COMPARATIVE FLIGHT DYNAMICS OF KNAPWEED GALL FLIES *UROPHORA QUADRIFASCIATA* AND *U. AFFINIS*(DIPTERA:TEPHRITIDAE)

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Abstract

By using laboratory flight mills, I tested the hypothesis that the differential distributions of knapweed gall flies, *Urophora quadrifasciata* and *U. affinis*, among knapweed sites can be predicted by the flight propensity and endurance of the flies. Results from tests did not support the prediction that the former species displays the greater propensity for flight and endurance. I discuss several reasons supporting the values obtained and their validity for use in interspecific comparisons. Finally, I point to the danger of extrapolating laboratory behaviour to the field.

INTRODUCTION

The distribution of insects in space is likely to be some function of the distribution of their resources (Karieva 1985) as well as their propensity (Jones 1977; Roitberg *et al.* 1984) and ability (Ralph 1977; Roitberg *et al.* 1979) to move among resources and resource sites.

An apt example of differential distribution among similar resource sites is represented by two species of palaearctic tephritid flies in British Columbia. The larvae of *Urophora quadrifasciata* (Meigen) and *U. affinis* Frauenfeld induce galls and feed within the seed heads of diffuse knapweed (*Centaurea diffusa* Lam.). Adults of both species were released into knapweed-infested sites in the interior of BC during the early 1970's to control the spread of this highly pestiferous host (Harris and Myers 1984). Following release, however, each species has displayed different spatial distributions, within and between sites. *Urophora affinis* typically achieves moderately high population levels and low rates of spread between sites. By contrast, *U. quadrifasciata* is generally found at low population densities, but spreads rapidly and can be found at remote resource sites (Harris and Myers 1984; Story and Nowierski 1984). Within-site differences in the spread of these flies has been explained in terms of differential use of seed heads (Berube 1980). Here, I propose an hypothesis to explain the different inter-site spread rates of the two species:

H_a : *Urophora quadrifasciata* displays greater flight propensity and endurance than *U. affinis*.

If it was supported, this hypothesis could explain differential fly distribution purely on the basis of emigration tendency. Such differences have been demonstrated among closely related species of milkweed bug and in different geographic populations within the same species (Dingle 1978). In this paper, I describe a test of the differential flight hypothesis that uses laboratory flight mills.

MATERIALS AND METHODS

All experiments were conducted in the laboratory with wild-type, lab-maintained flies. To obtain the flies, knapweed seed heads were collected during November 1985 from roadsides near Penticton, BC. The seed heads, some of which were infested with overwintering *Urophora* larvae, were then held at 2°C for several months. Following this, the seed heads were held at *ca.* 20°C for several weeks until the flies emerged. Emergent flies were placed in 15 X 15 X 15 cm plexiglas-screen cages and were provided with water and food (sugar + enzymatic yeast hydrolysate (Prokopy and Boller 1971)) ad lib, and knapweed stems which served as resting and mating sites for the flies.

Upon reaching 11 ± 1 days-of-age, mature female flies were removed from the maintenance cages and then placed in petri dishes with water and abundant food for 2 h prior to testing. Then the flies were individually placed in glass vials and held at -5°C for *ca.* 30 s or

until they became immobile. The chilled flies were then attached at the dorsal thorax, to flight mills as described in Roitberg *et al.* (1984). Tarsal contact was provided by a glass microscope slide. To induce flight, tarsal contact was removed within a few seconds after it appeared that the flies had recovered from chilling. If no flight occurred, tarsal contact was reinstated and then again removed. If the fly still did not initiate flight, that trial was terminated. Similar procedures were employed to induce further flight from flies that initiated but terminated flights.

I chose 11-day-old females for testing because, at that age, flies had mated and had been reproductively mature for several days. Since flies had been deprived of oviposition sites I reasoned that they would be more likely to display flight response (e.g. Roitberg *et al.* 1984) thus providing a larger data base for comparing fliers of both species. This was an appropriate decision since my comparison of flight parameters were not absolute measures of field performance.

