A study of Urophora affinis (Diptera : Tephritidae) released on spotted knapweed in Western Montana
by Jim Maynard Story

A thesis submitted in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE in Entomology
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Abstract:
A gall-producing fly, Urophora affinis Frfld., was introduced into western Montana for the biological control of spotted knapweed (Centaurea maaulosa Lam.). Releases were made in 1973, 1974, and 1975 on spotted knapweed infestations. In 1973, 150 u. affinis were released into a field cage, while 279 u. affinis were field released. The u. affinis population within the field cage was found to have increased significantly over a two-year period, u: affinis galls were found at a distance of 50 m from the initial release point after two years; the adults were found throughout the field in very small numbers. A spider, Dietyna major Menge, was found preying on U. affinis adults; the impact of the spider on the U. affinis population was not determined. It is concluded that u. affinis successfully overwintered and became established at the primary study site in western Montana. The life history of V. affinis was found to be closely synchronized with the flower head development of its host plant, spotted knapweed. An increase in the number of v. affinis galls was found to decrease spotted knapweed seed production. Pronounced variation for morphological traits occurred among spotted knapweed plants. Phenology of spotted knapweed generally agreed with previous reports.

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A STUDY OF *UROPHORA AFFINIS* (DIPTERA: TEPHRITIDAE) RELEASED ON SPOTTED KNAPWEED IN WESTERN MONTANA

by

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A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Entomology

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ABSTRACT

A gall-producing fly, *Urophora affinis* Frfld., was introduced into western Montana for the biological control of spotted knapweed (*Centaurea maculosa* Lam.). Releases were made in 1973, 1974, and 1975 on spotted knapweed infestations. In 1973, 150 *U. affinis* were released into a field cage, while 279 *U. affinis* were field released. The *U. affinis* population within the field cage was found to have increased significantly over a two-year period. *U. affinis* galls were found at a distance of 50 m from the initial release point after two years; the adults were found throughout the field in very small numbers. A spider, *Dictyna major* Menge, was found preying on *U. affinis* adults; the impact of the spider on the *U. affinis* population was not determined. It is concluded that *U. affinis* successfully overwintered and became established at the primary study site in western Montana. The life history of *U. affinis* was found to be closely synchronized with the flower head development of its host plant, spotted knapweed. An increase in the number of *U. affinis* galls was found to decrease spotted knapweed seed production. Pronounced variation for morphological traits occurred among spotted knapweed plants. Phenology of spotted knapweed generally agreed with previous reports.

INTRODUCTION

Spotted knapweed (*Centaurea maculosa* Lam.), a member of the Compositae family, is a serious problem in pastures, rangeland, and waste areas of western Montana. The plant is described by Watson and Renney (1974) thus:

> Spotted knapweed is a biennial or short-lived perennial, reproducing by seeds; stems erect or ascending, branched, pubescent, 30-100 cm high; leaves alternate, much divided, upper leaves linear; flower heads eradiate, 6mm diam., 16-20 mm high, mainly terminal, numerous, corymbs or corymbose panicles, bracts with a black-fringed tip 1-2 mm long; flowers tubular, purple, rarely white; achenes brownish, 3 mm long; pappus of simple bristles, 1-2 mm long, persistent.

The plant was first introduced into North America in the nineteenth century and has since spread to many parts of the United States and Canada (Fletcher and Renney, 1963). Moore (1972) reported that spotted knapweed occurs in all areas of the United States except possibly the Southeast. Watson and Renney (1974) showed that spotted knapweed can be found in the Canadian provinces of British Columbia, Alberta, Ontario, New Brunswick, Quebec, and Nova Scotia. The plant was first collected in Canada in 1893 at Victoria, British Columbia (Watson and Renney, 1974). The earliest collection of spotted knapweed in the Montana State University herbarium was made in 1927 in Gallatin County, Montana. The first herbarium specimen from western Montana was collected in 1933 and a note accompanying this specimen stated that the weed was probably introduced from states east of Montana. In 1975, a survey based on estimates by the County Extension

Agents and weed supervisors in those Montana counties having spotted knapweed infestations showed that approximately 647,511 ha (1.6 million acres) are infested with spotted knapweed in Montana. The majority of the infestation occurs west of the continental divide but it is rapidly spreading eastward into many areas of the State. It is so common in western Montana that it is referred to locally as "Bitterroot alfalfa." In Ravalli and Missoula Counties, spotted knapweed can be found on almost any unattended ground, especially on dry waste areas where the soil has at one time been disturbed. Spotted knapweed can be found on a wide variety of soil types (Watson and Renney, 1974) and it apparently requires very little moisture. The prevalence of spotted knapweed along the high mountain trails in the Bitterroot Mountains apparently is not unusual as Watson and Renney (1974) reported observations of the plant at altitudes over 1200 m in British Columbia.

Watson and Renney (1974) and Renney and Hughes (1969) report that spotted knapweed is an undesirable plant due to its unsuitability as a forage plant for livestock and its tendency to suppress desirable plant species. They report that the mature plant has a high fiber content, has very little nutritional value, and has a bitter taste all of which make the plant unacceptable to livestock except in overgrazed areas. Observations in the Bitterroot Valley were in agreement with the aforementioned statement with one exception. Sheep were observed to not only eat the plant but to actually seek it out in pastures where abundant grass and other forage were available.

Spotted knapweed's tendency to suppress other vegetation is due to its dense overstory and its production of a substance inhibitory to other plant species (Watson and Renney, 1974). The inhibitor has been partially characterized as an indole, probably an indole alkaloid or an auxin precursor (Fletcher and Renney, 1963).

The suppression of vegetation by spotted knapweed was evident in western Montana. Study Site B (see page 8) was a good example of an area where gradual suppression by spotted knapweed had resulted in the complete elimination of all other competing vegetation. The economic losses due to spotted knapweed can be significant. Watson and Renney (1974) have described range in good condition and the adverse affects of spotted knapweed on range productivity. They cited the discussion by McLean and Marchand (1968) in which it was pointed out that: "'Bluebunch wheatgrass-rough fescue' range in 'good' condition produces, on the average, 896.8 kg/ha (800 lb/acre) of forage and would have a stocking rate of 0.61 ha (1.5 acre) per animal unit month.'" Watson and Renney (1974) report that: "Knapweed-infested range may produce only 112 kg/ha (100 lb/acre) of forage resulting in a stocking rate of 4.86 ha (12.0 acre) per animal unit month."

The beneficial aspects of spotted knapweed according to Watson and Renney (1974) are: (1) the plant serves as a valuable pioneer species due to its rapid establishment which prevents soil erosion; (2) the plant serves as an important source of nectar for domestic bees; and (3) the plant has an esthetic value due to its attractive purple flowers.

Although chemical control has been effective against spotted knapweed (Furrer and Fertig, 1965; Renney and Hughes, 1969) it is limited to those infestations which are readily accessible and not located near waterways and livestock. Since spotted knapweed is found in a wide variety of habitats and soil types (Watson and Renney, 1974) control methods are needed which can be effectively used against the plant in all of its habitats and geographical locations.

Goeden (1975) states that biological weed control is the deliberate use of natural enemies (predators, parasites, or pathogens) to reduce weed densities to more acceptable levels. Since this control technique is environmentally safe and, under certain situations, more practical than other control methods, it is being considered as a possible alternative to the chemical control of spotted knapweed.

Urophora affinis Frfld. is a fly (Diptera: Tephritidae) that attacks the flower heads of *Centaurea maculosa* and *Centaurea diffusa* Lam. Like its host plants, the fly is native to Europe and probably western Asia (Zwölfer, 1970; Watson and Renney, 1974). Zwölfer (1970) describes the biology of *U. affinis* thus:

> If the flower head is accepted for oviposition the eggs are deposited singly or in small groups (2-5) on the small, undeveloped tubular flowers; between the tubular flower and the interior bracts; into the tissue of the receptacle. Up to 35 and 40 eggs may be deposited by an individual female per day, but the average number of eggs deposited per day seems to be much lower (5-10). After 3-4 days the first instar-larva hatches and penetrates into the ovariole of the undeveloped tubular flower, where it mines and causes the latter to develop into a fusiform gall deeply rooted in the receptacle and open at the apical end. Larval development takes several weeks during which time the walls of the gall become lignified. There are usually one to three galls per flower head but in some cases up to 8 galls had been found within an individual flower head. Varying proportions of larvae pupate without diapause and give rise to an additional generation. Most larvae, however, having reached maturity (i.e. third instar) remain in diapause within their galls until early summer when the diapause ends. Before a larva pupates it turns within the gall so that its head is orientated against the distal opening of the gall, the position in which pupation takes place. The adults emerge after two to three weeks and force their way through the opening of the gall by using their ptilinum.

Zwölfer further states that:

> The effect of *U. affinis* upon its host plant consists in the destruction of achenes and in the deformation of the receptacle of the capitulum which leads to a reduction of the production of viable seeds.

After being tested to insure its safety for release, the insect has been released into Canada and in the United States in Montana, Idaho, Oregon, and Washington (Harris and Hubbard, 1970; Andres, 1975).

The purposes of the present study were to: (1) study the behavior and life history of *U. affinis* in conjunction with the phenology of spotted knapweed and to determine if the relationship between the two organisms is affected in any way by environmental factors in western

Montana; (2) measure the ability of *U. affinis* to successfully over-winter, increase its population, and disperse at the initial (1973) release site in western Montana.

Field work was conducted from May to September, 1974 and from May to September, 1975 at the Western Agricultural Research Center at Corvallis, Montana.

DESCRIPTION OF STUDY AREA

All of the sites used for this study are located in or near the Bitterroot Valley of Western Montana. The Bitterroot Valley is approximately 104 km (65 miles) from north to south and 16 km (10 miles) wide. It extends from Lolo, Montana, on the northern boundary to Connor, Montana, where the East Fork of the Bitterroot River and the West Fork of the Bitterroot River merge to form the Bitterroot River. The valley is bordered on the west by the Bitterroot Mountains and on the east by the foothills leading to the Sapphire Mountains. The soils of the valley vary from highly calcareous on some east-side benches to moderately acid on west-side benches. Soil textures range from loamy coarse sand to clay loam (U.S. Department of Agriculture, 1959).

