shows heterogeneity among litters in the proportions of the two behavioral morphs. These results suggest a genetic basis for differences in slug-eating behavior, but some alternative hypotheses cannot be ruled out. A maternal effect might explain some of the results, but the prey preferences of newborn snakes apparently are unaffected by the mother's diet during gestation (*19*). Other explanations are possible, however. For example, one can construct a purely phenotypic model consistent with the results on the assumption that some snakes develop an aversion to slugs at their first exposure to this prey.

If slug-eating proves to be a heritable trait, then sympatry with slugs may be the selective force responsible for the geographic variation found. Snakes sympatric with slugs are congenitally disposed to eat them, while allopatric snakes often avoid slugs. Although the advantages of a slug-eating disposition are obvious if slugs are abundant, the disadvantage of a slug-eating trait where slugs are rare or absent is not apparent. It is possible that a slug-eating propensity causes unprofitable attacks on shelled molluscs, but I have no evidence that this occurs or represents a liability for inland *T. elegans*.

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10. Gravid females were captured in July in California at the following inland localities (the numbers of progeny from these females are indicated in parentheses): extended vicinity of Eagle Lake (Eagle Lake, Colman Lake, Papoose Creek), Lassen County, 12 (75); Gardner Meadows, Tuolumne County, 4 (15); 5.3 km south-southeast of Woodfords, Alpine County, 2 (11); and at the following coastal localities: 8 km south-southwest of Orick, Humbolt County, 7 (60); Scott Creek, 16 (221), and Waddell Creek, 1 (12), in San Mateo and Santa Cruz counties.
11. Gravid females and newborn snakes were maintained at 27°C. All snakes were individually housed in plastic cages (15 by 30 by 9 cm) with a paper towel substrate and a water dish. Newborn snakes were separated from their mothers within 18 hours of birth and moved to individual cages.
12. Newborn *T. elegans* cannot eat adult *Ariolimax* because of the large size of these slugs. Consequently, *Ariolimax* were frozen, and the body wall was cut into pieces of uniform size (5 by 10 mm). One freshly thawed piece was then placed on the paper substrate of each cage.
13. The snakes were fed dead tree frog tadpoles (*Hyla regilla*) twice each week during the interval between the second and third slug trials. Frozen tadpoles were thawed for 20 minutes before presentation.
14. Frozen supplies of both control food species were thawed just before presentation. Two control species were used because *B. boreas* was initiated as a control, and the supply of this species was insufficient for the entire experiment. Consequently both *B. boreas* and *H. regilla* were used as controls for both groups at trials 1 and 2, but only *H. regilla* was used for trials 3 and 4. Each snake received only one of the two control foods after each slug trial.
15. The ten slug presentations began 8 days after trial 4 of experiment 1, so the age of the snakes ranged from 11 to 14 weeks.
16. *Ariolimax* preparation has been described (*12*). *Deroceras* were killed by freezing and presented whole after a thawing period of 20 minutes. Pieces of *Ariolimax* (0.28 ± 0.06 g) and whole *Deroceras* (0.29 ± 0.08 g) were approximately the same size (means and standard deviations are for samples of 10). Both types of slugs were placed in each cage simultaneously and 5 cm apart.
17. The test was conducted 19 days after the final slug presentation in experiment 2. The snakes were fed dead tree frog tadpoles (*H. regilla*) on five occasions during the interim period. The last maintenance feeding occurred 5 days before the test.
18. The data were tested using the McNemar test for significance of change [R. R. Sokal and F. J. Rolf, *Biometry* (Freeman, San Francisco, 1969), pp. 614–615]. Of 59 Eagle Lake snakes, 22 ate both *Deroceras* and *Ariolimax*, 3 refused *Deroceras* but ate *Ariolimax*, 6 ate *Deroceras* but refused *Ariolimax*, and 28 refused both types of slugs ($\chi^2 = 0.44$, d.f. = 1, $P > .05$). For 148 Scott Creek snakes, the comparable data are 134, 7, 4, and 3 ($\chi^2 = 0.36$, d.f. = 1, $P > .05$). Thus, at neither locality can we reject the hypothesis that the proportion of snakes eating slugs is identical for both slug genera.
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Resource Partitioning in Bumble Bees: The Role of Behavioral Factors

Abstract. *Small* Bombus ternarius *workers forage most frequently on the distal parts of goldenrod flower clusters when large* B. terricola *workers are present. This shift results from* B. ternarius *avoiding* B. terricola. *In this way* B. ternarius *can exploit, without conflict, resources whose availability changes constantly because of fluctuating numbers of larger consumers.*

Many ecologists believe that changes in feeding or habitat by animals often result directly from interactions among individuals (*1*, *2*). However, they have made few efforts to test this hypothesis experimentally with controls under natural conditions (*3*), given its potential importance in structuring communities (*1*, *2*). Further, none of the latter studies unequivocally show the mechanism responsible for the observed changes. Here I demonstrate shifts in the use of resources by bumble bees (*Bombus* spp., Apidae) in response to congeners and the mechanism by which it takes place.

