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and *B. Pennsylvanicus***

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## INTRASPECIFIC RESOURCE PARTITIONING IN THE BUMBLE BEES *BOMBUS TERNARIUS* AND *B. PENNSYLVANICUS*<sup>1</sup>

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**Abstract.** I tested for an association between intraspecific size differences and differences in resource utilization in worker bumble bees (*Bombus ternarius* and *B. pennsylvanicus*). Bees were observed foraging in two old fields in Minnesota where flower species with short corollas and species with long corollas occurred in both single-species and mixed-species stands. In mixed-species stands, foragers on the species with short corollas were found to have shorter proboscides than conspecific foragers on the species with long corollas. However, proboscis lengths of foragers on the species with long corollas in single-species stands did not differ from those on the species with a short corolla in single-species stands. Thus, where a choice exists, bumble bee foragers select the species having a corolla most compatible to their proboscis length. I then compared conspecific foragers on a single flower species in one-species versus mixed-species stands. For foragers on flowering species with a short corolla, proboscis length was significantly shorter in the mixed-species than in the single-species stand, but this difference was not found for the species with a long corolla. Thus, presence of other flowering species can influence the pollinator population of a species, relative to a single-species stand.

Resource choice by foragers was analyzed using a probability function, calculated as the ratio of foragers with a given proboscis length on the species with a long corolla to the number with that proboscis length collected on both species. The shape of the probability function was fitted to a sigmoidal curve using probit analysis. Regression of the linearized probabilities was significant. This procedure is a better measure of intra- or interspecies association than are measures such as niche overlap, because it quantifies a continuous distribution and accounts for variance in the species distribution.

**Key words:** *Bombus*; bumble bees; corolla length; foraging; intraspecific resource partitioning; large and small workers; probit analysis; proboscis length; sigmoidal curve.

### INTRODUCTION

Optimal foraging theory predicts that animals harvest food to maximize net energy gain or to minimize foraging time (Emlen 1966, Schoener 1971, Pyke et al. 1977). Energetic gain is often maximized by selecting a limited range of available prey items (Kislalioglu and Gibson 1976, Inouye 1980), with size of the feeding apparatus determining size of the food particles ingested (Hutchinson 1959, Hespeneide 1966, Schoener 1974). Little information is available on how intraspecific differences affect resource selection (but see Selander 1966, Storer 1966, Schoener 1967, 1977, Earhart and Johnson 1970, Pianka 1973, Rissing 1981, Polis 1984), although studies demonstrating that similar species differ in spatial or temporal resource use suggest that intraspecific differences might also lead to differential resource utilization (MacArthur 1958, Holm 1966, Morse 1977, Werner 1977, Inouye 1980).

Bumble bees are excellent for examining differences in resource selection because: (1) there is variation in size, especially in the length of the proboscis, which is used to gather nectar, (2) the morphological traits in-

involved are easily measured, and (3) resources are chosen individually and not by recruitment (Heinrich 1979a).

Previous studies show a correlation between corolla length and proboscis length of bumble bees foraging in mixed-species stands (Brian 1957, Hobbs et al. 1961, Hobbs 1962, Inouye 1978). I extended such studies by examining intraspecific correlations between proboscis length and corolla length using *Bombus ternarius* and *B. pennsylvanicus* (Apidae). Two hypotheses were tested: first, in two-species stands, one species with short and the other with long corollas, proboscis length of foraging workers is positively associated with corolla length; second, proboscis length is not associated with corolla length when comparing single-species stands of different corolla length.

### METHODS

I collected *Bombus ternarius* in two old-field sites (Knoll's and Lagoon) at Itasca State Park, Minnesota, for 2 wk in August 1980. Criteria for selecting a site were that two flowering species with quite different corolla lengths predominated in the area and dispersion of each species was random throughout the site. The species at Knoll's were Spotted Knapweed (*Centaurea maculosa*) and White Sweet Clover (*Melilotis alba*), and at the Lagoon, *M. alba*, Yellow Sweet Clover