A waste field containing a heavy infestation of spotted knapweed was selected as the primary study site. The field was approximately 5000 m^2. This field will be referred to as "Site A" throughout the remainder of this paper. The field was located near the Western Agricultural Research Center at Corvallis, Montana, 46^{o} 20' N. and 114^{o} 4' W., at an elevation of 1,096 m (3,597 feet). A soil survey of the Bitterroot Valley reports the soil at Site A as Burnt Fork Loam and is described as "deep permeable soils that are high in natural fertility and have good water-holding capacity" (U.S. Department of Agriculture, 1959). The field was generally dry although the eastern half was usually more moist as a result of seepage from a nearby irrigation ditch. Consequently, the vegetation in the eastern half was much taller. In August 1975, the absolute densities of spotted knapweed and kentucky bluegrass (*Poa pratensis* L.) in the moist half of the field were 107.92 and 24.50 shoots/m^2, respectively while the absolute densities of the same plants in the dry half were 201.53 and 92.67 shoots/m^2 (see page 20). The field was bordered on the west by an alfalfa-hay field, on the south and east by a pasture, and on the north by a garden.

Table 1 summarizes the weather data at the Western Agricultural Research Center during the 1973-1975 period. The highest temperature recorded at the Center over the three summers was 39 C (102 F) in July 1973. High temperatures of 36 C (97 F) and 37 C (99 F) were recorded for the summers of 1974 and 1975, respectively. The coldest temperature recorded at the Research Center during the 1973-1975 period was -32 C (-26 F) in January 1974; for an 11 day period in January 1974, the mean minimum temperature was -25 C (-13 F). The coldest temperature recorded during 1975 was a January reading of -26 C (-15 F).

Site B, the only study site located outside the boundaries of the Bitterroot Valley was located near Missoula, Montana, a distance of 80 km (50 miles) north of Site A. Spotted knapweed, the only plant inhabiting the area, was recorded at an absolute density of 60.65 shoots/m^2.

Table 1. Monthly maximum and minimum temperatures (in degrees Celcius) and precipitation recorded at the Western Agricultural Research Center from June 1973-Sept. 1975. (Converted from U.S. Weather Bureau Climatological Data.)

Date	Temperature					Precipitation (in cm)
	Avg. Mean	Avg. Max.	Avg. Min.	High Temp.	Low Temp	
June 1973	15	23	7	34	0	4.85
July 1973	18	30	8	38	3	.38
Aug. 1973	18	28	8	35	3	1.47
Sept. 1973	12	20	4	31	0	4.24
Oct. 1973	7	14	1	23	-7	3.43
Nov. 1973	0	3	-4	12	-20	5.38
Dec. 1973	0	3	-4	13	-14	2.46
Jan. 1974	-6	-1	-10	12	-32	3.78
Feb. 1974	1	7	-3	13	-8	.41
Mar. 1974	2	8	-3	19	-15	2.49
Apr. 1974	7	15	0	25	-6	.51
May 1974	8	18	1	24	-6	3.07
June 1974	17	26	7	36	0	2.49
July 1974	18	28	8	32	5	2.31
Aug. 1974	16	26	7	31	3	5.00
Sept. 1974	13	23	3	29	-2	.89
Oct. 1974	8	17	0	25	-8	.86
Nov. 1974	2	7	-3	16	-11	.86
Dec. 1974	-1	2	-5	10	-15	.51
Jan. 1975	-3	1	-8	10	-26	3.23
Feb. 1975	-5	0	-10	8	-25	2.49
Mar. 1975	1	6	-4	11	-17	1.50
Apr. 1975	3	10	-2	17	-7	5.16
May 1975	8	16	2	28	-3	5.33
June 1975	13	21	5	26	0	2.54
July 1975	21	30	11	36	6	-
Aug. 1975	16	25	7	33	2	5.64
Sept. 1975	12	22	2	28	-2	.76

Site C was located 4.8 km (three miles) northwest of Site A. Plant densities were not recorded at this site.

Site D was located 16 km (10 miles) southwest of Site A. The absolute density of spotted knapweed at this site in 1975 was 62.29 shoots/m^2. The rest of the vegetation was not measured.

Site E was located 6.4 km (four miles) south of Site A. The absolute density of spotted knapweed at this site in 1975 was 73.17 shoots/m^2. The rest of the vegetation was not measured.

Field cages were placed on Study Sites A, B, and C.

MATERIALS AND METHODS

A total of 1,329 *U. affinis* adults was received from the Biological Control of Weeds Laboratory (U.S.D.A., A.R.S.) in Albany, California from 1973-1975. The insects were released on spotted knapweed infestations immediately after they were received. The dates and locations of the releases are shown in Table 2. Of the total, 659 *U. affinis* were field-released at Sites A and C while 550 *U. affinis* were released into 3.6 m long x 1.8 m wide x 1.8 m high field cages placed on heavy infestations of spotted knapweed at Sites A, B, and C. A field cage is shown in Fig. 1A. The cages consisted of a wooden frame enclosed by a light colored, No. 32-mesh, nylon net. The cages were used to aid in studying the behavior of *U. affinis* adults since their small size (2.5-5 mm long) and protective coloration made them not only difficult to observe but also difficult to locate in a typical spotted knapweed infestation. In 1974, the field cage at Site A was removed in late July at the onset of flowering by spotted knapweed. The cages were not removed from the other sites until September. The only cage used in 1975 was the one at Site A and, again, it was removed in late July.

The remaining 120 *U. affinis* were released into three small cages placed around single spotted knapweed plants located in the western half of Site A. The three small cages will be referred throughout the paper as mini-cage A, mini-cage B, and mini-cage C. These cages are

Table 2. Date, number released, and location of *U. affinis* releases.

Dates of *U. affinis* releases	Number of *U. affinis* released	Release Sites
June 12, 1973	150	Site A-field cage
June 12, 1973	279	Site A-field
July 10, 1974	200	Site B-field cage
July 12, 1974	200	Site C-field cage
July 12, 1974	200	Site C-field
July 9, 1975	180	Site A-field
July 9, 1975	120	Site A-mini cages
Total	1,329	

A

B

Figure 1. Study cages. A. Field cage for behavioral studies.
B. Mini-cages over individual plants.

shown in Fig. 1B. The cages consisted of 25 cm long x 25 cm wide x 1 m high wooden frames enclosed by a green, No. 32-mesh, nylon net. The three spotted knapweed plants used for the experiment were carefully selected on the basis that: (1) they were of equal height, (2) had the same number of shoots, (3) had approximately the same number of flower heads, and (4) possessed many flower heads of the size range preferred by ovipositing *U. affinis* females. Releases of 10 pair, 20 pair, and 30 pair of *U. affinis* adults were made into mini-cages A, B, and C, respectively in July 1975. A pair represented one male *U. affinis* and one female *U. affinis*. The purpose of this experiment was to determine the effect of *U. affinis* on spotted knapweed seed production. The cages were removed at the onset of flowering. Seed heads from each plant were harvested and examined in August.

Spotted knapweed plants were collected along transects at Sites A (dry half), B, C, and D in 1974. In 1975, a collection was made at Site E in addition to the other four sites. Also, in 1975, plants were collected in both the moist and dry halves of Site A. The plants were measured for height and scored for the number of flower heads per plant. In 1975, the number of shoots per plant was also scored. A line transect was established at each of the sites and the nearest plant to the transect at intervals of 50 cm along the transect was measured. Approximately 30 plants were measured at each site. One collection of plants was made at each of the sites per year.

Unopened but nearly mature seed heads of spotted knapweed were randomly collected at the five study sites in August 1975 for the purpose of determining the average number of seeds per head at the five sites. The seed head collections from each site were bagged and stored. When the heads were examined five months later, it was found that some of the seed heads had shattered. Therefore, to calculate an accurate variance, the "seeds-per-head" data were taken from only those heads which did not appear to have lost any of their seeds. Seeds that were immature or obviously abnormal were not counted. Depending on the availability of "nearly mature" seed heads, collections of 82 to 112 seed heads were made at the five sites. The "nearly mature" designation refers to those seed heads on which the green color, characteristic of flower heads, was beginning to be replaced by a straw color. The straw color first appeared on the seed heads about two to five days prior to their opening for seed dispersal. It was essential that the seed heads be collected in this "nearly mature" stage for two reasons:

(1) It was necessary that the seeds be almost mature to facilitate accurate analysis of the numbers of normal seeds. It is often difficult to distinguish between small, immature seeds and abnormal seeds.

(2) It was essential that the number of seeds counted per head was accurate. Since the mature seed heads are hygroscopic (i.e.,

they close due to the absorbtion of moisture), a collector cannot be sure that a closed head has not been previously opened and has already shed some of its seeds.

In May 1974, five spotted knapweed plants in the eastern half of Site A were randomly selected, tagged, and assigned a number. Measurements of plant height, based on the average of three randomly selected shoots measured from ground level to the top flower head, and flower head width, based on the diameter of the top flower head on each of the three measured shoots were made. Measurements of the five plants were recorded on a weekly basis throughout the summer until maximum growth was reached and all of the heads were flowering. By the end of the summer it was obvious that this technique had a major drawback. Since the shoots chosen for measurement on the tagged plants were randomly selected each week, occasionally the shoots measured on a plant one week would be shorter than the ones measured on that plant the previous week. Thus, the average height recorded would be less than the previous week representing a negative growth pattern. To eliminate this problem, in 1975 five shoots were tagged on each of the "test" plants and the average height of those five shoots was recorded on a weekly basis. Since the same five shoots were measured each week, there was no longer any chance of recording negative growth rates.

It was also noticed by the end of the summer of 1974 that the spotted knapweed plants in the eastern half of the field were considerably larger than those plants in the western half. Therefore, in 1975, 10 spotted knapweed plants were randomly selected, tagged, and assigned a number in each of the two halves of the field. Following the procedures of 1974, the 20 plants were measured on a weekly basis throughout the summer until they reached maturity. In each half, the plants selected were at a distance of at least 40 meters from the initial *U. affinis* release point. The correlations of plant height and flower head width were based on specific calendar dates which were converted to numerical scores on a linear scale corresponding to the number of days following the first measurement; e.g., in 1974, June 10 = 1, June 18 = 9 and so on to July 18 = 39 and in 1975, June 12 = 1.

