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Fecundity, development and behavior of *Ceratapion basicorne* (Coleoptera: Apionidae), a prospective biological control agent of yellow starthistle

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Abstract

A laboratory colony of *Ceratapion basicorne* (Illiger) was established from adults reared from infested plants of yellow starthistle, *Centaurea solstitialis* L. (YST, Asteraceae), that were collected in eastern Turkey. Newly emerged adults fed on yellow starthistle foliage and mated, but females did not oviposit. The feeding rate of females decreased to almost zero by 16 d after emergence, whereas males continued to feed for at least 26 d. Dispersal activity was initially high but decreased to low levels in 2-3 weeks. After 6 weeks, most adults were hiding inside tightly curled dry leaves and in the crevices of crumpled paper towel. Insects were held in a cold dark incubator (5°C) for at least 3 months to terminate reproductive diapause. Females began ovipositing 4.4 d after being placed on YST leaves at 19°C. The oviposition period lasted a mean of 20.6 d, and lifetime fecundity was 34.5 eggs. Daily fecundity was high during the first 14 d of oviposition (1.8 eggs per d), then declined to low levels (0.3). Feeding rate of ovipositing females during the first two weeks was 19.2 holes per day, but this decreased to 4.7 for the remainder of the 45-d experiment. Female feeding rate was highly correlated to oviposition rate. Development time of eggs until eclosion of larvae at 19°C was 8.5 d and survivorship until eclosion was 73%. Development time from oviposition until adult emergence at about 19°C was 77 d. These results provide a foundation for conducting experiments to evaluate host plant specificity and potential impact on the weed.

Key words: life history, laboratory rearing, fecundity, longevity, weed biological control

Introduction

YELLOW STARTHISTLE (YST, *Centaurea solstitialis* L., Asteraceae: Cardueae) is a serious invasive alien weed in the western U.S. (Sheley et al. 1999). It originates from Eurasia and is a winter annual adapted to Mediterranean climate (Maddox 1981). Seeds generally germinate in the fall after the onset of winter precipitation, rosettes grow during winter and spring, then bolt in May to June, and continue flowering until frost or lack of moisture kill the plant. The plant has been the target of classical biological control since the late 1960s but, despite the introduction of six seedhead insects, it is not yet under control over most of its range (Turner et al. 1995, Piper 2001, Pitcairn et al. 2004). This suggests the need for agents that attack vegetative parts of the plant, and *Ceratapion basicorne* (Illiger) (Coleoptera: Apionidae) was considered a likely prospect (Zwölfer 1965, Rosenthal et al. 1994).

Ceratapion basicorne was studied as a prospective biological control agent of yellow starthistle by Clement et al. (1989). Larval transfer experiments and no-choice oviposition tests with five females captured in the spring in Italy indicated that the insect could oviposit and develop on safflower. However, in the wild this insect has been reared only from *C. solstitialis*, *C. cyanus* L., *C. depressa* M. Bieb., and *Cnicus benedictus* L., which suggests that it is highly host specific (Table 1; Alonso-Zarazaga 1990, Wanat 1994, Campobasso et al. 1999). The insect is common on yellow starthistle in Turkey, Greece, and Georgia (Rosenthal et al. 1994, Balciunas 1998, Uygur et al. 2005) and is widely distributed in Europe and western Asia (Alonso-Zarazaga 1990, Wanat 1994).

Ceratapion basicorne appears to be univoltine (Clement et al. 1989). Adults emerge from hibernation in the early spring, feed on leaves of YST rosettes and lay eggs in the leaves (from late March to early May in Italy). Larvae mine down the leaf midribs, feed mainly in the upper root (root crown) and lower stem, when the plant begins to bolt. Larvae pupate inside the plant, and adults emerge in late May to early July, which is when YST is bolting, and soon disappear. They are thought to aestivate and hibernate until the next spring. Adults have been found hiding under bark of apricot and peach trees in July in eastern Turkey (Hayat et al. 2002). The species is described and illustrated in two publications (Clement et al. 1989, Alonso-Zarazaga 1990, Wanat 1994).