Flight propensity was indexed as the distance flown by individuals (number of 1 m revolutions) during the initial flight only. Flight endurance, by contrast, was indexed as the total distance flown until individuals refused to fly further following two tarsal-contact removals.

Following completion of each flight trial, the fly was frozen and then placed in a desiccator. Desiccated flies were weighed and their wing areas were measured through employment of an Apple™ Computer Graphics Tablet.

RESULTS

Frequency distributions of initial flight distances are shown in Fig. 1. Contrary to predictions, *U. quadrifasciata* did not fly significantly further during initial flights than did *U. affinis* ($\bar{x}$ = 84.3 m ± 45.3 SE, n = 28 vs. $\bar{x}$ = 161.8 m ± 59.1 SE, n = 51; $p > 0.5$ Mann Whitney U). Most initial flights covered less than 100 m for both species (*U. quadrifasciata*, 25/30; *U. affinis*, 38/51).

As with initial flight, and again contrary to the prediction, *U. quadrifasciata* covered less distance during total flight than did *U. affinis* (x = 140.1 m ± 62.1 SE vs. x = 381.5 m ± 108.0 SE; $p > 0.05$ Mann Whitney U). While the majority of total-distance flights again covered less than 100 m, (*U. quadrifasciata*, 24/30; *U. affinis*, 31/51) the distribution had an extended tail for *U. affinis*, with a small proportion of flies covering more than 500 m (*U. quadrifascita*, 2/30; *U. affinis* 10/ 50) (Fig. 2).

No significant correlations were found between the size characteristics of the flies and their initial or total flight distances. Two parameters, dry weight and wing loading (= weight/ wing area) *vs.* initial and total distance had little explanatory power as shown by the values below, all of which are NS:

		U. quadrifasciata	*U. affinis*
Dry weight	vs. intial distance	r = 0.06	r = 0.06
	vs. total distance	r = 0.11	r = 0.16
Wing loading	vs. initial distance	r = 0.17	r = 0.02
	vs. total distance	r = 0.14	r = 0.08

DISCUSSION

Tethered flight can be a reliable, qualitative means of comparing inherent vagility within and among populations and species of insects (Davis 1981; Nakamori and Simizu 1983; Roitberg *et al.* 1984; Dingle and Evans 1987). For both species of fly studied here, the distributions of flight distance were leptokurtic (*i.e.* skewed toward short distance), a common feature of many insect species (Davis 1980). Thus, the results reported here probably reflect relative within-field differences in vagility for these two *Urophora* species.

The conclusion is that species-specific vagility in *Urophora quadrifasciata* and *U. affinis* does not explain their differential distributions among knapweed sites. Indeed, *U. affinis*, the species which I predicted would display lower flight propensity and endurance, actually appeared to be more vagile than its congener. There are reasons for being cautious about

generalizing from these results, in that each individual was tested only once (Davis 1980) and a single age class was tested, but given the restricted set of conditions employed, the experimental design seems appropriate and the conclusions warranted.

A possible explanation of my results is that the flight mill itself caused some bias in the flight propensity and endurance estimates. Since *U. quadrifasicata* is the somewhat smaller species (Fig. 3), any friction within the mill system should have a greater impact on its flight. I