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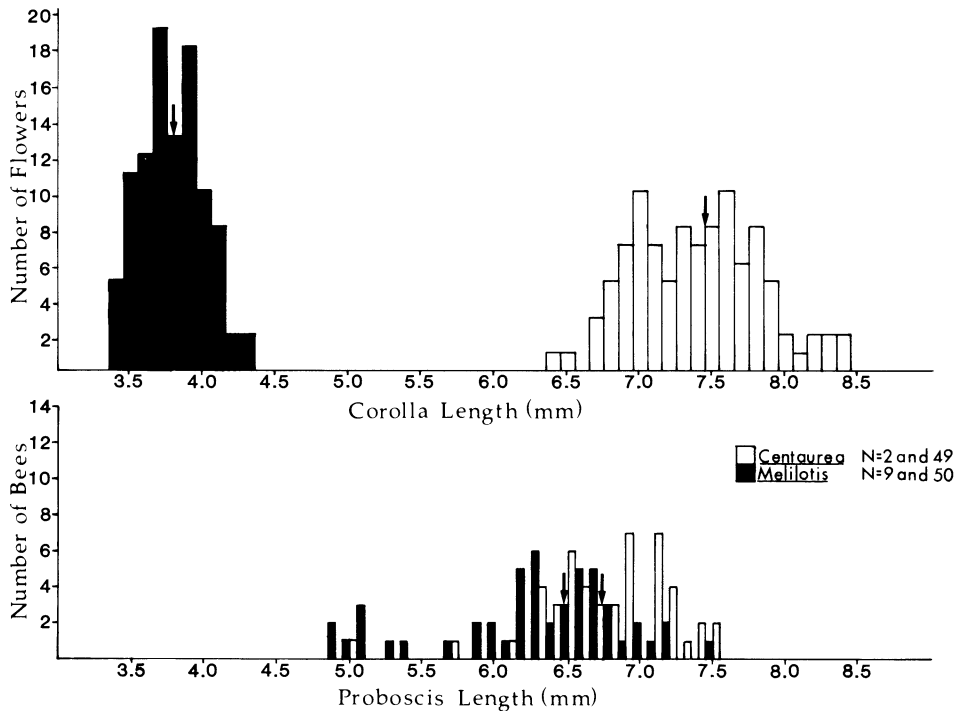


FIG. 1. Frequency distributions of corolla lengths of flowers visited by *Bombus ternarius*, and proboscis lengths of the bees visiting them, at Knoll's old field site during 1980. *N* gives the number of small workers and the total number of bumble bees collected on each species, respectively. ■ the species with a short corolla and bumble bees captured thereon. □ the species with a long corolla and bumble bees captured thereon. Arrows indicate population means. Bumble bee population means omit the small workers.

(*M. officinalis*), and Blue Giant Hyssop (*Agastache foeniculum*). The two *Melilotis* species at the Lagoon were treated as one flower class since they only differed in color and were visited indiscriminately by bumble bees. The *Melilotis* species was the species with a short corolla at each site; either *A. foeniculum* or *C. maculosa* was the species with a long corolla.

During one week in August 1981, I compared flower selection by *B. pennsylvanicus* in single- and mixed-species stands of *A. foeniculum* (long corolla) and goldenrod (*Solidago canadensis*) (short corolla) in the vicinity of the Lagoon.

Prior to collection, all bees were followed until they had consecutively visited inflorescences on 5–10 conspecific plants. Additional evidence for flower constancy was the observation that bumble bees flew over flowers of the second species to visit their preferred flower.

After collection, bumble bees were placed in 70% aqueous ethanol; proboscides were dissected and measured (to the nearest millimetre) with an ocular micrometer at 10 $\times$  using a binocular microscope. Proboscis measurements included the prementum and glossa (see Inouye 1980). Corolla lengths of all species in both years were measured (10 florets from each of 10 inflorescences) with an 8 $\times$  hand micrometer. Corolla length was measured from the base of the nectary to the base of the corolla limb, i.e., the corolla tube.