Previous efforts to learn more about host specificity of *C. basicorne* have been limited by the inability to colonize the insect. The purpose of this study was to establish a laboratory colony and collect detailed information on fecundity, survivorship, and development time of the insect to facilitate rearing it, testing host specificity, and modeling population dynamics.

Materials and Methods

Colony origin, maintenance and insect behavior. Yellow starthistle plants infested with apionid larvae and pupae were collected by L. Smith at 15 sites near Kayseri, Sivas, Erzincan, Erzurum, and Malatya, Turkey between 28 May and 2 June 2001. Most of the foliage and stems, if present, were removed, and the plants were put in plastic bags with screen ventillation panels to minimize condensation, and kept in an insulated container. Ice was added to the container, when available, to retard deterioration of the plants. The plants were hand-carried to the USDA-ARS quarantine laboratory in Albany, CA on 6 June and were placed in sleeveboxes at room temperature to allow the adults to emerge. Plants were checked daily and emerged adults were collected and identified by L. Smith

before using them in experiments or to establish a colony. Identification of representative specimens was confirmed by B.A. Korotyaev, and vouchers were deposited at the USDA-ARS Systematic Entomology Laboratory in Beltsville, MD. We are continuing to maintain the colony on potted YST plants in the Albany quarantine laboratory.

Newly emerged adults of the field-collected generation were held in glass-topped sleeve boxes in the quarantine greenhouse for 6 weeks to observe their behavior and habitat preference (25 June to 7 Aug. 2001). Twenty-five males and 25 females were placed in each of 4 sleeve boxes (73 x 43 x 43 cm; length, width, height) in a greenhouse. Males are distinguished by apically dilated protibae and a strong ventral spine on the first metatarsomere, whereas females have uniform protibae and lack the spine on the first metatarsomere (Clement et al. 1989). Each sleeve box contained two potted YST plants, a flower pot containing sand (1.2 L), a petri dish with sand placed inside a box lying on its side to provide shade, and a paper cup lying on its side containing a crumpled paper towel. These provided different microhabitats for the insects to choose. Daily observations were made of the location of the insects that could be seen without disturbing the plants or habitats. After 6 weeks, the plants, sand, etc. were closely examined to determine the location of all the insects. A subsample of males and females were then weighed (live wt.), and the length of the elytra was measured using an ocular micrometer at 20x magnification. Elytra length was considered more reliable than body length because the latter can be affected by the angle of the head.

To measure adult feeding rate, newly emerged adults of the fourth generation were held individually with an excised YST leaf in a plastic tube in the laboratory at 22°C . In all experiments with excised leaves, the leaf (ca. 10 cm long) was inserted in a 4-ml vial containing tap water, sealed with an open-foam stopper, and positioned vertically. A small piece of tightly crumpled paper towel provided a place for the insect to hide. The experiment was conducted using two cohorts that emerged a week apart, and observations were made between 10 Sept. and 10 Oct. 2003.

We had to terminate reproductive diapause before we could conduct fecundity experiments. Newly emerged adults were kept in groups in paper cans containing excised YST leaves at room temperature and light for at least 1 week to permit feeding and mating. Adults were then held in a cold, dark incubator (24h dark, 5° C) for three or more months to terminate reproductive diapause. In the absence of information on what stimuli were required, it was hoped that the extreme photoperiod and cool temperature would be sufficient (Tauber et al. 1986). In later generations, we used 1: 23 h L: D and 25: 5°C diurnal cycle to allow the incubator to defrost. Insects were held in groups of about 20 in paper cans with excised YST leaves and crumpled paper towel to provide hiding places. Insects were removed from the incubator one day per week to change the YST leaves and to allow the insects to feed for about 6 hours on YST foliage at room temperature and ambient light. Insects were held at these hibernal conditions until used in the fecundity experiment.