I tested individually marked (*4*) *B. ternarius* Say workers in the presence and absence of *B. terricola* Kirby workers on Canada goldenrod (*Solidago canadensis* L.), the major food source of bumble bees along the Maine coast in mid-August. The shallow florets of this plant can be categorized as proximal, medial, or distal depending on their position in a continuum from the central stalk of the flower cluster to its exterior (Fig. 1).

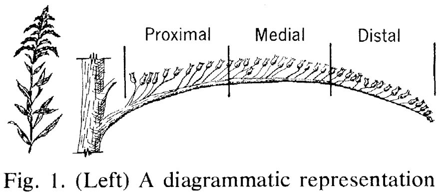

Fig. 1. (Left) A diagrammatic representation of a goldenrod plant with its flower cluster (inflorescence). (Right) Branch of a goldenrod flower cluster showing the parts recognized: proximal, medial, and distal. When the flower cluster is in full bloom the proximal and distal parts often lie at an angle to the horizontal, and the medial part is essentially horizontal in a position superior to the other parts. Each of the three divisions contains a similar number of florets.

Goldenrods were regularly visited for nectar by both species of bees. Workers of a wide size range feed from the same florets, but they seldom make bodily contact or near contact with each other. Given these conditions and the knowledge that individuals of large species usually are behaviorally dominant to those of small ones (*2*), I predicted that large *B. terricola* workers (the largest bees regularly visiting goldenrod) would replace *B. ternarius* workers, which were among the smallest bumble bees visiting the goldenrod.

Cages (1 m^3) of coarse window screening were placed over a group of ten goldenrod plants, each with flower clusters of several hundred florets. Immediately, I introduced a marked *B. ternarius* worker that had just been captured in the field. After 30 seconds, I recorded the location of the next 50 florets that it visited. Ten *B. ternarius* were tested in this way.

About one-third of the bees would not forage on the caged flowers and were immediately released. Others commenced foraging immediately and often continued to do so for more than 10 minutes, well in excess of the experimental period.

Table 1. Foraging scores of *Bombus ternarius* workers on 50 florets of goldenrod flower clusters. Each floret visited on the proximal part of the flower stalks was scored 3; each medial observation, 2; and each distal observation, 1. The basis for scoring is illustrated in Fig. 1. Each score is the mean ± the standard error of the mean. (Experiment A) Foraging of individual *B. ternarius* workers on goldenrod in cage before and after introduction of three *B. terricola* workers. (Experiment B) Same as experiment A, except that the second measurement was taken with no *B. terricola* present. (Experiment C) Foraging of *B. ternarius* in cage and when flying free in the field. (Experiment D) Foraging of *B. ternarius* in cage when no *B. terricola* had foraged there immediately previously, and immediately after *B. terricola* had foraged in cage.

Treatment	*N*	Score	*P*
	Experiment A		
Before *B. terricola* added	10	96.1 ± 1.7	.005*
After *B. terricola* added	10	79.4 ± 1.8	
	Experiment B		
Before *B. terricola* added	12	90.4 ± 1.9	.003*
No *B. terricola* added, 5 minutes later	12	99.1 ± 3.0	
	Experiment C		
Before *B. terricola* added	12	96.4 ± 2.1	>.05*
Flying free in field	12	92.9 ± 2.8	
	Experiment D		
No *B. terricola* present immediately before	15	92.1 ± 1.7	>.05†
B. terricola present immediately before	7	92.7 ± 2.0	

*Two-tailed Wilcoxon test. †Two-tailed Mann-Whitney U test.

After a *B. ternarius* completed an initial foraging run, I added three large *B. terricola* workers to the cage, a density commonly encountered in the field. Three minutes later I counted the next 50 florets visited by the just-tested *B. ternarius*. After the last foraging run, all individuals were released. The 3-minute period should ensure that the forager perceived the presence of the newly introduced bees. Six of the same *B. ternarius* were recaptured on a following day and tested as before, except that no additional *B. terricola* were introduced prior to the second run of observations. This second observation period corresponded to the time at which the *B. terricola* were introduced in the first experiments and should control for possible cage effects. I also tested six previously untested *B. ternarius* in this way to ensure that results obtained in the reruns did not derive from habituation. Last, I obtained similar data from 12 of the same *B. ternarius* when they foraged in the field under unrestrained conditions. Groups were pooled where appropriate when they did not differ among themselves. The flowers were left uncaged except during tests.