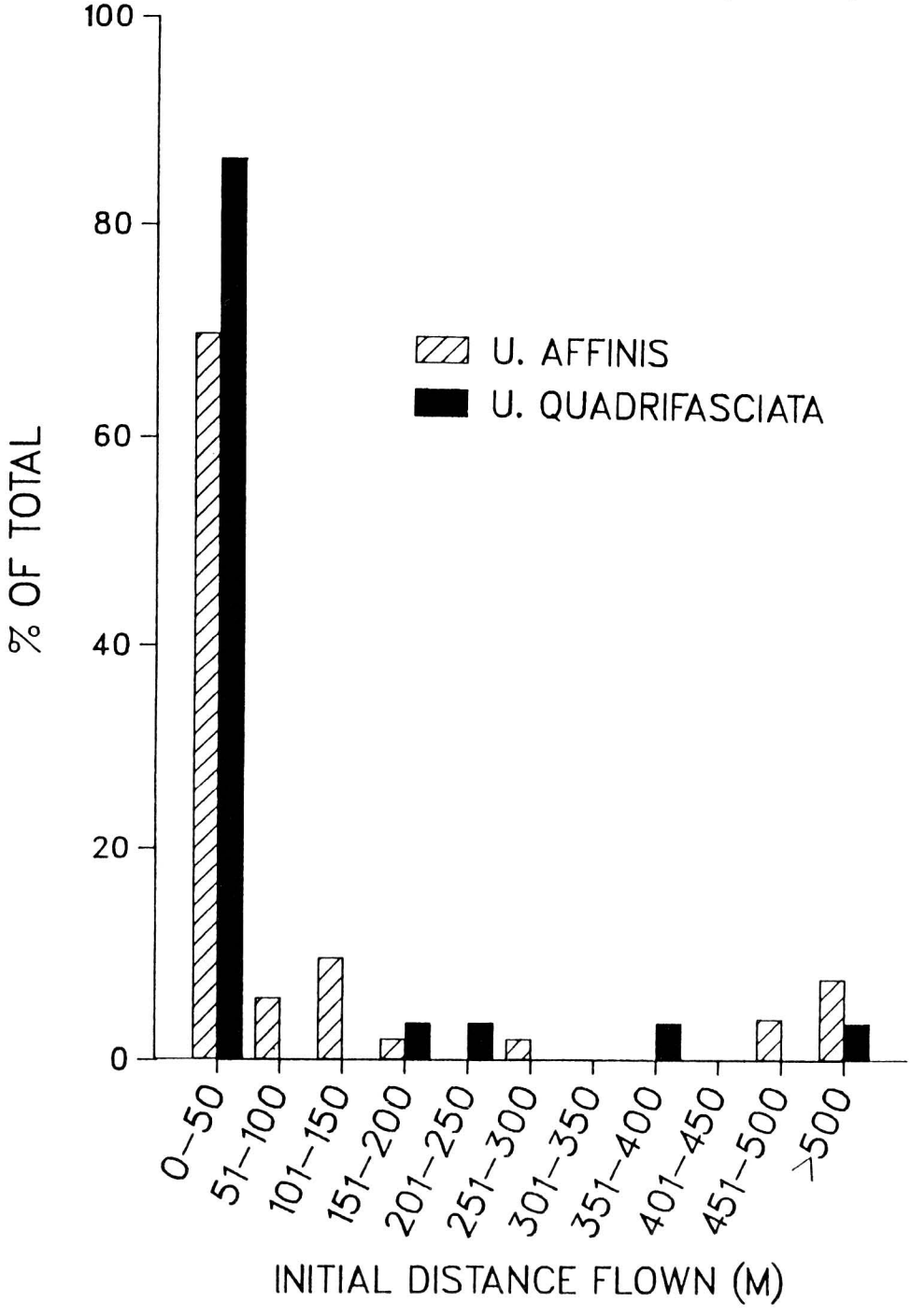

Fig. 1 Frequency distributions of initial flight distances by tethered *U. quadrifasciata* and *U. affinis* females.

tested this hypothesis by comparing the proportion of flights greater than 100 m (= long flight) among the different size classes of flies in both species. The results showed that long flights were independent of fly size in both species (*U. quadrifasciata* $\chi^2 = 2.29$, df = 3, NS; *U. affinis* $\chi^2 = 6.6$, df = 8, NS). Since even the smallest individual within the smaller species appeared equally likely to engage in long flight, I concluded that the mill estimates are not biased against size.

