 μv at LoE, 34.6 μv at UpE, 28.0 μv at Fz, 21.9 μv at Cz, and 11.8 μv at Pz. [In a few children, P3-like waves (latency of about 650 msec) were seen at Pz in response to novel and dim slides (five of ten subjects in each case)]. A comparison of amplitudes of Nc waves for novel and dim slides at Fz gave $t = 2.60$, $P < .03$ (two-tailed test); a comparison of latencies at Fz gave $t = 2.88$, $P < .02$ (two-tailed test).
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15. Lateral eye movements may be discounted as the source of the Nc and Pc waves for the same reasons. Movements to the right produced positive potentials in the upper eye lead and negative ones in the lower eye lead. The opposite was true for movements to the left. Also these eye movement potentials were largest in the upper eye lead with Fz, Cz, and Pz derivations having successively smaller potentials.
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18. The mean P3 amplitudes in adults for novel slides were 1.5 μv at LoE, 5.5 μv at UpE, 15.2 μv at Fz, 15.5 μv at Cz, and 12.7 μv at Pz; the mean P3 amplitudes in adults for dim slides were 0.0 μv at LoE, 0.9 μv at UpE, 11.4 μv at Fz, 17.2 μv at Cz, and 17.5 μv at Pz. The mean P3 latencies at Cz were 411 and 448 msec for novel and dim slides, respectively.
19. The mean target P3 amplitudes were 9.6 μv at Fz, 24.0 μv at Cz, and 28.6 μv at Pz for children; and 11.0 μv at Fz, 18.4 μv at Cz, and 19.5 μv at Pz for adults. The mean P3 amplitudes for background stimuli were 5.3 μv at Fz, 9.9 μv at Cz, and 9.1 μv at Pz for children; and 4.4 μv at Fz, 7.0 μv at Cz, and 8.1 μv at Pz for adults.
20. A comparison of the mean amplitudes of target P3 waves at Pz for adults and children gave $t = 203$, $P > .06$ (two-tailed test). Comparisons of the distribution of P3 waves to background and target stimuli for adults and children each yielded $P > .50$.
21. This does not suggest that all paradigms using such deviant stimuli will produce such differences or that P3 waves to these stimuli are never found in children.
22. Adults made less than 1 percent errors in target counts and the children made only 2 percent errors. Both groups used similar methods to keep count (such as repeating to oneself the current count each time a stimulus flashed and incrementing this count each time a target flashed). Also, subjects in each age group stated that they were surprised when they saw the first dim or novel slide. However, unlike the adults, most children attempted to label or identify (often in idiosyncratic ways) the novel slides by using concrete constructs (for example, "one slide looked like a horse," or "was there one with a house and flowers?").
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Two Genes Control Seasonal Isolation in Sibling Species

Abstract. Interspecific hybridization tests between *Chrysopa carnea* and *Chrysopa downesi* show that single allele differences at two unlinked autosomal loci cause large differences in photoperiodic responses. These differences produce asynchronous seasonal reproductive cycles, thus forming an effective temporal reproductive barrier between the two sympatric species. The results subserve the development of a genetic model for allochronic speciation.

Evolutionary biologists generally imply or state directly that a prerequisite for sympatric speciation in bisexual animals is the attainment of a high degree of reproductive isolation through very simple genetic changes (*1*, *2*). However, there are very few proposed cases of sympatric speciation in which this requirement is shown to be fulfilled, and all of these cases deal with speciation in monophagous or parasitic animals through host race formation (*2*). For example, in monophagous tephritid flies alteration of a single allele can produce a shift in host plant preference (*3*). Such a change sets the stage for sympatric speciation because these insects generally mate on the preferred host, and a single allele difference at the locus controlling host selection can thus confer a substantial amount of reproductive isolation between host races (*4*). Similar mechanisms of sympatric speciation through host race formation have been proposed for other monophagous insect species (*5*). In comparison to these examples, proposed cases of sympatric speciation through seasonal isolation (that is, allochronic speciation) are not as well supported either experimentally or theoretically; and these deficiencies have contributed appreciably to the controversy of whether or not seasonal isolation is indeed a mechanism of speciation (*6*). Specifically, the primary impediment to the development of an acceptable model (or models) for allochronic speciation is the lack of the necessary experimental evidence that a simple genetic change can produce a functional asynchrony in the seasonal occurrence or cycles of reproduction in animals (*7*). In fact, there exists considerable evidence to the contrary; numerous studies have illustrated that polygenes or complex genetic mechanisms underlie interracial and interspecific differences in seasonality (*8*). Our recent experiments with interspecific hybrids indicate that gross differences in the seasonal reproductive cycles between two sympatric species result from single allele differences at each of two autosomal loci. These small genetic differences produce an asynchrony in the species' seasonal patterns of reproduction that is sufficient to provide a high degree of reproductive isolation. Thus, our findings provide a basis for developing a realistic

Table 1. Diapause characteristics of F_1 progeny from hybrid and conspecific crosses of *C. carnea* and *C. downesi*, reared under LD 16:8 at 24° ± 1°C. The numbers in parentheses indicate the number of animals.

F^1 progeny*	Percent diapause: Male	Percent diapause: Female
d–c	0 (31)	0 (33)
c–d	0 (33)	0 (32)
c–c	0 (25)	0 (25)
d–d	100 (25)	100 (24)

*d, *C. downesi*; c, *C. carnea*; female parent indicated first.

Table 2. Diapause characteristics of progeny from F_1 hybrid × F_1 hybrid crosses, reciprocal F_1 hybrid × *C. downesi* backcrosses, and conspecific pairings (LD 16:8, 24° ± 1°C). The numbers in parentheses indicate the number of animals.