The *B. ternarius* individuals (entire wing length, 8.2 to 9.7 mm) (*5*) foraged significantly more distally when with *B. terricola* workers (entire wing length, 12.5 to 14.0 mm) than they did when alone (Table 1, experiment A). This shift occurred even though both previously tested and untested *B. ternarius* foraged significantly more proximally in the second foraging period than in the first when the experiment was run without *B. terricola* (Table 1, experiment B). Because this trend counters the one seen when *B. terricola* were introduced, it strengthens the argument that the foraging changes in the first experiment resulted from the presence of *B. terricola*. Outside of the cages the bees tested did not visit florets significantly differently from the way that they foraged when in cages without *B. terricola* (Table 1, experiment C). The results support the hypothesis that large *B. terricola* workers spatially displace *B. ternarius* workers, demonstrating experimentally a shift of resource use resulting from behavioral interactions.

Bombus ternarius probably forage most distally in the presence of large *B. terricola* because of the latter's rather low use of the pendant branch tips, an area in which they feed with difficulty because the ends of these branches will not support their weight. Small *B. ternarius*, on the other hand, crawl over this part without apparent difficulty (*6*). Only 14.0 percent of the florets visited by *B. terricola* outside of the cage were in this area, as compared to 38.4 percent for *B. ternarius* ($P < .001$, one-tailed Mann-Whitney U test on original data; $N_1 = 7$, $N_2 = 10$). The tendency for *B. ternarius* to feed more proximally in the absence of *B. terricola* probably ensures that *B. ternarius* obtain the greatest rewards then, since they appear equally adept at foraging on all parts of a flower cluster. Feeding more proximally over time when *B. terricola* is absent could result from initially exhausting the resources of first-encountered distal florets.

I saw no overt aggressive behavior; however, on three occasions a *B. ternarius* quickly vacated a flower cluster when a *B. terricola* began to feed on the same branch. I then compared the foraging patterns of *B. ternarius* alone in the cage immediately after foraging bouts by *B. terricola* and when alone in the cage when *B. terricola* had not preceded them. No significant difference occurred (Table 1, experiment D). If *B. ternarius* were only avoiding the sites where *B. terricola* fed because *B. terricola* had exhausted the resources there, *B. ternarius* should have foraged more distally in the runs following *B. terricola*'s presence. These data point strongly to active avoidance of *B. terricola* as the major factor causing *B. ternarius* to shift its foraging location. Active avoidance probably is not uncommon in animals (*2*, *7*); however, it usually is difficult to demonstrate, and I know of no other experimental tests that occur in the context of resource partitioning.

Bombus ternarius workers thus possess considerable phenotypic plasticity in their foraging repertoire, a highly advantageous trait for animals that meet a diversity of other foragers, many of which are behaviorally dominant to them (*2*), and which experience food sources whose reward size and physical characteristics are changing constantly in time (*8*). Their avoidance of physically superior individuals eliminates the probably fruitless expenditure of time and energy that would occur if they did not give way; on the other hand, they retain the ability to exploit these resources when other individuals are not present (*2*).

This report deals with only the *Bombus* species with the smallest and largest workers that frequent goldenrod in the study area. One might predict that spatial relationships between the other segments of the guild (for example, small *B. terricola* workers and large *B. ternarius* workers, which may overlap in size) will not be as clearly delineated as those reported above.

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Toxicity of Mild Prenatal Carbon Monoxide Exposure

Abstract. *Rats prenatally exposed to a low concentration of carbon monoxide which results in carboxyhemoglobin levels equivalent to those maintained by human cigarette smokers, show reduced birth weight and decreased weight gain. Neurobehavioral and biochemical testing of the offspring reveals lower behavioral activity levels through the preweaning period, altered central catecholamine activity, and reduction in total brain protein at birth.*