Seed heads from spotted knapweed plants were collected from within the field cage at Site A in May 1974; in May 1975, collections were made within the field cages at Sites A, B, and C, and from the field at Site A. During both years, the collected seed heads were placed in quart jars. Sections of nylon stockings, secured by rubber bands, were placed over the mouths of the jars to protect the seed heads while allowing for air movement. To prevent moisture accumulation and excessive heat, the jars were placed upside down in a well-ventilated, shaded box with a wire-mesh floor positioned in the field. A total of 138 seed heads was randomly gathered in the 1974 collection while 6,918 seed heads were gathered in 1975. Daily observations were made to note the emergence of *U. affinis* adults. Mean dates of emergence of *U. affinis* adults were estimated by converting calendar dates to numerical scores on a linear scale; e.g., in 1974, June 24 = 1, June 27 = 4 and in 1975, June 30 = 1. After emergence, the adult *U. affinis* were released into the field cage at Site A.

The 138 seed head and 305 seed head collections made from within the field cage at Site A in 1974 and 1975, respectively, were also used in a study to determine the rate of increase of the *U. affinis* population within the cage. An additional 150 seed heads were collected and dissected in August of 1975 (i.e., any galls in these heads would contain the progeny of the May 1975 *U. affinis* generation). Each of these three collections of seed heads represented a separate *U. affinis* generation. The 1974 collection of 138 seed heads was placed in three jars, each containing about 46 heads. The 1975 collection of 305 seed heads was divided among 12 jars, each containing about 25 heads. The collected seed heads were dissected in late August of each year and scored for the presence of galls. In 1975, the total number of infested seed heads in the 12 jars as well as the number of infested heads in each jar was recorded. The only data recorded in 1974 were the total number of galls in the 138 seed head collection; the number of galls found in each of the three jars was not recorded. The galls were examined to detect the percentage of empty galls (i.e., the percentage of successfully emerging adults).

Galls which were not empty were examined to note the stage of development of the dead *U. affinis* within.

Seed heads were collected in both May and October of 1975 along five compass-based transects at Site A. The five transects ran east, southeast, south, southwest, and west from the initial *U. affinis* release point. The nearest 100 seed heads to the transect at 10 meter intervals out to 50 meters were collected on each of the five transects in May 1974. In October 1975, all of the seed heads in a ¼m^2 plot at each of the 10 meter intervals were collected. The collected heads were dissected and examined for the presence of galls in January 1976.

Random sweeps for *U. affinis* adults were made throughout the field at Site A in July 1975. The sweeps were directed at the top of spotted knapweed plants and the contents within the net were examined after each sweep. Approximately 50 sweeps were made during each of four trials. The distance and direction from the initial release site to the points at which *U. affinis* adults were captured were recorded.

Random searches for infested seed heads on spotted knapweed plants in the field were also made at Site A. The distance and direction from the initial release site to any seed heads containing galls were recorded.

A study of the flower head size preferred by ovipositing female *U. affinis* was made in the field cages at Sites A and B in 1974 and in the field cage at Site A in 1975. Spotted knapweed flower heads being probed by ovipositing female *U. affinis* were tagged. At the time of tagging, the width of the selected flower heads was measured with a vernier caliper. In August of both years, the heads were collected and dissected. The number of heads containing galls and the number of galls per infested head were recorded.

In July 1975, an attempt was made to measure the population density of the spider, *Dictyna major* Menge, at Site A. Ten $2m^2$ plots were randomly set up throughout the field. The number of *D. major* and *D. major* webs found in each plot were recorded on July 16 and July 21. The study was limited to two surveys due to cool, wet weather which hampered later attempts to census the population. When fair weather finally returned in early August, only a few spiders and webs were seen, apparently due to normal attrition and the surveys were, consequently, abandoned.

The densities of spotted knapweed plants were measured at Sites A, B, D, and E during the summers of 1974 and 1975 using a modification of the point-centered quarter method described by Dix (1961). Modifications of the procedures described by Dix (1961) used in this experiment were: (1) approximately 30 individuals of a particular species had to be encountered before the density of that species was recorded; (2) of the herbaceous plants like spotted knapweed, only those plants with differentiated leaves were recorded (i.e., established plants); (3) the transect in the western half of Site A was a permanent transect while the transects at the other study sites were randomly selected during each trial; and (4) in 1975, vegetation (other than spotted knapweed) which had gone to seed was not measured. The results are shown in Appendix A.

The definitions of the statistical symbols and botanical terms used throughout the paper are as follows:

N = number of individuals

$\bar{x}$ = estimate of the mean

μ = mean

S^2 = variance

SE = ($S_{\bar{x}}$) = standard error (standard deviation of the mean)

r = correlation coefficient

a = y-intercept

b = slope of the regression line

The term "seed" is equated with the achene typical of the Compositae family.

The term "flower" is equated with the individual head inflorescences.

RESULTS AND DISCUSSION

Observations and Measurements of Spotted Knapweed

Observations on the phenology of spotted knapweed were generally in agreement with Watson and Renney (1974). Spotted knapweed plants began their growth in late April or early May and by mid-June tiny stems bearing immature flower heads appeared on the shoots. The stems elongated and began to branch with new flower heads appearing at the end of each branch. This growth and branching continued until about mid-July when flowering began. The continual branching and appearance of new flower heads on the plants resulted in each plant having a wide variety of flower head sizes. Once a plant had reached maximum growth, most of the immature flower heads (less than 4 mm) ceased growth.

Each flower bloomed from two to six days (Fig. 2). After the flower had wilted, a period of 18 to 26 days passed before the bracts of the head pulled back exposing the seeds within. A seed head approaching maturity could be recognized in the field by a straw color that appeared on the seed head about two to five days prior to its opening. Once the seed head had opened, friction between the stiff, white receptacle hairs on the floor of the head and the short pappus hairs on the dorsal end of the seed pushed the seeds up to the mouth of the head. Any sudden movement of the plant produced by wind, etc., caused the seeds to be ejected within a radius of about 1 meter from the plant. The seed heads were found to be hygroscopic, closing at

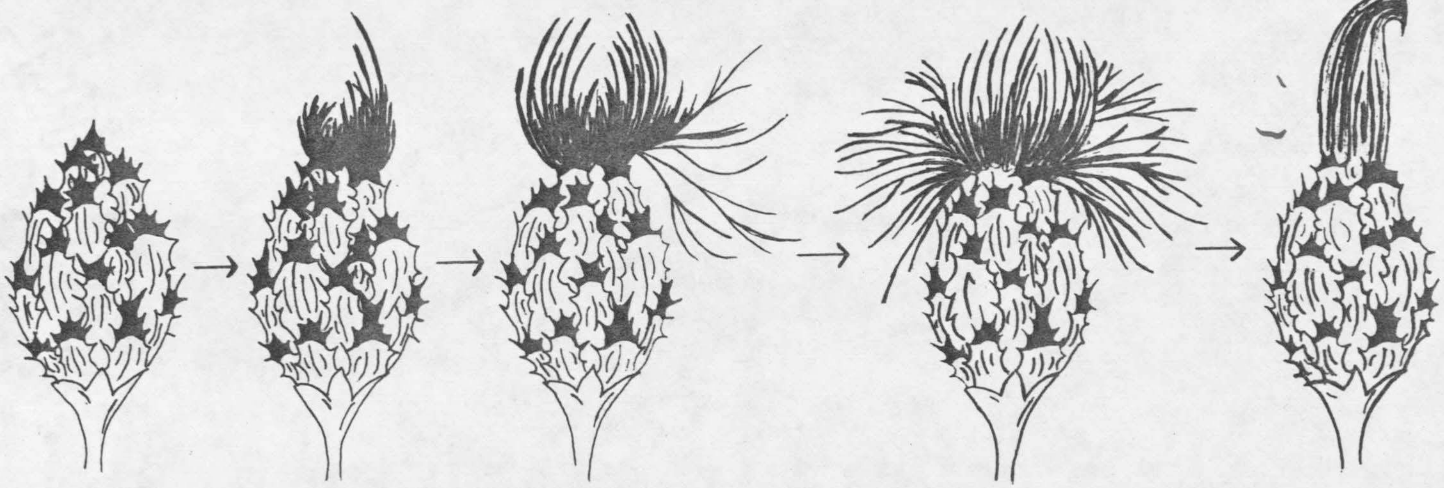

Figure 2. Flowering sequence of a typical spotted knapweed flower head during a period of 4-7 days.

night and also during the day under conditions of cool, wet weather.

Periodical measurements of spotted knapweed plant heights were made during 1974 and 1975 at Site A. The results are shown in Table 3. In 1974, mean height of spotted knapweed, based on one sample of five plants, increased linearly from nearly 68 cm on June 10 to 127 cm on July 2, with little additional height increase from July 2 to July 18. The correlation of height with time is highly significant, r = 0.87 (a = 82.07 and b = 1.52).

Mean height, in 1975, was based on two samples of 10 plants each. The mean height of the 10 plants sampled in the eastern half of the field increased linearly from slightly less than 31 cm on June 10 to slightly more than 69 cm on July 14. There was little additional height increase from July 14 to August 6. The correlation of height with time is highly significant, r = 0.89 (a = 39.48 and b = 0.71).

Measurements on the 10 plants sampled in the western half of the field did not begin until June 30. The pattern of growth was comparable to the plants sampled in the eastern half of the field, r = 0.78 (a = 39.28 and b = 0.17).

The r values for the three samples (one in 1974 and two in 1975) are comparable and they all indicate a strong correlation between time and height. However, the wide variation in b values among the three samples indicates that the rate of height increase varies with each sample.

Table 3. Periodic measurements of spotted knapweed plant heights in 1974 and 1975.

Year	Location	6/10	6/12	6/18	6/23	6/26	6/30	7/2	7/7	7/12	7/14	7/18	7/21	7/28	8/6	r	a	b
		Date																
1974	Site A (eastern half-moist)	67.8		99.4		123.4		127.2		130.0		130.0				0.87	82.07	1.52
1975	Site A (eastern half-moist)		30.96		46.76		56.46		67.06		69.36		70.16	70.7	70.86	0.89	39.48	0.71
1975	Site A (western half-dry)						39.74		45.52		46.87			47.46	47.53	0.78	39.28	0.17

The difference in growth pattern between the plants sampled in the western half of the field and those sampled in the eastern half was probably due to the seepage of irrigation water onto the eastern half of the field while the western half of the field remained relatively arid. These data suggest that there is an increase in height with time and that the amount of increase is probably influenced by water. In addition, the marked differences in plant height between 1974 and 1975 may reflect the plants' responses to yearly, environmental differences. The spring of 1975 was markedly cooler than 1974; thus, plant growth was less on comparable dates.

In 1974, flower head width increased linearly from June 18 through July 25. The correlation between flower head width and time is highly significant, $r = 0.95$ ($a = 2.73$ and $b = 0.13$).