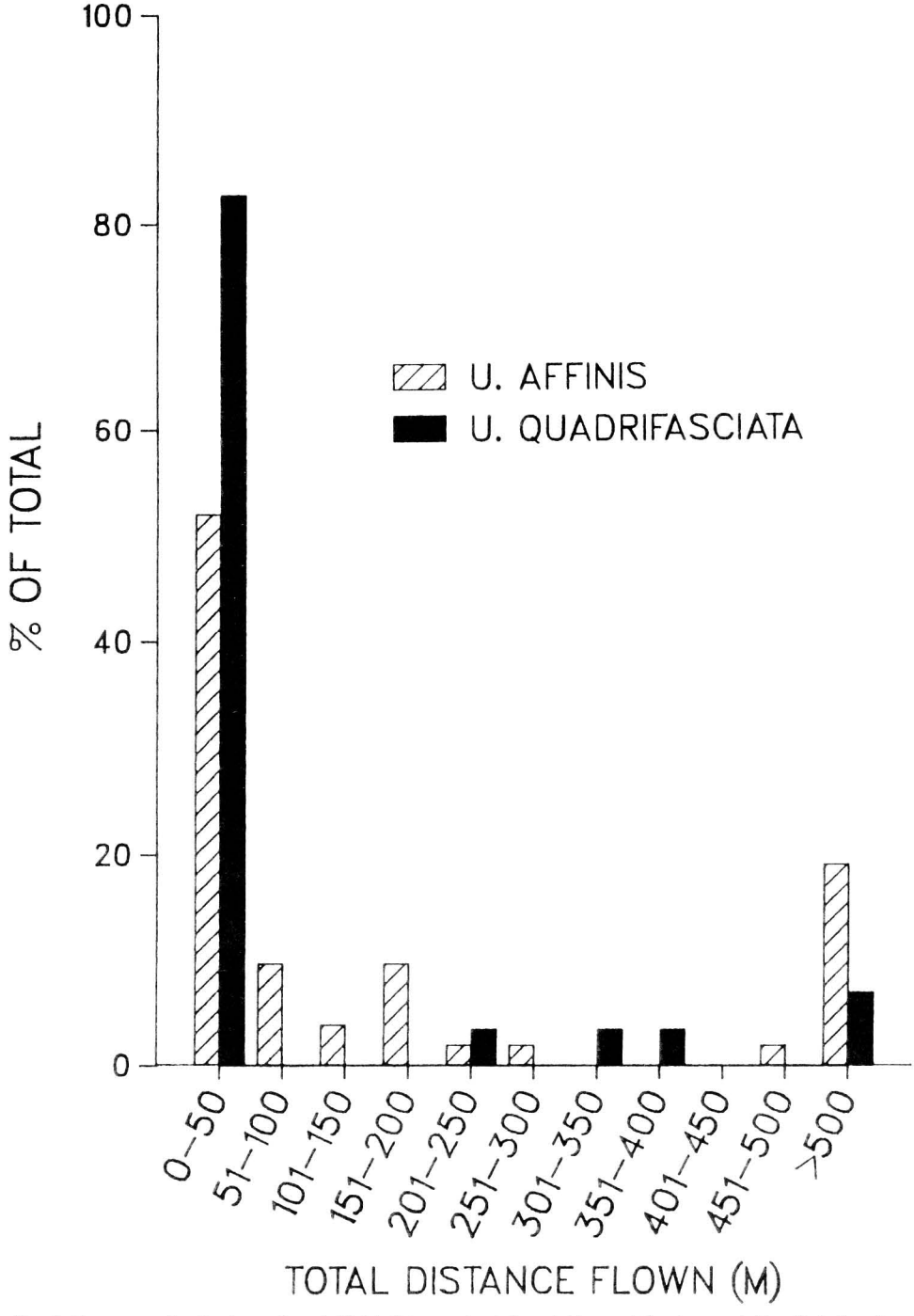

Fig. 2 Frequency distributions of total flight distances by tethered *U. quadrifasciata* and *U. affinis* females.