Fecundity and adult survivorship. The females used in this experiment were from the second and third generation of the laboratory colony which had developed on potted YST plants. Five females emerged between 9 and 22 April 2002, (put into hibernal incubator 30 April 2002) and 28 females emerged between 13 Sept. and 15 Oct. 2002 (into hibernal incubator between 15 Oct. to 5 Nov.). Oviposition of 15 females (all emerged in Oct.) was observed from 22 Jan. to 7 March 2003, and a second group of 18 females (5 emerged in Apr., 13 in Oct.) was tested from 3 March to 21 April 2003. Pairs of male and female *C. basicorne* were placed in transparent plastic tubes (3.5 x 11 cm)

with screen lids containing an excised YST leaf. Males were removed after 2 days to minimize possible disturbance of the female. The experiment was conducted in a growth chamber at 25°C and 12: 12 h L: D photoperiod. One excised YST leaf, replaced every 2-3 d, was provided as food and oviposition substrate. Leaves were then held for 3 to 5 days at room temperature (12:12 h L: D, 22: 17°C; (mean 19.0°C), which permitted time for the eggs to darken and become more visible. Number of feeding holes (regardless of size) and eggs were counted under a microscope (20x) using back-lighting. Midribs were dissected to verify the presence of eggs. The experiment was terminated two weeks after all females had stopped ovipositing.

Egg Location and Development. Development time of eggs was observed during Nov. 2001 using eggs oviposited by the first generation adults (the generation that was collected as immatures in Turkey) using the same procedures and conditions above using excised YST leaves. Leaves were checked every 1 to 3 d and were removed from the female as soon as eggs appeared. Leaves were then checked every 1 to 3 d for egg eclosion to record survivorship, and all leaves were eventually dissected to confirm the presence of egg chorions and larvae, especially for those concealed in the midrib. For development time, leaves were checked daily for both oviposition and for larval eclosion. We studied 224 eggs produced by 39 females for location, 200 of these were suitable for survivorship and 54 for development time. Leaves that deteriorated before possible completion of egg development were omitted from survivorship analysis, and precise date of oviposition and emerence (within 24 h) was observed for only a subset of the eggs to obtain development time data.

Immature Development. Data on development time (egg to adult) were collected from 3 cohorts starting 4 Dec. 2002, 20 Feb. 2003, and 26 June 2003 for a total of 57 insects. For each cohort, individual females were held on single leaves inside a clear plastic tube with one end sealed to the petiole of a potted YST rosette by a slit foam plug and the other end covered with tulle. The leaves were checked every 1 to 3 d until eggs were observed. Plants were then held in sleeve boxes in the laboratory for about 2 weeks to check for presence of larval tunneling and then were transferred to screen cages in the quarantine greenhouse. In the laboratory the temperature oscillated between 22 and 17°C (day: night); mean = 19.0°C. Photoperiod was not controlled in the greenhouse, and the temperature was allowed to fluctuate between 16 and 27°C; mean = 18.9 $\pm$ 3.1 **(**sd**)** °C.

Results and Discussion

Identification and colony establishment. Insects were reared from 785 YST plants field-collected in Turkey, yielding 827 *C. basicorne* and 7 *C. orientale*. Of these, 51 specimens were sent to B. Korotyaev to confirm their taxonomic identification: all 47 specimens reared from YST collected in Turkey and used to establish the laboratory colony were identified as *C. basicorne*. Additional specimens reared from *Centaurea triumfetti* All. (probable identification) included 2 *C. basicorne* and 2 *C. orientale* (from plants collected near Goreme, Turkey on 28-V-01). *Centaurea triumfetti*, *C. cyanus* and *C. depressa* are very similar plants, all in the section *Cyanus* (Wagenitz 1975). Adult *C. basicorne* began emerging in the laboratory before 12 June and continued emerging until 1 July from YST plants collected in Turkey (Fig. 1). Samples were kept as cool as possible during the collection trip in Turkey, using insulated containers and ice, when available, so the observed emergence pattern may be delayed by several days relative to natural emergence in the field.

Sex ratio. The sex ratio of adults emerging from YST plants collected in Turkey was 53.9% female, which was not significantly different from 50% (chi-square test, $P > 0.5$). The sex ratio of second generation adults reared from YST plants in the quarantine laboratory (54.5% female; n = 220) was also not significantly different from 50%. Males did not emerge earlier than females (Fig. 1). Females tended to be larger than males based on fresh body weight (1.12 $\pm$ 0.03 vs. 0.92 $\pm$ 0.03 mg [SE]; n = 86 females, 74 males; *T*-test, $P < 0.001$) and elytra length (1.76 $\pm$ 0.02 vs. 1.61 $\pm$ 0.02 mm) (n = 34 females, 26 males; $P < 0.001$). Clement et al. (1989) observed similar differences in body size.