The results of the 1975 flower head width study for the two populations in the eastern and western halves of the field, respectively, are highly significant and comparable to the 1974 data (Table 4). Mean flower head width increased with time for both populations. Correlations of flower head width with time were identical, $r = 0.97$. Regression equations for the populations in the eastern and western halves of the field are: $a = 4.03$, $b = 0.13$ and $a = 4.33$, $b = 0.10$, respectively. The apparent effects of moisture, discussed previously for plant height, did not appear to affect flower head widths.

The relationship of spotted knapweed height to number of shoots

Table 4. Periodic measurements of spotted knapweed flower head widths in 1974 and 1975.

		Date													
Year	Location	6/18	6/26	7/2	7/7	7/12	7/14	7/18	7/21	7/25	7/28	8/4	r	a	b
1974	Site A (eastern half-moist)	2.00	4.40	5.40		6.40		6.80		7.33			0.95	2.73	0.13
1975	Site A (eastern half-moist)				3.83		5.20		6.21		7.03	7.31	0.97	4.03	0.13
1975	Site A (western half-dry)				4.17		5.42				6.90	7.05	0.97	4.33	0.10

and flower heads and number of flower heads to number of shoots is shown in Tables 5, 6, and 7. Very little correlation was found between spotted knapweed height and number of shoots. The highest correlation occurred in the moist half of Site A where about 34% of the variation in number of shoots was due to plant height (r = 0.58).

The correlations between plant height and number of flower heads also were not significant. The highest correlation occurred in the dry half of Site A where about 55% of the variation in number of flower heads was associated with differences in plant height (r = 0.74). The r values are comparable in 1974 and 1975, although they are slightly lower in 1974.

The correlation between the number of flower heads and the number of shoots was highly significant at Sites A and D. The correlation was especially high in the moist half of Site A where r = 0.96. The r values for Site D and the dry half of Site A were 0.88 and 0.85, respectively. The r values for Sites B, C, and E were 0.59, 0.65, and 0.58, respectively.

The average spotted knapweed seed production at the five study sites is shown in Table 8. The mean numbers of seeds per head at the six sampling sites were fairly uniform, averaging about 32 seeds per head except for Site B where only 19.59 seeds per head was recorded. The SE values ranged from 0.59 at Site E to 0.92 at Site B. The mean number of flower heads per plant was comparable at Sites A (moist half),

Table 5. Means, variances, correlations and regression estimates for plant height (x) and number of shoots (y) of spotted knapweed, based on single plants in 1975.

Site	N	$\bar{x}$	$\bar{y}$	S^2x	S^2y	r	a	b
A (eastern half-moist)	30	41.57	4.50	336.74	108.81	0.58	-9.09	0.33
A (western half-dry)	30	35.50	2.67	112.81	3.26	0.49	-0.27	0.08
B	29	75.10	5.41	343.74	25.25	0.14	2.52	0.04
C	29	48.86	2.93	90.05	4.42	0.38	-1.19	0.08
D	31	53.52	6.48	211.86	46.79	0.30	-1.05	0.14
E	30	33.73	7.53	96.27	11.50	0.24	4.69	0.08

Table 6. Means, variances, correlations, and regression estimates for plant height (x) and number of flower heads (y) of spotted knapweed, based on single plants in 1975.

Site and Year	N	$\bar{x}$	$\bar{y}$	S^2x	S^2y	r	a	b
A(eastern half-moist) 1974	27	37.15	15.11	90.98	150.79	0.58	-12.84	0.75
B-1974	30	59.60	129.70	168.25	22289.18	0.53	-231.49	6.06
C-1974	31	47.39	33.65	127.58	1988.77	0.50	-60.78	1.99
D-1974	27	37.78	40.11	83.95	891.26	0.46	-16.79	1.51
A(eastern half-moist) 1975	30	41.57	28.40	336.74	5294.73	0.66	-79.96	2.61
A(western half-dry) 1975	30	35.50	9.20	112.81	92.86	0.74	-14.55	0.67
B-1975	29	75.10	62.24	343.74	3679.33	0.64	-94.29	2.08
C-1975	29	48.86	27.93	90.05	677.42	0.67	-61.28	1.83
D-1975	31	53.52	30.84	211.86	1278.34	0.54	-39.78	1.32
E-1975	30	33.73	27.33	96.27	328.09	0.69	-15.94	1.28

Table 7. Means, variances, correlations, and regression estimates for number of flower heads (x) and number of shoots (y) of spotted knapweed, based on simple plants in 1975.

Site	N	$\bar{x}$	$\bar{y}$	S^2x	S^2y	r	a	b
A(eastern half-moist)	30	28.40	4.50	5294.73	108.81	0.96	0.61	0.14
A(western half-dry)	30	9.20	2.67	92.86	3.26	0.85	1.19	0.16
B	29	62.24	5.41	3679.33	25.25	0.59	2.36	0.05
C	29	27.93	2.93	677.42	4.42	0.65	1.47	0.05
D	31	30.84	6.48	1278.34	46.79	0.88	1.31	0.17
E	30	27.33	7.53	328.09	11.50	0.58	4.58	0.11

Table 8. Average seed production of spotted knapweed in western Montana in 1975.

Location	Flower heads per plant			Seeds per head			Seeds per plant	Assumed Annual Reproductive Capacity
	N	$\bar{x}$	SE	N	$\bar{x}$	SE		
Site A (eastern half-moist)	30	28.40	13.28	82	35.12	0.73	997	798
Site A (western half-dry)	30	9.20	1.76	112	30.00	0.61	276	221
Site B	29	62.24	11.26	100	19.59	0.92	1219	975
Site C	29	27.93	4.83	97	36.74	0.72	1026	821
Site D	31	30.84	6.42	96	28.83	0.81	889	711
Site E	30	27.33	3.31	110	32.52	0.59	889	711

C, D, and E, averaging about 29 flower heads per plant. The mean number of flower heads per plant at Site A (dry half) was very low (9.20) while at Site B it was extremely high (62.24). The wide range of SE values (1.76 to 13.28) indicates a tremendous variation among spotted knapweed populations in regard to flower head numbers per plant.

Assuming 80% survival of all seeds (as did Watson and Renney, 1974), the annual reproductive capacities of spotted knapweed ranged from 221 seeds in the dry half of Site A to 975 seeds at Site B. The expected high seed production in the moist half of Site A was not evident in this study due to the large number of small plants sampled along the transect. The wide spacing of the large plants and the high density of small plants made the chance of sampling the large plants along the transect slight. Watson and Renney (1974) reported the annual reproductive capacity of spotted knapweed on rangeland in British Columbia to be 349 seeds per plant.

Spotted knapweed growing in irrigated areas often exhibits tremendous growth and seed production. Since the above study did not adequately show the reproductive potential of spotted knapweed growing under moist conditions, flower heads were counted on 10 large plants in the moist half of Site A in 1975. The average number of flower heads per plant was 1247.90 (SE = 111.06). Using the average number of seeds per head listed in Table 8 for the moist half of Site A

(35.12) and assuming 80% survival of all seeds, the annual reproductive capacity for the 10 plants was 35,061 seeds per plant. The large number of flower heads per plant in the moist half was less than the number recorded on 10 plants in the same area in 1974; the average number of flower heads per plant in 1974 was 2028.60 (SE = 247.87). The mean number of flower heads per plant, mean number of seeds per head, and annual reproductive capacity of irrigated spotted knapweed in British Columbia was 706.66 ± SE 64.81, 35.75 ± SE 4.00, and 20,210, respectively (Watson and Renney, 1974).

Extremely low seed per head numbers were recorded from spotted knapweed seed heads within the field cages at Sites B and C in 1974. At that time it was not known whether the low seed numbers were due to *U. affinis* or the exclusion of insect pollinators by the cages. The cages were removed in 1975 to isolate the causative factor. The resulting seed production within the cage areas increased appreciably (Table 9). The cage at Site A was removed at the onset of flowering in both 1974 and 1975 to allow access for insect pollinators. Seed production of plants in the Site A field cage (removed at the onset of flowering) was comparable to that of plants outside the cage in both 1974 and 1975. This indicates that: (1) *U. affinis* was apparently not the cause of the low seed numbers and (2) the cage affected seed production only during the time of flowering because it served as an exclosure to pollinators. The fact that spotted knapweed is

Table 9. The effect of cages on spotted knapweed seed production.

Location	Date	No.of seed head Collections	No.seed heads Collected	Cage Removed?	Avg. No. Seeds/head
inside cage Area	Aug. 1974	1	10	yes*	30.7
Site A					
Field	Aug. 1974	2	a)10	-	38.7
			b)30	-	31.7
inside cage Area	Aug. 1975	1	43	yes*	29.6
Site A					
Field	Aug. 1975	1	82	-	35.1
inside cage Area	Aug. 1974	1	16	No	0.6
Site B					
Field	Aug. 1974	1	30	-	25.3
inside cage Area	Aug. 1975	2	a)29	yes	16.8
			b)26	yes	19.9
Site B					
Field	Aug. 1975	2	a)100	-	19.6
			b) 35	-	29.8
inside cage Area	Aug. 1974	1	8	No	0.4
Site C					
Field	Aug. 1974	2	a)10	-	43.0
			b)28	-	34.7
inside cage Area	Aug. 1975	1	25	yes	39.8
Site C					
outside cage	Aug. 1975	2	a) 97	-	36.7
			b)115	-	30.8

*removed before onset of flowering

entomophilous was also reported by Watson and Renney (1974); they stated that the plant is self-compatible.

Observations and Measurements of *U. affinis*

U. affinis is a small fly belonging to the family Tephritidae. The male and females average about 3mm and 4½ mm in length, respectively (Fig. 3 and 4). Like most members of the family, *U. affinis* has distinct markings on its wings.

The life cycle of *U. affinis* was found to be closely synchronized with the flower head development of its host plant, spotted knapweed (Table 10). Adults of *U. affinis* first appeared in the field cage at Site A on June 10 in 1974 and on June 17 in 1975. The adult population reached its peak during 1974 and 1975 on June 24 and July 6, respectively. In both cases, the populations reached their peak at a time when the majority of spotted knapweed flower heads were about 3½ - 4½ mm in width, the size range preferred by ovipositing female *U. affinis* (discussed later). The majority of *U. affinis* emerged much later in 1975 than in 1974 apparently due to the unusually cool, wet spring in 1975. The cool weather had the same delaying effect on spotted knapweed since the plant development was considerably behind that of 1974 on comparable dates.