Bumble bees of two size groups occurred in the collections, a finding which agrees with previous studies (Cumber 1949, Brian 1952, Free 1955). Large workers are consistent foragers, while small workers are inconsistent foragers. Small workers may be "house bees" that maintain the nest and are not normally foragers, or, alternatively, older workers that emerged from early broods, which produce small individuals (D. Inouye, *personal communication*). The two size groups were separated by graphing the cumulative normal distribution of all individuals at a site over a range of possible break points (Sokal and Rohlf 1981). The points giving the best graphical fits were 5.8 mm for *B. ternarius* and 6.4 mm for *B. pennsylvanicus*. An individual with a proboscis length equal to or above the break point for its species was regarded as a forager; others were treated as small workers. The two groups were analyzed separately in order to take into account possible behavioral differences.

At each site, corolla lengths of the two species were compared, and proboscis lengths of bumble bees visiting those species were compared, by *t* tests. A *t* test, however, assesses sample differences using the mean and standard error, and does not examine the relation between two continuous distributions. Similarly, intraspecific niche overlap (Colwell and Futuyma 1971) is a discrete comparison of two continuous distributions. I used a continuous probability function to ex-

amine the distributions with respect to intraspecific resource partitioning.

Intraspecific resource partitioning was examined at each site by calculating the probability of foragers of each proboscis length visiting the species with a long corolla. This was the number of foragers of a particular proboscis length observed on the species with a long corolla divided by the number of foragers of that proboscis length on both species.

The shape of the probability function was compared to a sigmoidal curve using a probit analysis (SAS; Barrett et al. 1979). Probit analysis assumes a threshold (proboscis length) below which a response (selection of a particular flower species) does not occur and above which it always occurs. Under this assumption a bumble bee with a proboscis above the threshold length should always visit the species with the long corolla, while a bee with a proboscis below the threshold should always visit the species with the short corolla. The intermediate portion of the function is nearly linear.

Similarity between the data and a sigmoidal curve was assessed by a chi-square test. Sigmoidal parameters were calculated by maximum likelihood estimates of the intercept, slope, and natural (threshold) response rate using a modified Gauss-Newton algorithm. Probability values  $<.05$  indicate the data are significantly different from a sigmoidal curve. Increasing probability values indicate the data are more sigmoidal. These probabilities can be linearized using a probit transformation (Finney 1971). Regression analysis of linearized data provides a goodness-of-fit measure for the

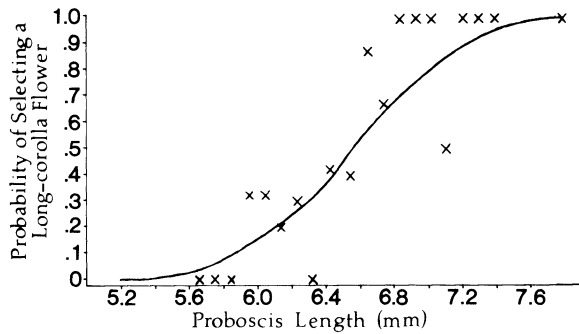


FIG. 3. Probability of selecting a flower species based on a given proboscis length. These data (from the Lagoon old field site during 1980) demonstrate the continuity of the flower selection response, and are compared with a calculated sigmoidal curve.

model. Thus, probit analysis was used to examine the entire gradient of response to corolla length in a single statistic, with a subsequent regression of linearized probabilities quantifying the function in a simplified statistical manner, as well as accounting for variance in the probability of flower choice.

RESULTS

1980

Corollas of *Melilotis* were shorter than those of *Centaurea maculosa* at Knoll's ( $t$  test,  $P < .001$ ; Fig. 1) and *Agastache foeniculum* at the Lagoon ( $P < .001$ ; Fig. 2). Similarly, proboscis length of *Bombus ternarius*