Behavior of newly emerged adults. Most adults in the sleeve boxes were not visible without disturbing the plants, sand or paper towel. However, the behavior of visible insects clearly changed during the course of the experiment. During the first 1-2 weeks, insects were more common on the glass ceiling, ventilation screen and sleeves, suggesting a short period of dispersal activity (Fig. 2). Insects were seen flying only rarely during the day. The number of insects observed on YST plants gradually increased during 5 weeks, probably because the bolting of the plants and decrease in number of rosette leaves made them easier to see. The large difference in the number of insects on the plants between the final observation and week 6 indicates how well the insects were hidden on the plants. They often were found hiding inside tightly curled dried-up leaves. It is probable that the vast majority of the insects were on the YST plants throughout the course of the experiment. At week 6, the crumpled paper towel, representing a shady, narrow-spaced microhabitat, was the second most preferred hiding place (chi-square, $P < 0.001$). Insects did not hide in loose sand or in the soil under the YST plants. Couples in mating posture were occasionally observed, either on the plants or in hiding places. Although there was evidence of adult feeding on the YST foliage, no eggs were observed. This suggests that the natural behavior of the insects is to feed and mate for a few weeks and then to find aestivation sites. The fact that most insects were still on the YST plants at the end of the experiment (7 Aug.) may be abnormal behavior, possibly due to a combination of 1) the inability to disperse from the sleeve box to find more preferred hiding places and 2) the presence of YST plants that were more immature and lush than would normally be encountered in the field at this season. Adults have not been seen on YST plants in the field any later than early July (M. Cristofaro [ENEA C.R. Casaccia, Rome, Italy], personal communication).

Adult feeding and oviposition. Adults feed on the leaf blade by creating a small hole and consuming all the tissue between the upper and lower epidermis as far as the rostrum can reach. This produces a characteristic transparent window with a small entry hole on one side (Fig. 3). In the laboratory, adults feed on both adaxial and abaxial surfaces, but in the field in early spring adults are usually found under the rosette leaves (Clement et al. 1989, M. Cristofaro & R. Hyatt [Ataturk University, Erzurum, Turkey] personal observation). Eggs are usually placed in small holes the same diameter as the egg. In the laboratory, these were often located on the leaf blade (60%), but in the field they may more often be located in the midrib (Clement et al. 1989). Placing a diffuse light source behind the leaf facilitated detecting the presence of eggs, which are yellow at first then darken to tan after about 3 days.

There was sexual dimorphism in the feeding rate of newly emerged adults (Fig. 4; $F_{(1,170)} = 24.3$, $P < 0.0001$, ANOVA). Feeding by females steadily decreased during the first two weeks from 9 to about 0.5 feeding holes per day (slope = -0.37, $P < 0.0001$), whereas that of males decreased more slowly during the 26-d study, from about 9 to

about 5 feeding holes per day (slope = -0.19, $P < 0.027$). The higher feeding rate of males may be related to mating activity. Colleagues in Russia also observed that newly emerged adults actively fed and mated. They dissected 6 individuals on 15 Aug. and 50% had well-developed fat bodies, suggesting that they were ready to diapause. At this time, many insects exhibited thigmotaxis, hiding in dry leaves and folds of filter paper (M. Yu. Dolgovskaya [Zoological Institute, St. Petersburg, Russia], personal communication).

Ovipositing females produced a mean of 19.2 $\pm$ 10.2 sd feeding holes per day during the first two weeks (Fig. 5B), when oviposition rate was high (Fig. 5A), but this decreased to 4.7 $\pm$ 2.0 for the remainder of the experiment. The feeding rate of non-ovipositing females (4.1 $\pm$ 1.0, Fig. 5C) was similar to that of ovipositing females during the post-oviposition period (Fig. 5B).