Having reached its peak, the *U. affinis* population slowly declined with the last adults being seen on July 30 in 1974 and August 7

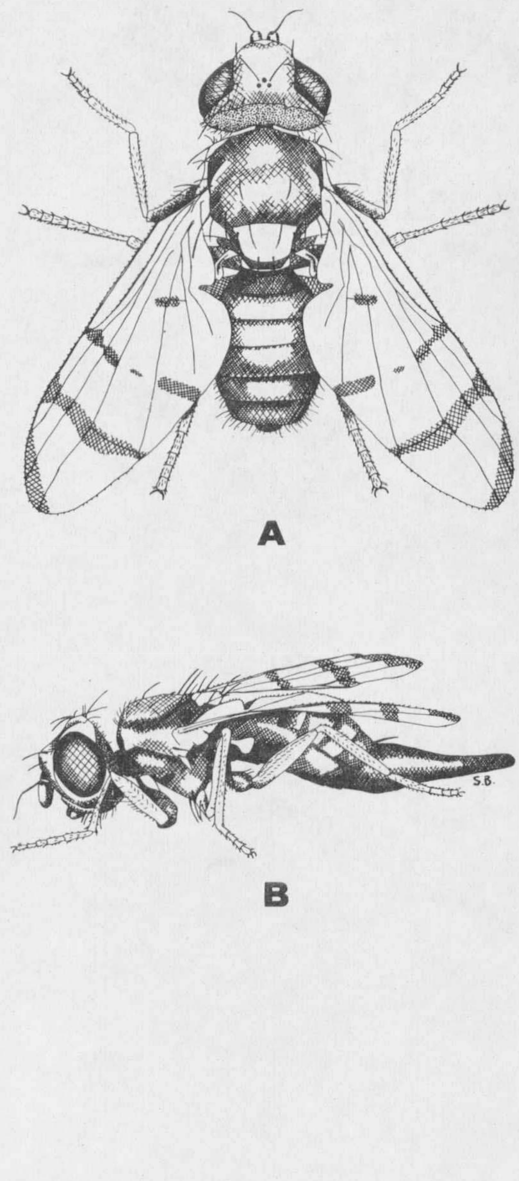

Figure 3. *U. affinis*. A. Male (x 18). B. Female (x 14).

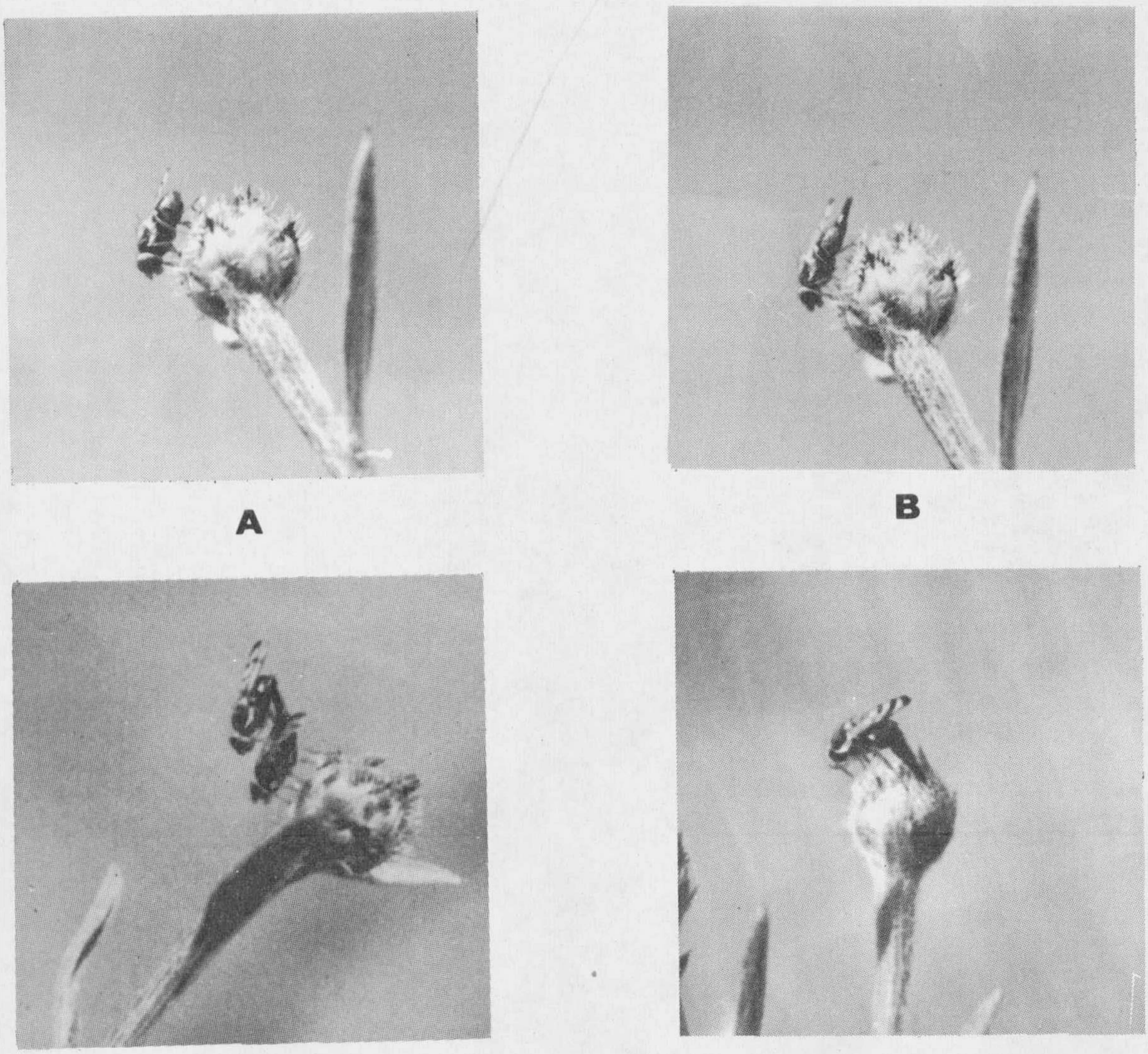

Figure 4. *U. affinis* on spotted knapweed (*C. maculosa*). A. Male *U. affinis* (x 4). B. Female *U. affinis* (note ovipositor) (x 4). C. Copulation (x 4). D. Oviposition (x 4).

Table 10. Seasonal history of *U. affinis* in relation to the phenology of spotted knapweed

		U. affinis		
Month	Status of spotted knapweed	Overwintering generation	Summer generation	Overwintering generation
January-mid-April	dried shoots and seed heads from old plants	Larval diapause	-	-
April 2nd half	small rosettes		-	-
May	growing rosettes		-	-
June 1st half	shoots	emergence of adults	-	-
June 2nd half	branching and flower heads	emergence of adults;beginning of oviposition	egg stage	egg stage
July 1st half	flower heads; few flowers	oviposition	eggs;larvae	eggs;larvae
July 2nd half	flowering	-	larvae; pupae	larvae entering diapause
August	seed heads progressively maturing	-	emergence of adults; oviposition	larval diapause
September-December	plants progressively dying	-	-	larval diapause

in 1975. A periodic census of the cage population in 1975 is shown in Table 11. Due to the very small size of the flies, it is possible that a number of flies were overlooked in the census; thus, the validity of the census is questionable.

In both 1974 and 1975, small numbers of *U. affinis* adults were found emerging in late August and early September from seed heads produced that summer. This showed that a period of diapause was not essential. Individuals of this second generation were seen in both the field and in the field cage at Site A. This early emergence was mentioned by Zwölfer (1970). Any biological advantage of this early emergence is questionable since the availability of flower heads of proper size for the ovipositing females is almost negligible. No evidence has been found to indicate that *U. affinis* can overwinter as an adult.

Adults emerged from the seed heads in the quart jars much later than the normal-emerging (i.e., those adults that underwent diapause and thus, did not emerge "early") "wild" population. This delayed emergence was probably a result of the cooler temperatures associated with the shaded conditions under which the jars were maintained.

The dates and frequency of *U. affinis* emergence from the jars is shown in Fig. 5. The first emergence from the jars occurred on June 24 and June 30 in 1974 and 1975, respectively. Based on a total of 39 individuals, the mean date of emergence in 1974 occurred on July 9

Table 11. Sightings of *U. affinis* adults in the field cage at Site A in 1975.

Date	Number of *U. affinis*		
	male	female	total
June 16	3	1	4
June 22	5	2	7
June 24	14	2	16
June 28	18	1	19
July 2	34	5	39
July 3	45	13	58
July 6	89	27	116
July 17	73	29	102
	281	80	361