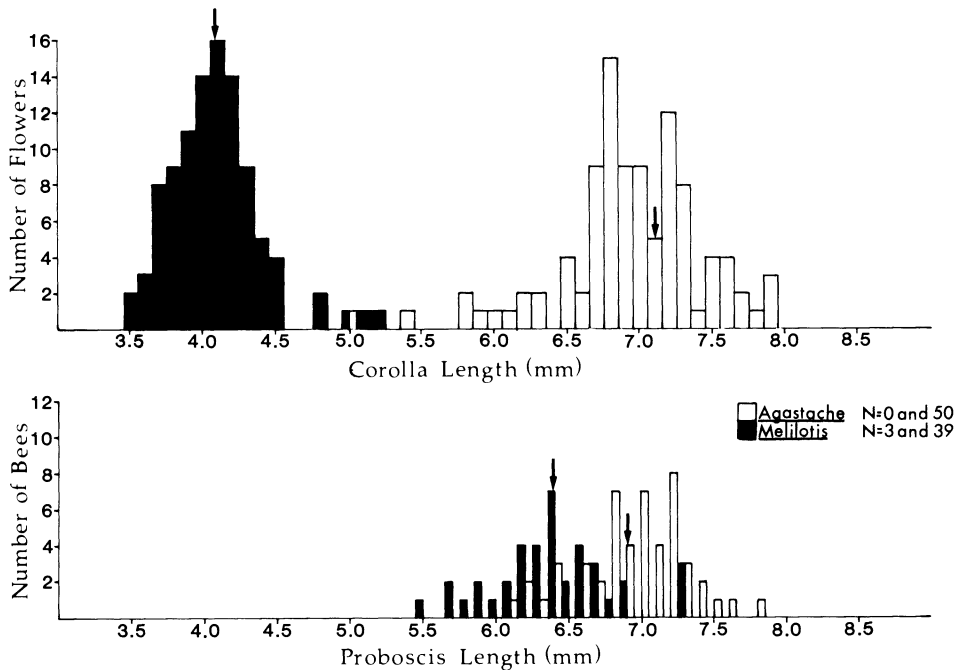


FIG. 2. Frequency distributions of corolla lengths of flowers visited by *Bombus ternarius*, and proboscis lengths of the bees visiting them, at the Lagoon old field site during 1980. Symbols as in Fig. 1.

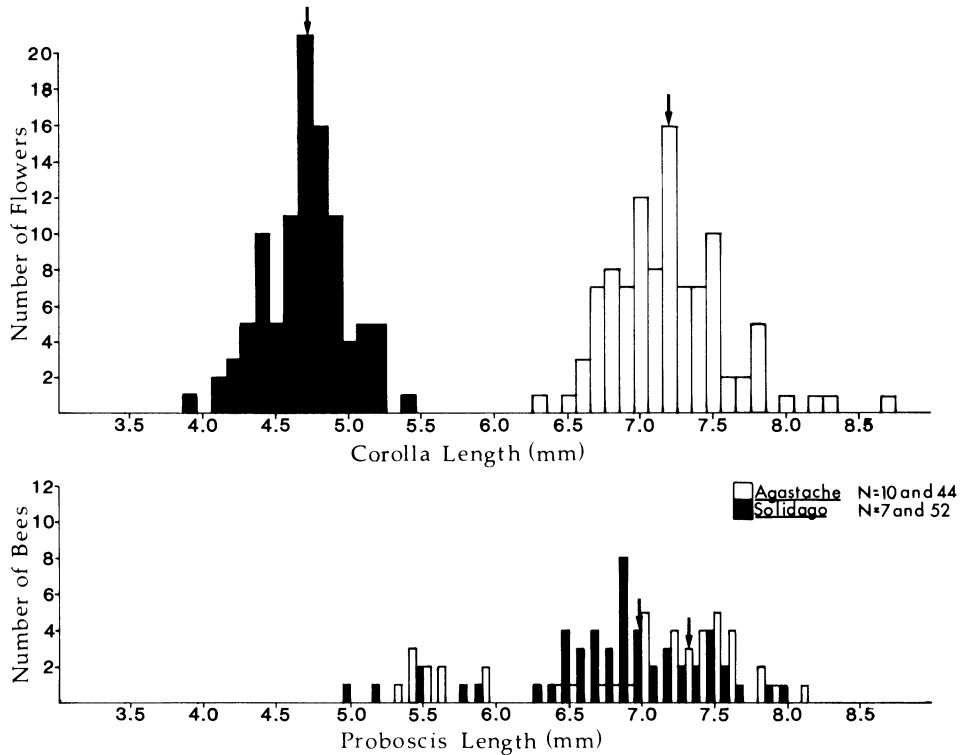


FIG. 4. Frequency distributions of corolla lengths of flowers visited by *Bombus pennsylvanicus*, and proboscis lengths of the bees visiting them, in the mixed-species stands during 1981. Symbols as in Fig. 1.

foragers was shorter on *Melilotis* than on *C. maculosa* (Knoll's:  $P < .001$ ; Fig. 1) or *A. foeniculum* (Lagoon:  $P < .001$ ; Fig. 2). There were too few small workers for statistical analyses (Lagoon,  $N = 3$  bees; Knoll's,  $N = 11$  bees; see Figs. 1 and 2).