Irreversible central nervous system damage reflected in widespread necroses and ultrastructual changes (*1*), alterations in cerebral energy production or metabolism (*2*), and depression of neurotransmitter synthesis or turnover (*3*) have all been reported following acute hypoxic or anoxic exposures. Such findings are useful in predicting the pattern of neurological changes that may result from asphyxia accompanying obstetric procedures and cerebrovascular accidents. Comparatively little is known about the effects of chronic hypoxia at levels relevant to human experience. This may result from natural causes such as high altitude and man-made causes such as chronic carbon monoxide exposure induced by cigarette smoking and industrial sources. We have concentrated on the effects of CO exposure during the prenatal period. Carbon monoxide readily crosses the placenta, and mild maternal exposures in animals result in decreased fetal oxygen partial pressures in the descending aorta and inferior vena cava (*4*). Rats and rabbits prenatally exposed to high-altitude conditions or to CO show a variety of abnormalities at birth, including reduced birth weight (*5–7*), heart hypertrophy (*7, 8*), and reduced brain protein levels suggestive of smaller neurons (*9*). There is evidence, too, that mild prenatal CO exposure in rabbits may be teratogenic (*5*). The long-term consequences of these effects as well as their functional significance have not been elucidated. Moreover, studies of central nervous system toxicity following chronic CO exposure are lacking.

Table 1. Growth rate of preweanling rats exposed prenatally to CO [150 parts per million (ppm)] or to air. Values are given as mean ± standard error of the mean (S.E.M.).

Treatment	Body weight (g)				
	Day 1	Day 4	Day 10	Day 14	Day 21
Air	5.77 ± 0.05	9.68 ± 0.2	21.82 ± 0.34	27.16 ± 0.6	45.81 ± 0.77
CO	5.49 ± 0.05	8.16 ± 0.17†	18.19 ± 0.45*	24.40 ± 0.42†	39.90 ± 1.5*

*Significantly different from comparable control group at $P < .01$. †Significantly different from comparable control group at $P < .05$.

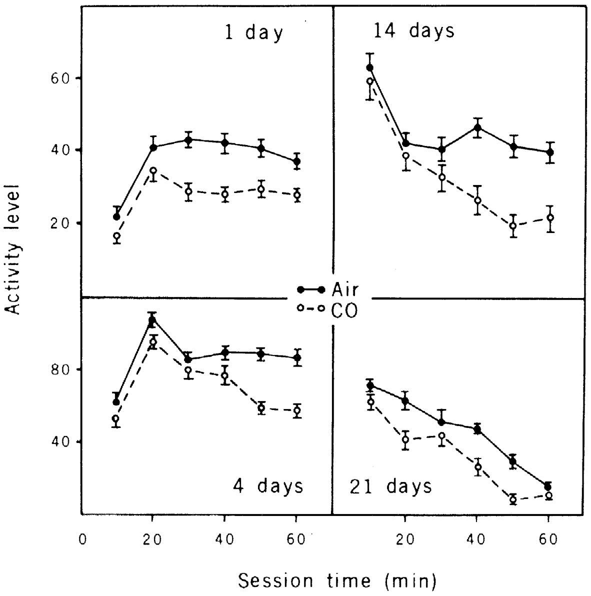

Fig. 1. Open-field activity levels of rats exposed prenatally to CO concentrations of 150 parts per million (ppm) or to room air. Subjects 1 and 4 days old were injected with L-dopa (100 mg/kg) at time zero. Subjects 14 and 21 days old were not injected. Activity was averaged across 10-minute intervals for a 1-hour period.

Maternal cigarette smoking and domicile at high altitude are major causes of chronic prenatal hypoxia. Both conditions represent important risk factors, having been associated with excess prenatal mortality (*10, 11*), premature (preterm) birth (*10–12*), and decreased birth weight (*10, 13*). Experimental evidence (*5*) confirms that these sequelae are related to the hypoxic exposure in a dose-related manner regardless of the source of hypoxia (CO or diluting air with nitrogen). We report here that chronic prenatal exposure of rats to CO has behavioral, neurochemical, and physiological consequences which last well beyond birth and that these effects are measureable at CO levels approaching those experienced by offspring of mothers who smoke.

Adult female Long-Evans hooded rats were maintained in the laboratory with continuous access to food and water, a diurnal light cycle (12 hours light, 12 hours darkness), and room temperature at 22°C. The rats were bred and, after a sperm-positive vaginal smear, were transferred to exposure chambers for the duration of gestation. Spectrophotometric measurements (*14*) were used to verify that maternal carboxyhemoglobin (HbCO) concentrations of 15 percent resulted among the subjects exposed to CO. By comparison, human cigarette smokers show HbCO concentrations ranging from about 1 to 16 percent (*15*).

Within 12 hours after birth the subjects were removed from the exposure chambers and placed in a normal air environment. The neonates were counted, weighed, and examined for superficial deformities. Litter sizes were then ad-