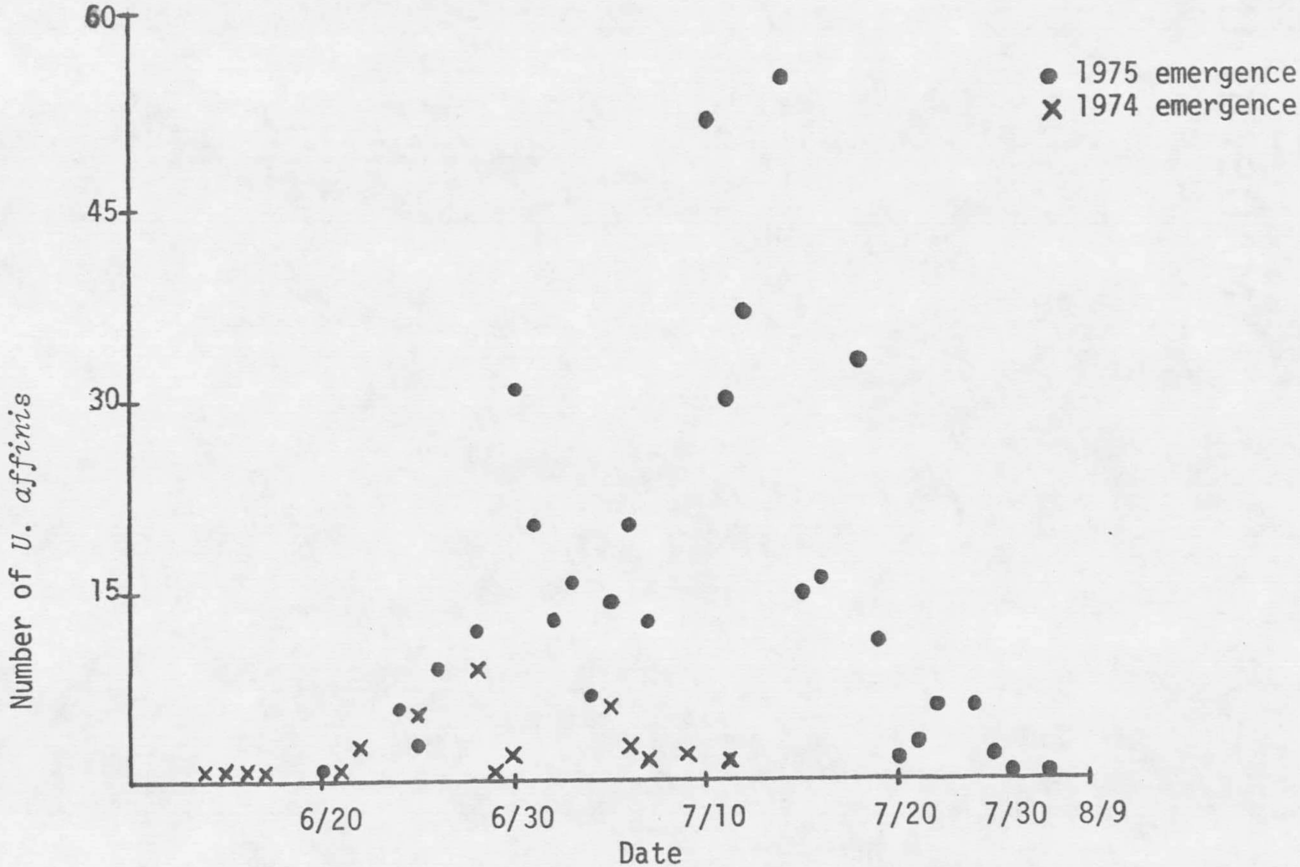

Figure 5. Dates and frequency of *U. affinis* emergence from the seed heads stored in jars.

($\bar{x}$ = 15.90). In 1975, the mean date of emergence, based on 435 individuals, was July 19 ($\bar{x}$ = 20.46). The S^2 and SE values for the 1974 and 1975 emergence dates were 49.88, 1.13 and 50.68, 0.34, respectively.

A high level of confidence in $\bar{x}$ is suggested by the low value of SE in 1975. The distribution of emergences suggests a concentration slightly early in the season with relatively few flies emerging at the end of the season.

Analysis of emergence by sex was also made in 1975. The mean emergence date for males (N = 244) was July 18 ($\bar{x}$ = 18.60) while for females (N = 191) it was July 22 ($\bar{x}$ = 22.82). The corresponding values of S^2 and SE for males are 44.82 and 0.43 while for females they are 48.39 and 0.50. The difference between mean emergence dates of the two sexes of 4.22 is highly significant, $P < .01$ ($t = 6.39$).

The earlier emergence of males is apparently typical of *Urophora* spp. Wadsworth (1914), in his observations of *U. solstitialis* Linn., reported that the number of males emerging in early June greatly outnumbered the females, but the disproportion in the sexes decreased towards the end of the month. The biological significance of the earlier emergence of males is not known.

The emergence data in 1974 were comparable to 1975 but on a much smaller scale due to the limited sample size (N = 39). The SE value (1.13) was relatively high and may be due to the small sample size.

Emergence dates by sex were July 7 ($\bar{x}$ = 14.40) for males and July 10 ($\bar{x}$ = 17.47) for females. The difference between the two emergence dates (3.07) was not statistically significant which may be due to high S^2 and SE values associated with smaller samples.

The jar emergence was also later in 1975 than in 1974. Again, this was probably due to the cool spring in 1975.

The successful establishment of *U. affinis* in the field cage at Site A was evident in late 1975. The percentage of infested seed heads increased linearly over three *U. affinis* generations (Table 12). The correlation between infestation percentage and *U. affinis* generations was highly significant, r = 1.00 (a = -13.17, b = 28.05). It is obvious that a positive change in the percentage of heads with galls occurred over the three generations but confidence in a perfect correlation is low in any biological system. With additional seed head samples and generations, the value of r can be expected to change but hopefully the conclusion that *U. affinis* is becoming established will not change.

Other traits such as the total number of galls, the average number of galls per head, and the highest number of galls found in any one seed head also increased over the three generations but they were not statistically analyzed due to the variability occurring among the number of seed heads sampled for each generation. The 10 galls found in one seed head in the August 1975 collection is of interest in that

Table 12. Analyses of seed heads in field cage at Site A from May 1974-August 1975. (3 *U. affinis* generations)

Date	No. seed heads examined	% of seed heads with galls	Total No. galls	Avg. No. galls/seed head*	High No. galls/seed head	No. empty galls	% galls empty	No. of dead *U. affinis*	Stage of development of dead *U. affinis*	
									Larva	Pupa
May 1974	138	15.2	46	2.19	5	39	84.8	7	4	3
May 1975	305	42.3	242	1.88	6	151	62.4	91	48	43
August 1975	150	71.3	337	3.15	10	**				

*only those seed heads containing galls, not the total number examined.

**the galls were not dissected to note contents within.

it is the highest number of galls per head that has been reported. Prior to this study, the highest number of galls found in a single spotted knapweed seed head was eight (Zwölfer, 1970).

The percentage of empty galls (i.e., the percentage of successfully emerging adults) decreased from 1974 to 1975. Although the dead *U. affinis* within the galls were examined, it is not known what caused the mortality or why the mortality increased in the 1975 generation. The stage of development of the dead *U. affinis* was noted. Since *U. affinis* larvae and pupae are very similar in appearance, the developmental stage of the dead *U. affinis* was determined by noting whether the head was oriented toward the distal opening of the gall. Zwölfer (1970), as mentioned earlier, reported that prior to pupation, the larva reverses its position in the gall such that its head is oriented distally in the gall. Therefore, all immature *U. affinis* that died with their head oriented distally were considered to be pupae, while those in the reverse position were considered larvae. Many of the dead immature *U. affinis* were in such a shrivelled, desiccated condition that it was impossible to determine where the head was oriented. Consequently, the validity of these data is questionable. Dissection of the galls did not reveal the presence of parasites.

An attempt to estimate the total *U. affinis* population within the field cage at Site A was made in September 1975. This estimate represents the population that should appear as adults in the summer of

1976. Based on the total number of seed heads in the cage (6,132), the infestation percentage of the 150 seed heads collected in August (71.3), and the average number of galls per seed head (3.15), a population estimate of 13,772 *U. affinis* was calculated. Potential *U. affinis* mortality was not considered.

Assuming the number of seed heads within the field cage to be fairly uniform in both 1974 and 1975, the estimated population in the summer of 1975 (based on an infestation percentage of 42.3, an average of 1.88 galls per head, and 62.4% successful emergence of adults) was 3,027 *U. affinis*. This figure is far in excess of the number of *U. affinis* recorded in Table 11. It is not known which of the two population counts most accurately describes the *U. affinis* population within the field cage as it occurred in the summer of 1975.

From Site A in May 1975, a total of 305 seed heads, separated into 12 jars of about 25 heads each, was scored for percent infestation and number of galls per head. The average infestation was about 42% (SE = 3.05). Infested heads had an average of 1.88 galls (SE = 0.09). Thus, for percent infestation, $\mu = 42.3 \pm 6.71$ and for number of galls per head, $\mu = 1.88 \pm 0.20$. These data suggest that any collection of about 25 seed heads collected within the field cage during the summer of 1974 would have shown an infestation percentage of about 42. Similar data were not recorded for the May 1974 collection of seed heads.

Due to the very small number of *U. affinis* in the field at Site A, adequate data describing the success of the field population were not obtained. Galls of *U. affinis* were found at a distance of up to 50 m from the initial release point (Fig. 6, 7, and 8). The frequency of spotted knapweed plants was fairly uniform throughout the sampling area; thus, the number of galls per sampling site was probably fairly indicative of the entire sampling area in regard to distance and direction from the initial release point. Adults were seen throughout most of the field, but in very small numbers (Fig. 9). On July 15, 1975, two male *U. affinis* were found on spotted knapweed in the farthest corner of the field, a distance of 94 m from the initial release point. Although no supporting data are available, it is felt that the *U. affinis* population is established in the field at Site A, is dispersed throughout the field, and is increasing in numbers, although very slowly. Reports on the *U. affinis* population increases in British Columbia (Harris, 1974) suggest that the Canadian *U. affinis* population is increasing at a considerably faster rate than in western Montana. A population of 174,000 *U. affinis* was estimated at the Chase colony in 1973 after apparently the same period of *U. affinis* establishment in western Montana (two years). The number of *U. affinis* involved in the initial release at Chase, British Columbia is not known.

Observations of *U. affinis* behavior mainly involved those

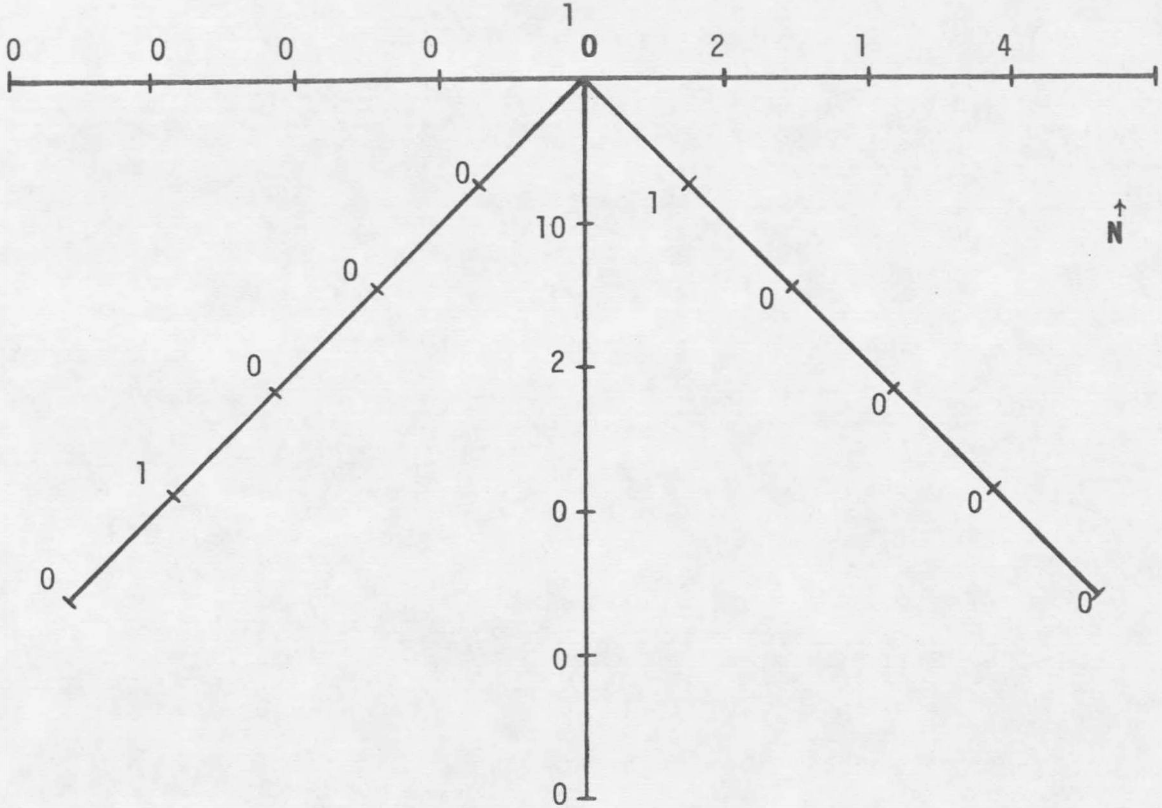

Figure 6. Number of galls found in collections of 100 seed heads at the release point and at 10 m intervals along compass-based transects in June 1975.