The probability function of flower choice is not different from a sigmoidal curve for either site (Knoll's:  $P < .31$ ; Lagoon,  $P < .21$ ; Fig. 3), indicating a continuous and unidirectional change in the probability of flower selection with change in proboscis length. Regression of the linearized probabilities (probit-transformed values,  $Y$ ) with proboscis length ( $X$ ) was significant (Knoll's:  $Y = 0.19X + 5.69$ ,  $R^2 = 0.47$ ,  $N = 17$  proboscis lengths,  $P < .01$ ; Lagoon:  $Y = 0.23X + 5.41$ ,  $R^2 = 0.75$ ,  $N = 20$ ,  $P < .001$ ), giving a quantification of the entire gradient of intraspecific flower selection. The slopes of the two regression lines did not differ significantly ( $P > .05$ ).

#### 1981

Corollas of *S. canadensis* were shorter than those of *A. foeniculum* in mixed-species ( $t$  test,  $P < .001$ ) and single-species ( $P < .001$ ) stands (Figs. 4 and 5). Similarly, in mixed-species stands, proboscis length of *B. pennsylvanicus* foragers was shorter on *S. canadensis* than on *A. foeniculum* ( $P < .005$ ). However, proboscis length of foragers did not differ among stands (Duncan's multiple range test,  $P > .05$ ), which suggests that partitioning occurs within each stand.

I then compared conspecific foragers on a single flower species in one-species vs. mixed-species stands. For *B. pennsylvanicus* foraging on *S. canadensis*, mean proboscis length was significantly less ( $P < .04$ ) in mixed-species stands; this difference did not exist on *A. foeniculum*. Corolla length of *S. canadensis* in the mixed-species stand was also significantly shorter than in single-species stands ( $P < .001$ ; variances unequal,  $P < .003$ ). Proboscis lengths of small workers did not differ between flower species with short and long corollas in single- or in mixed-species stands. There were too few small workers for further statistical analysis (two-species stands,  $N = 17$  bees; single-species stands,  $N = 22$  bees; see Figs. 4 and 5).

*Bombus pennsylvanicus* foragers fit the sigmoidal function in the mixed-species stands ( $P > .50$ ) but not in the single-species stands ( $P < .05$ ). Similarly, regression of the linearized probabilities with proboscis length was significant in mixed-species ( $Y = 0.20X + 6.27$ ,  $R^2 = 0.38$ ,  $N = 18$  proboscis lengths,  $P < .01$ ) but not in single-species stands. This indicates that a bumble bee species partitions flower species based on proboscis length in mixed-species stands but not in isolated single-species stands.

#### DISCUSSION

My data support the hypothesis that bumble bees foraging in a mixed population of plants, some with short and others with long corollas, segregate intra-

specifically such that those with short proboscides visit short corollas and those with long proboscides visit long corollas. Whereas previous studies focused on interspecific resource partitioning, my work demonstrates intraspecific resource partitioning for workers of both *B. ternarius* and *B. pennsylvanicus*. There was no evidence of discrimination between single-species stands differing in corolla length. However, proboscis length of bees foraging on a given species may vary between single- and mixed-species stands, indicating that the presence of other flowering species can influence the pollinator population relative to a single-species stand.

Intraspecific partitioning of floral resources is advantageous to the bumble bee colony. Size-related foraging differences among individuals could maximize the colony's overall efficiency of resource exploitation (see Morse 1978), since handling time per flower (Holm 1966, Inouye 1977, Harder 1983) and nectar extraction efficiency (Harder 1983) are a function of proboscis length relative to corolla length. Such foraging may also increase the colony's production of offspring (Strickler 1979).