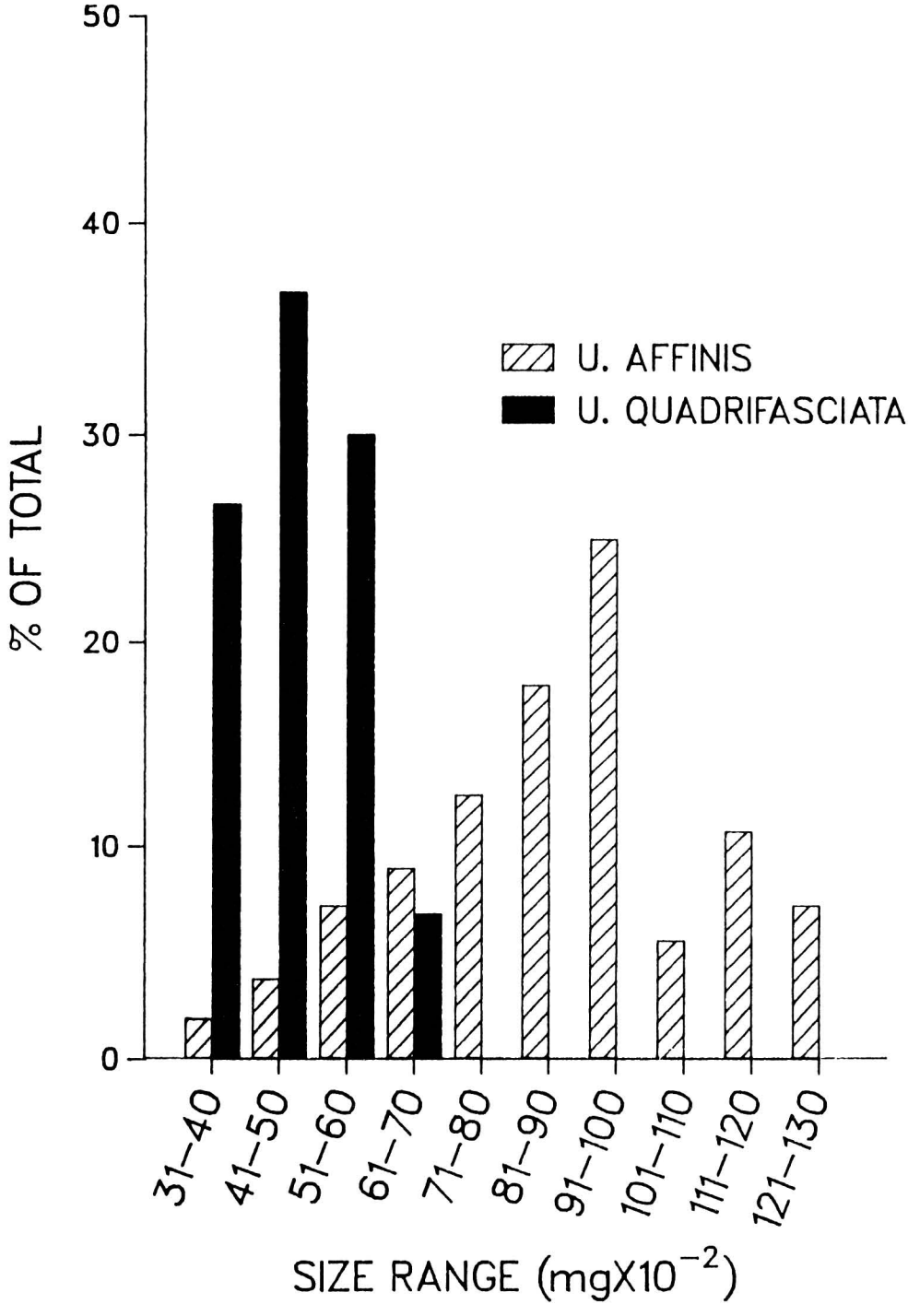

Fig. 3 Frequency distributions for weight classes (dry weight (mg x 10^{-2}) of female *U. quadrifasciata* and *U. affinis*.