Progeny*	Percent diapause
F_1 hybrid × F_1 hybrid	
dc–dc	5.2 (96)
cd–cd	8.6 (70)
Backcrosses	
dc–dd	25.0 (52)
cd–dd	36.5 (52)
dd–dc	15.6 (45)
dd–cd	21.2 (52)
Conspecific	
dd–dd	100.0 (27)
cc–cc	0.0 (36)

*d, *C. downesi*; c, *C. carnea*; female parent indicated first.

model for sympatric speciation through seasonal isolation (*9*).

In our experiments we used the green lacewings, *Chrysopa carnea* Stephens and *Chrysopa downesi* Banks (Neuroptera: Chrysopidae), sibling species that readily hybridize under laboratory conditions (*10*) but that remain reproductively isolated in nature because of differences in their seasonal periods of reproduction. *Chrysopa carnea* is multivoltine and produces three generations each summer in the Ithaca, New York, area before the adults enter diapause in September (*11*). In contrast, *C. downesi* is univoltine, and its reproductive activity occurs only during early spring; summer, as well as autumn and winter, are spent in reproductive diapause (*12*). Underlying the seasonal differences between the two species are their characteristically different patterns of response to photoperiod (*13*).

The quantitative criteria we used for analyzing the genetic basis for the seasonal differences between the two species was based on their differential responses to photoperiod. In *C. carnea* no particular stimulus, other than long day lengths, is needed to avert diapause and allow continuous reproduction (*11*). In contrast, *C. downesi* requires an increase in day length, from short day to long day, during the late larval or pupal stages to avert diapause and promote reproduction by the emerging adults (*13*). Therefore, when individuals with a *C. carnea* genotype are reared under a light dark period of 16 hours and 8 hours, respectively (LD 16:8), reproduction begins without the intervention of diapause; however, when individuals with a *C. downesi* genotype are reared and maintained under LD 16:8, no reproduction occurs and diapause is induced. Consequently we used the numbers of diapausing and nondiapausing adult progeny from each cross (reared and maintained under an LD 16:8 photoperiodic regimen) as a quantitative measure for our analysis.

Under LD 16:8, the F_1 hybrids of reciprocal *C. carnea* × *C. downesi* crosses all showed typical *C. carnea* characteristics; that is, they reproduced without entering diapause (Table 1). Thus, the gene or genes controlling *C. carnea*'s seasonal characteristics are clearly dominant over *C. downesi*'s. Subsequent intercrosses of the F_1 hybrids produced F_2 progeny containing approximately 7 percent of individuals (both males and females) with *C. downesi*'s diapause characteristics, and the progeny (both male and female) of reciprocal backcrosses between F_1 hybrids and pure *C. downesi* stock did not differ significantly from a 1:3 (*downesi*:*carnea*) ratio when tested by chi-square ($P \geq .2$) (Table 2). These results are consistent with the ratios produced by the segregation of a pair of alleles at each of two unlinked autosomal loci; the *C. downesi* phenotype results from homozygous recessive alleles at both loci (*14*).

In summary, our results provide experimental evidence that seasonal isolation between two sympatric insect species is based on small genetic differences. These findings support the proposal that speciation in *C. carnea* and *C. downesi* occurred through seasonal isolation (*9*). We propose that analogous genetic changes may have had a similar function in allochronic speciation in other groups.

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14. We propose that each of the two recessive alleles plays a spearate role in controlling the expression of the *C. downesi*'s seasonal cycle. Homozygous *downesi* alleles at one locus probably underlie the short day–long day requirement for diapause prevention and, therefore, control the *induction* of diapause under constant long day conditions. Whereas the *downesi* alleles at the second locus probably act in diapause *maintenance* under long day conditions (*8*).
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Coevolution of Foraging in *Bombus* and Nectar Dispensing in *Chilopsis*: A Last Dreg Theory

Abstract. *Flowers of* Chilopsis linearis *dispense nectar into pools and grooves. The bumblebee,* Bombus sonorus, *extracts pool nectar at a rate seven times faster than groove nectar. The result is the coevolution of a plant-pollinator system in which bees, while foraging efficiently, increase the number of flowers visited per calorie of nectar reward provided by the plant.*

The coevolution of plants and their pollinators has received a great deal of attention. Much recent work has focused either on the coevolution of floral morphology and nectar secretion, which restricts visitors and guarantee rewards to a limited number of species (*1*), or on pollinator size, energetics, and behavior, which determine the dispersal of pollen and the nature of the plant breeding system (*2*). However, there has been little attempt to analyze the efficiency of pollinator movements in relation to optimal foraging theory (*3*) and the extent that this behavior is modified by plants. This may be due in part to the scant empirical evidence to support optimal foraging theory, even though its logic cannot be denied (*4*). The aim of this report is to demonstrate how desert willow, *Chilopsis linearis*, has taken advantage of the foraging behavior of bumblebees, *Bombus sonorus*, to increase the visitation rate to its flowers.

Chilopsis linearis is a shrubby tree 3 to 5 m tall, which occurs along dry water courses surrounded by desert scrub. It produces a profuse number of catalpalike blossoms, which secrete most of their nectar in a single peak of production before dawn (*5*). Plants of the family Bignoniaceae, of which *C. linearis* is a member, are typically pollinated by large to medium-sized bees and are thought to have a long history of morphological and phenological coevolution with their pollinators (*6*). *Bombus sonorus* queens are the most frequent visitors to desert wil-