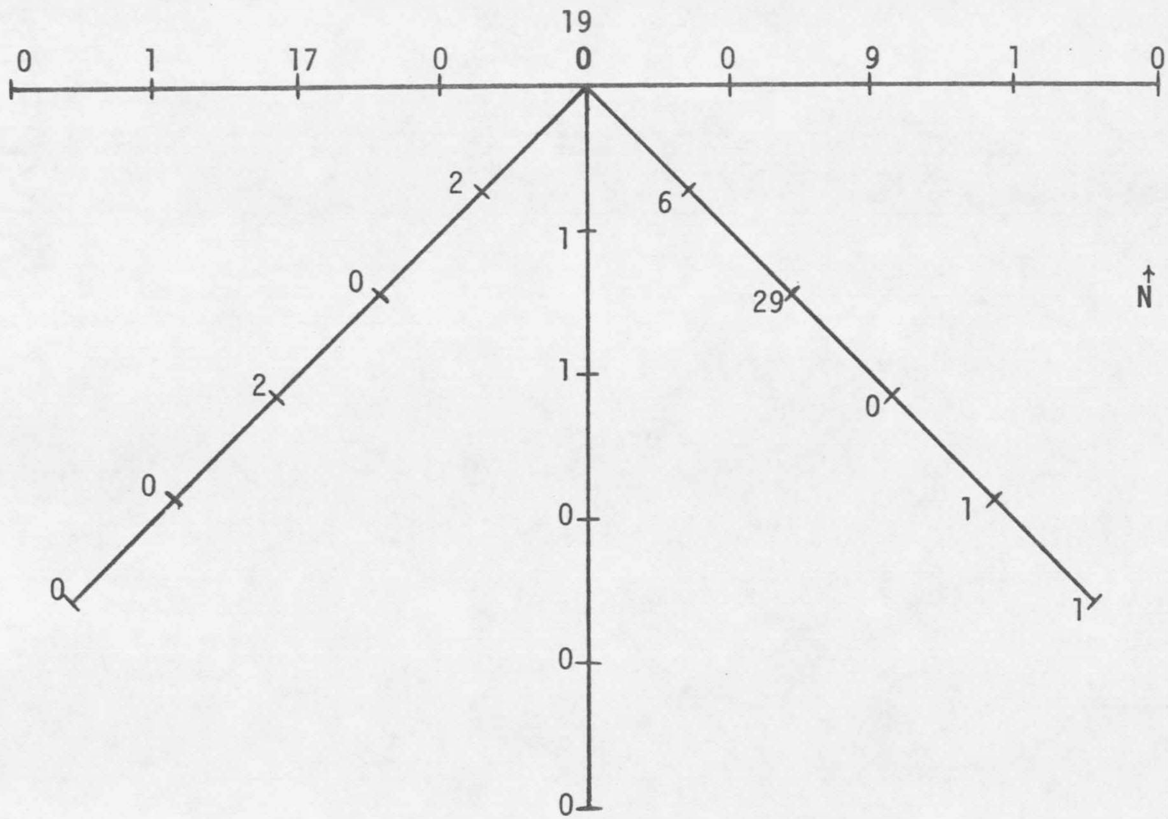

Figure 7. Number of galls found in ½ m^2 plots at the release point and at 10 m intervals along compass-based transects in October 1975.

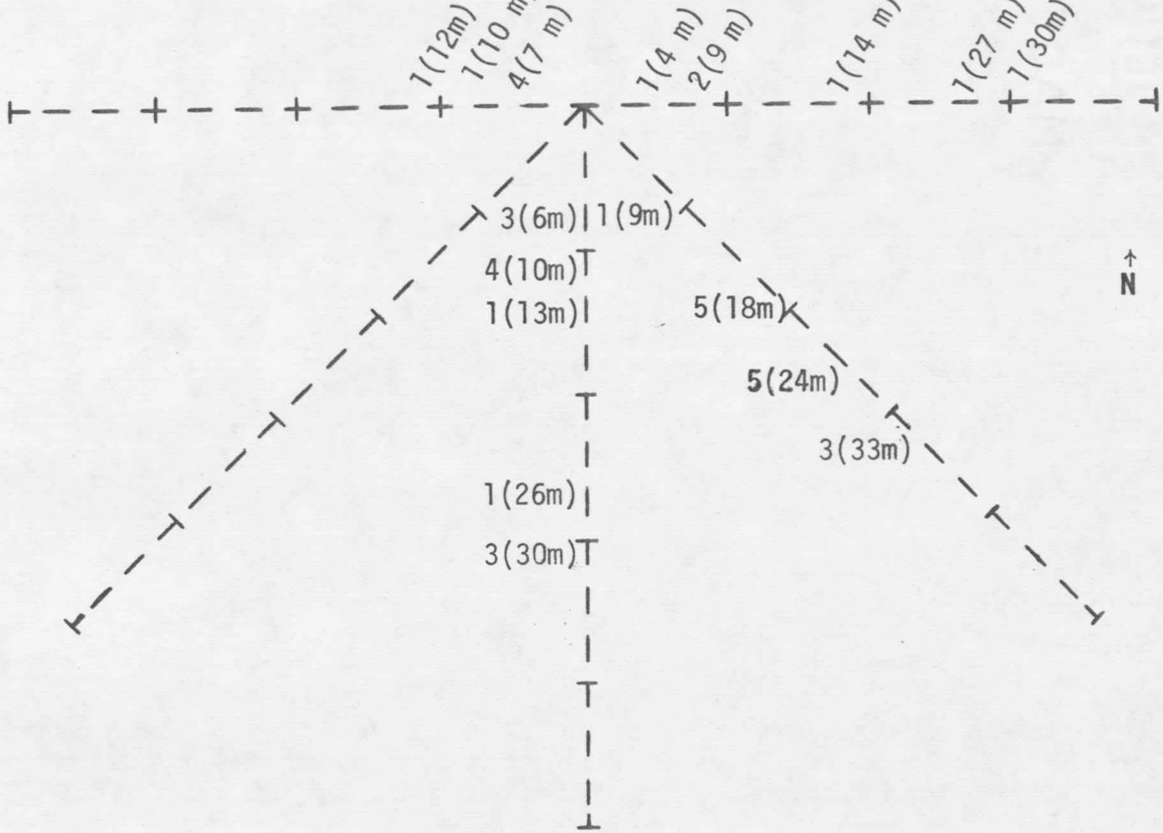

Figure 8. Results of random search for galls in compass-based directions from the initial release point.

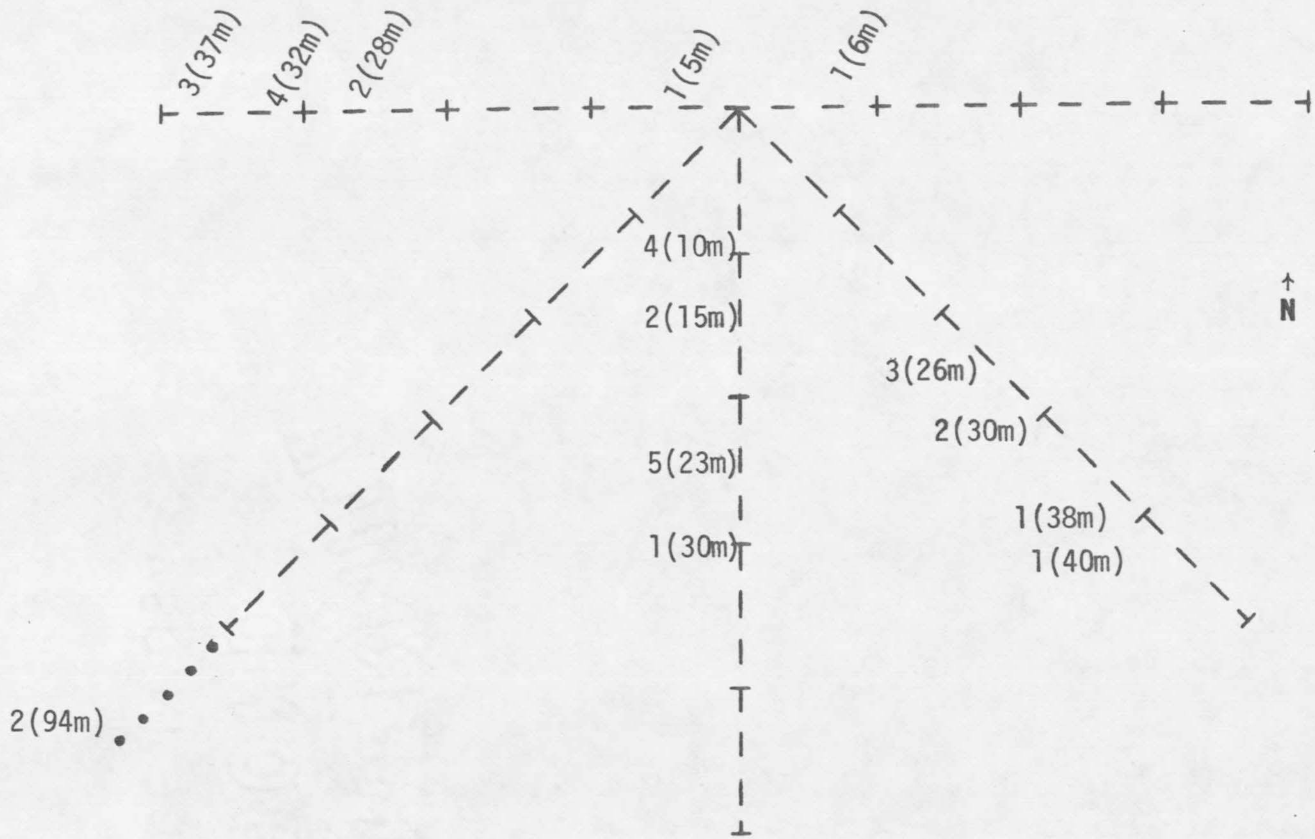

Figure 9. Results of random sweeps for adult *U. affinis* in compass-based directions from the initial release point.

individuals confined within the field cage at Site A. Although it is conceivable that the behavior exhibited by those individuals could have been altered as compared to behavior characteristic of "unconfined" flies, the observations generally agree with those of Zwölfer (1970).