Unlike larger foragers, small workers did not select a flower species based on proboscis length. This difference may have resulted from the inexperience of small workers that had never foraged (house bees) or had foraged only briefly before returning to nest duties (older workers). It is likely that the small workers had

recently abandoned nest duties to assume foraging duties (Richards 1946, Brian 1952, Free 1955, Miyamoto 1959), perhaps due to food shortages caused by depletion of foragers, and had not yet developed flower constancy (see Heinrich 1979b).

Change in an area's flowering species should modify the probability of visitation of a given species by a forager of given proboscis length. The shape of the probability function should change concomitantly. During 1980 the regression slope at the Lagoon was steeper than at Knoll's because mean corolla length of the two species was more similar at the Lagoon (Figs. 1 and 2). Obtaining significantly different regression lines may be difficult without a large sample size due to large variance in the frequency distribution.

Measuring individuals on each resource rather than obtaining a species mean and standard deviation on several resources permits better resolution of foraging behavior than was achieved in previous studies that considered the foraging species as a whole (see also Wilson 1975). There is a consensus that bumble bees with short proboscides visit flowers with short corollas and bees with long proboscides may visit flowers with both short and long corollas (Heinrich 1976, Ranta and Lundberg 1980). If my results are generally applicable, the pattern exhibited by bees with long proboscides may reflect intraspecific resource partitioning based on the relative fit of corolla and proboscis.

Use of probit analysis and regression can also quan-

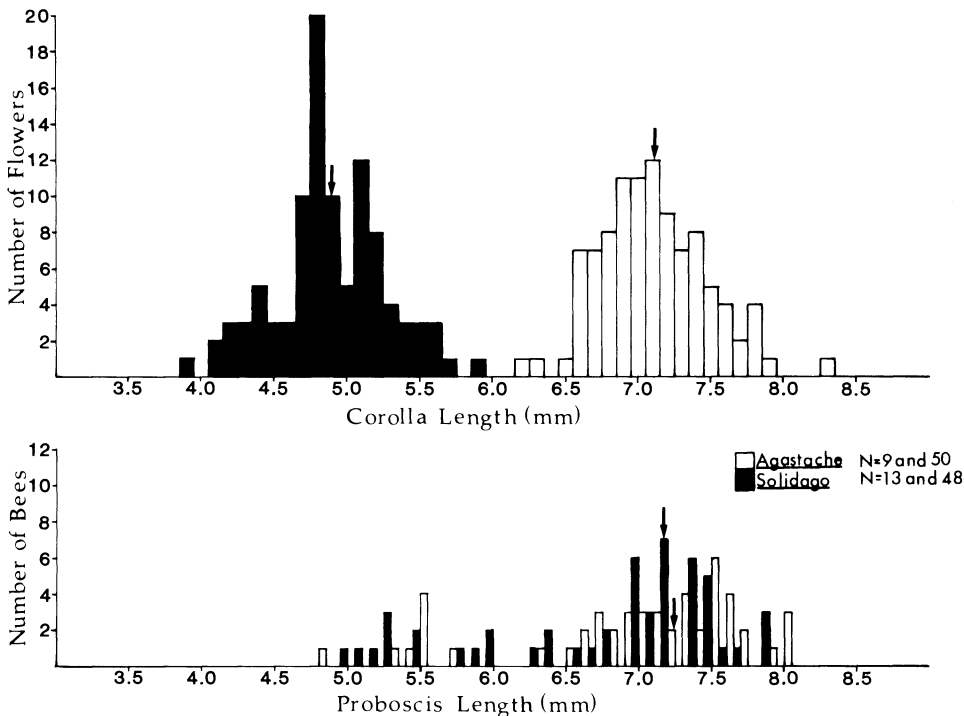


FIG. 5. Frequency distributions of corolla lengths of flowers visited by *Bombus pennsylvanicus*, and proboscis lengths of the bees visiting them, in the single-species stands during 1981. Symbols as in Fig. 1.

tify interspecific resource partitioning where distribution of prey size could be the resource continuum and the regression slope a measure of similarity between pairs of predator species. This procedure is a better measure of association than are measures such as niche overlap because it quantifies a continuous distribution and accounts for variance in the species interaction.

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