The demonstration of size class independence from long flight tendency is at odds with the finding of Roff (1977), who showed that, for *Drosophila melanogaster*, it was the larger individuals that were most prone to disperse from release sites. Similarly, Dingle *et al.* (1980) documented a positive relationship between body size and tethered flight distance both between species of milkweed bugs (*Oncopeltus* spp.) and within populations of *Oncopeltus fasciatus*. My results do indicate that, it is indeed the larger of the two *Urophora* species that may be more prone to engage in long tethered flight. Field samples, however, indicate the opposite trend (Myers and Harris 1984), which points to the danger of extrapolating lab behaviour to the field.

A more realistic explanation regarding the counterintuitive results reported here derives from Myers and Harris' (1980) observation of the distributions of *U. quadrifasciata* and *U. affinis* galls among plants. They reported that, although *U. quadrifasciata* displayed "better dispersion" among sites, that their within-plant distributions were more clumped than those of *U. affinis*. Thus, testing vagility on flight mills possibly ignores some crucial behavioral feature which causes *U. quadrifasciata* to switch from a within plant "clumper" to an active disperser.

Myers and Harris (1980) cite Gilbert's (1977) observation that analysis of insect distributions does not identify causal mechanisms, but might identify insect behaviors deserving further study. A corollary that arises from this study is that investigation of flight behaviour (*i.e.* movement) does not necessarily lead to indentification of insect distribution. Inherent tendencies must be considered against the ecological setting in which they are defined.

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REFERENCES

Berube, D.E. 1980. Interspecific competition between *Urophora affinis* and *U. quadrifasciata* (Diptera: Tephritidae) for oviposition sites on diffuse knapweed (*Centaurea diffusa*: Compositae). Zeit. fur ang. Entomol. 90: 299-306.

Davis, M.A. 1980. Why are most insects short fliers? Evol. Theory 5: 103-111.

Davis, M.A. 1981. The flight capacity of dispersing milkweed beetles, *Tetraopes tetraopthalmus*. Ann. Entomol. Soc. Amer. 74: 385-386.

Dingle, H., N. Blakley, and E.R. Miller. 1980. Variation in body size and flight performance in milkweed bugs (*Oncopeltus*). Evol. 34: 371-385.

Dingle, H. and Evans, K.E. 1987. Responses in flight to selection on wing length in non-migratory milkweed bugs, *Oncopeltus fasciatus*. Ent. exp. app. 45: 289-296.

Gilbert, N. 1977. Appendix to: Movement patterns and egg distributions in cabbage butterflies. J. Anim. Ecol. 46: 195-212.

Harris, P. and J.H. Myers. 1984. *Centaurea diffusa* Lam. and *C. maculosa* Lam. s. lat., diffuse and spotted knapweed. *In* J.S. Kelleher and M.A. Holmes, Biological Control Programmes Against Insects and Weeds in Canada. C.A.B., England.

Jones, R.E. 1977. Movement patterns and egg distribution in cabbage butterflies. J. Anim. Ecol. 46: 195-212.

Karieva, P. 1985. Finding and losing host plants by *Phyllotreta* : patch size and surrounding habitat. Ecol. 66: 1809-1816.

Myers, J.H. and P. Harris. 1980. Distribution of *Urophora* galls in flower heads of diffuse and spotted knapweed in British Columbia. J. Appl. Ecol. 17: 359-67.

Nakamori, H. and Simizu, K. 1983. Comparison of the flight ability between wild and mass-reared melon fly, *Dacus cucurbitae* Coquillett (Diptera: Tephritidae). Appl. Ent. Zool. 18: 371-81.