U. affinis adults, both inside and outside the field cage, were not highly active insects. Although they are extremely responsive to movement, an observer can readily move near them and can often coax one onto a finger without the insect flying away.

The adults are weak fliers; individuals rarely flew farther than 1 meter both inside and outside the field cage. Most of their traveling consisted of walking from one flower head to another via the branches of spotted knapweed panicles. After investigating two or three flower heads on one spotted knapweed plant, they usually flew a short distance to another plant and investigated a few flower heads on it. The flower heads investigated almost always were limited to the top five or six branches of the spotted knapweed plants; they rarely traveled below the top six branches.

The investigation of flower heads by the *U. affinis* adults within the field cage was generally a slow process. Depending on the time of day, the time spent on an individual flower head varied from 30 seconds to 1 hour. The short periods of investigation were typical of the more accelerated activity occurring in the cool (21 C) hours of the morning and evening. During the warmer parts of the day, the adults would generally rest on one flower head up to an hour in length.

Observations made on "un-confined" *U. affinis,* although few in number, did reveal a slight modification of behavior. These flies (both males and females) were much more active, spending far less time on individual flower heads than the caged flies. Also, the males appeared to be more persistent in their courting and mating attempts.

The flower heads of the host plant served different purposes for the male and female *U. affinis*. The main objective of a female *U. affinis* is to find acceptable flower heads in which she can lay her eggs. Therefore, her activities consist of methodically investigating many flower heads in an attempt to find those acceptable for oviposition. A flower head serves the male as a potential site for a rendezvous with a female. The male essentially spends most of his time waiting on a single flower head for a female to either approach "his" flower head or one in the near vicinity. If, after a period of about an hour, a confrontation with a female has not been made, the male will fly to a flower head on a nearby plant and will again assume his waiting position.

The behavior of a male waiting on "his" flower head changes immediately upon the approach of another *U. affinis,* regardless of the sex. If the intruder is another male, the two males show a territorial behavior involving display movements such as spreading of wings and "bobbing" motions of the body. After carefully stalking one another, they usually grapple and often attempt to mate before the loser takes flight. But, if the waiting male is confronted by a female both individuals spread and wave their wings and after the male slowly stalks the female he will fly onto her and attempt to copulate unless the female takes flight. The males are readily attracted to the movements of other *U. affinis* and will fly to any *U. affinis* they see moving, regardless of sex. Once he recognizes an individual *U. affinis* as being a female, he will continue to follow her from flower head to flower head and make repeated attempts to mate before either being successful or losing sight of her.

During the first two or three days after emergence, female *U. affinis* will reject all mating attempts by males. Any confrontation with a male during this period results in the female immediately taking flight. After this period, however, the females are very passive and confrontations with males will result in copulation nearly 100% of the time. The females mate many times during their adult life which, according to Zwölfer (1970), lasts up to three weeks.

The act of mating usually lasts about 90 minutes but it can vary from 15 minutes to 2 hours in length. After disengaging, the same pair may mate again after a resting period of about 10 minutes. Occasionally a mating pair will be confronted by another male in which case the latter male will also try to copulate with the female. In such a situation, the copulating male kicks his legs in an attempt to repeal the intruding male while at the same time maintain his copulatory position. Because of this activity, the usually passive female also attempts to remove the intruding male by kicking her legs. If the intruding male is not successful at dislodging the copulating male within a minute or two, he takes flight.

The procedures involved in *U. affinis* copulation (see Fig. 4C) were identical to those described for *Urophora siruna-seva* (Hg.) by Zwölfer (1969). The female turns her ovipositor sheath up to about a 45^{o} angle upon being mounted by a male. The male connects his genitalia to the tip of the ovipositor sheath while his legs simultaneously secure a position on the dorsal surface of the female's thorax. Copulation terminates when the male disengages his genitalia from the female's ovipositor sheath.

As mentioned earlier, the behavior of a female *U. affinis* is oriented toward finding spotted knapweed flower heads of a size acceptable for oviposition. The widths of flower heads preferred by ovipositing females in the field cages at Sites A and B varied slightly over the two years (1974 and 1975). A liberal estimate of the size preferred was determined by using the smallest sample which had the highest mean (4.06) and the highest standard error (0.24). Mean width (μ), was estimated: $\mu = 4.06 \pm 0.52$ mm. When the female found a flower head in this range, she investigated the head with her ovipositor sheath bent down touching the head. If the flower head was acceptable, she inserted her ovipositor between the bracts, usually on the lower half of the head (Fig. 4D). The female probed from 1 to 10 times on a single head with each probe lasting between 5 and 90 seconds. Most of the probes were short in duration but if the female was on an acceptable flower head, she would usually make two or three lengthy (one minute or longer) probes before leaving the head. At the start of the study it was assumed that the short probes were just exploratory probes and that is was during the lengthy probes that eggs were being deposited. Dissection of probed heads later proved that the latter was not necessarily true. During July 1974, tags were placed on those flower heads upon which female *U. affinis* were seen making lengthy probes. These observations were conducted in the field cages at Sites A and B. Dissections of the flower heads in August 1974 revealed the presence of galls in only 50.0 and 63.6% of the flower heads at Sites A and B, respectively. The pooled percentage of 55.6 suggests that either: (1) eggs were not deposited during many of the lengthy probes; (2) sterile eggs were deposited; or (3) mortality of some of the eggs or first-instar larvae occurred. The most likely explanation is that eggs were not deposited because Zwölfer (1970) states that: ". . . extensive probing of the bud [flower head] of the proper host plant (i.e. of a potential oviposition substrate) does not always lead to the deposition of eggs."

U. affinis was found to be highly host specific. All of the courting copulation, and egg-laying occurred on the host plant, spotted knapweed. Adults were observed to fly onto other plants of heights similar to spotted knapweed but the time spent on the other plants was usually quite brief. The high degree of host specificity of *U. affinis* is discussed by Zwölfer (1970). He states that *U. affinis* are highly specialized in their host selection due to: (1) the ability to induce gall formation, (2) the modification of the ovipositor length which restricts oviposition to flower heads of less than 10 mm in length and diameter, and (3) their almost exclusive use of physical tokens for host plant selection. Two additional specializations applicable to *U. affinis* were mentioned by Zwölfer (1969) when he described the adaptations of *U. siruna-seva* to its host plant, *Centaurea solstitialis*. These specializations were: (1) the synchronization with the phenology of its host plant, and (2) the restriction of courtship and copulation to the specific host plant.

An example of how effective *U. affinis* is in locating a spotted knapweed plant which has flower heads of the size appropriate for oviposition occurred on August 22, 1974. At this time, six "early-emerging" *U. affinis* adults were seen on a spotted knapweed plant that was only 40 cm tall in a field where all surrounding spotted knapweed was about 100 cm tall. This plant's shoots had been severed at ground level on June 28, 1974. The subsequent regrowth resulted in flower heads on August 22 being the size preferred for oviposition by *U. affinis* females. This plant was the only spotted knapweed plant in the entire field with appropriate sized flower heads and, consequently, it had attracted six *U. affinis* adults that were present in the field. Zwölfer (1970) reported that the branched pattern of spotted knapweed was the main factor attracting flying *U. affinis*. He further stated that olfaction is probably not an important factor in host plant recognition. Nevertheless, the plant that attracted the six *U. affinis* had very short shoots and branches with an abundance of large leaves, the combination of which essentially eliminated any branching pattern. The relative insignificance of this small plant in the field plus its lack of a pronounced branching pattern lend credence to the idea that olfaction plays a role in host plant selection and that the branching pattern is not the only attracting feature.

Food requirements of *U. affinis* adults were not determined. The adults were frequently observed touching the surface of spotted knapweed flower heads with their proboscises, but it is not known whether any food material was ingested. Zwölfer (1969), in his discussion of *U. siruna-seva*, suggested that honeydew might be an important source of food. *U. affinis* adults in the laboratory were observed feeding on honey solution but since no association between *U. affinis* and insects producing honeydew was noted in the field, the extent of honeydew-type food utilization by *U. affinis* was not determined.

The only organism observed causing any degree of consistent mortality to *U. affinis* was a small spider, *Dictyna major* Menge, that captured the adult flies in its web. The webs of these spiders were found most often on spotted knapweed due to the plant's extensive branching and superior height over the other plants associated with spotted knapweed communities (Fig. 10). The webs, although small, were very efficient. A number of honeybees (*Apis mellifera* L.) and small wasps were seen in the webs along with many small insects of sizes comparable to *U. affinis*. Although it is possible that the large insects, such as the honeybees, captured in the webs were sick or otherwise weakened, the strength and efficiency of this spider's web was obvious. There is no indication that the *U. affinis* ensnared in the webs were merely weakened or senescent individuals. The strength of the web plus the speed at which the spider attacked the struggling insect made the spider very capable of attacking and killing even the most vigorous of individuals in the *U. affinis* size range.

The spider was present throughout the Bitterroot Valley in very large numbers. A survey conducted to measure the population density of the spider showed a highly significant correlation between the number of webs and the number of spiders. For the July 16, 1975, survey, $r = 0.99$ ($\bar{x} = 9.40$, $\bar{y} = 10.70$) and for the July 21 survey, $r = 0.99$ ($\bar{x} = 10.10$, $\bar{y} = 11.20$). In both samples, $\bar{y}$ (mean number of