Prokopy, R.J. and E.F. Boller. 1971. Artificial egging system for the European cherry fruit fly. J. Econ. Entomol. 63: 1413-1417.

Ralph, C.P. 1977. Effect of host plant density on populations of a specialized seed-feeding bug, *Oncopeltus fasciatus*. Ecol. 58: 799-809.

Roff, D.A. 1977. Dispersal in dipterans: its costs and consequences. J. Anim. Ecol. 46: 443-456.

Roitberg, B.D., J.H. Myers and B.D. Frazer. 1979. The influence of predators on the movement of apterous pea aphids between plants. J. Anim. Ecol. 49: 111-122.

Roitberg, B.D., R.S. Cairl and R.J. Prokopy. 1984. Oviposition deterring pheromone influences dispersal distance in tephritid fruit flies. Ent. exp. appl. 35: 217-220.

Story, J.M. and R.M. Nowierski. 1984. Increase and dispersal of *Urophora affinis* (Diptera: Tephritidae) on spotted knapweed in Western Montana. Enivron. Entomol. 13: 1151-1156.

COMPARATIVE LARVAL GROWTH OF THE VARIEGATED CUTWORM, *PERIDROMA SAUCIA*, FROM A LABORATORY COLONY AND A WILD POPULATION

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Abstract

Larval growth of variegated cutworms from a laboratory colony (maintained for over 12 generations) was compared with that of the F_1 generation of field-collected larvae on an artificial medium. After eleven days of feeding, larvae from the wild population weighed, on average, over three times as much as those from the laboratory colony. However, when larvae from each population were reared on media spiked with an inhibitory plant extract, the degree of growth inhibition relative to their respective controls was equivalent.

INTRODUCTION

Insects from laboratory colonies are commonly used in both basic and applied research, especially in studies of pesticidal efficacy where large numbers of uniformly aged individuals are required for bioassay. One implicit assumption underlying such studies is that the response of insects from the laboratory colony is representative of that expected of insects from wild populations. Unfortunately, maintenance of a laboratory colony of insects often results in inadvertant selection of genotypes and phenotypes which diverge from the colony founders of natural origin. Often this fact is overlooked, and the insects chosen for the study are those which can be conveniently produced in the laboratory setting (Berenbaum 1986).

In our laboratory, we have been using a laboratory colony of the variegated cutworm, *Peridroma saucia* (Hbn.)(Lepidoptera: Noctuidae), for bioassay of natural insecticides and antifeedants (Isman and Proksch 1985). This species was selected because it is a polyphagous pest of occasional economic importance throughout North America (Simonet *et al.* 1981), and because it is relatively easy to maintain in the laboratory in continuous culture. In the present study, we compared larval growth and survival of cutworms from a two-year-old laboratory colony with those of the F_1 generation of field-collected larvae.

MATERIALS AND METHODS

The laboratory colony, maintained for over 12 generations, was founded from pupae supplied by Dr. G. Ayer, Agriculture Canada, Winnipeg. They were taken from a laboratory colony maintained at Winnipeg for at least one year. The field population in our study consisted of the offspring of larvae collected from cabbage plants growing at the Department of Plant Science field laboratory on the University of British Columbia campus in Vancouver, as well as from unsprayed gardens in the Kitsilano district.

Larvae were reared on an artificial medium (BioServ Inc., Frenchtown, NJ, no. 9682) as described previously (Isman and Rodriguez 1983). In the first experiment, neonate larvae from each population were reared on the standard diet for 11 days and then weighed. In the second experiment, neonate larvae from each population were reared on either the standard diet treated with 95% aqueous ethanol, or a diet spiked with an ethanolic extract from foliage of big basin sagebrush, *Artemsia tridentata*, at 50% of natural concentration (dwt/dwt). For each

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