Fecundity and adult survivorship. Only 48% of the females oviposited, suggesting that many had not yet completed reproductive diapause. Females began ovipositing 4.4 $\pm$ 5.2 (sd) d after being placed on YST leaves at 19°C. The oviposition period lasted 20.6 $\pm$ 10.2 d (range 3-42), and lifetime fecundity was 34.5 $\pm$ 27.1 eggs (range 1-87). Daily fecundity was high during the first 14 days of oviposition (1.8 $\pm$ 1.2), then declined to low levels (0.3 $\pm$ 0.3; Fig. 5A). Feeding rate was highly correlated to oviposition rate (Y = 0.09 [$\pm$ 0.01 SE] * X; $r^2 = 0.82$; $P < 0.001$).

All of the females survived the 45-d duration of the fecundity experiment, except for one female that was lost, and one accidentally stuck to tape. This high longevity raises the question of whether the insects are able to survive more than one year in the field. In the laboratory, some of our insects have survived up to 135 weeks, being primarily held at hibernal conditions. The oldest female that we have observed to oviposit was 68 weeks old. Because insects were held in groups during hibernation, we do not know if any that stopped ovipositing were able to oviposit again after further hibernation.

Egg Development. Development time of eggs until larval eclosion at 19°C was 8.5 $\pm$ 0.1 (SE) d (range 7-10). Egg survivorship until larval eclosion was 73%. Some of the mortality was caused by cannibalism by other larvae that encountered an egg, apparently by chance. Occasionally the plant had a galling reaction that ejected the egg from the leaf tissue, which always resulted in death of the insect, regardless of whether the egg hatched. Eggs were primarily located in the leaf blade (60%), with 33% in the midvein or secondary veins and 7% beside a vein. Larvae eclosing from eggs in the leaf blade mined to the midrib and then directly down to the base of the petiole, which took 1-2 d. When more than one larva occurred on a leaf, they often made separate tunnels down the midrib, but if two larvae followed the same tunnel, the first larva was likely to be eaten by the second.

Immature Development Time. Development time from oviposition until adult emergence at approximately 19°C was 76.7 $\pm$ 15.0 (sd) d (Fig. 6, range 46-123, n = 57). Clement et al. (1989) reported a development time of about 24 d from larval eclosion to pupation at about 18°C. We measured egg development to require 8.5 d at 19°C, but have no data on pupation time. Assuming that the Italian and Turkish populations have similar development times, and that the two experimental conditions were similar, then this suggests a long pupation period (24 d).

Significance and future work. Successful establishment of a laboratory colony will allow us to conduct more extensive studies on the host specificity and biology of this prospective biological control agent. Previous work on this prospective agent was severely constrained by the difficulty of obtaining specimens that were reproductively

active (Clement et al. 1989, J. K. Balciunas [USDA-ARS, Albany, CA] personal communication). Although it is relatively easy to collect host plants containing maturing larvae and pupae, the newly emerged adults do not oviposit. However, by holding them in cold dark conditions for at least 3 months, it is possible to terminate reproductive diapause. Further studies need to be done to determine the specific requirements for terminating diapause. Our results on oviposition rate and oviposition period provide a foundation for planning host specificity tests, which will be crucial to determine the suitability of this insect as a biological control agent.

Acknowledgements

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Tables

Table 1. Host plants of *Ceratapion basicorne* collected in the field.

Adult reared from	Adult resting on
Centaurea solstitialis L.[a,b,c,d,e]	*Centaurea calcitrapa* L.[a,b,c]
Centaurea cyanus L.[b]	*Centaurea jacea* L.[a,b]
Centaurea depressa M.Bieb.[d]	*Centaurea rhenana* Bor.[b] (=*stoebe*, = *maculosa*, = *paniculata*)
Centaurea triumfetti All.[e]	*Centaurea scabiosa* L.[a,b]
Cnicus benedictus L.[d]	*Centaurea virgata* Lam.[a,b]
	Arctium lappa L.[a,b]
	Carduus pycnocephalus L.[a,b]
	Carduus tenuiflorus Curtis[a,b]
	Onopordum tauricum Wild.[a,b]

[a] Alonso-Zarazaga (1990).
[b] Wanat (1994).
[c] Campobasso et al. (1999).
[d] J. Balciunas and B. Korotyaev (personal communication).
[e] this paper.

Figures

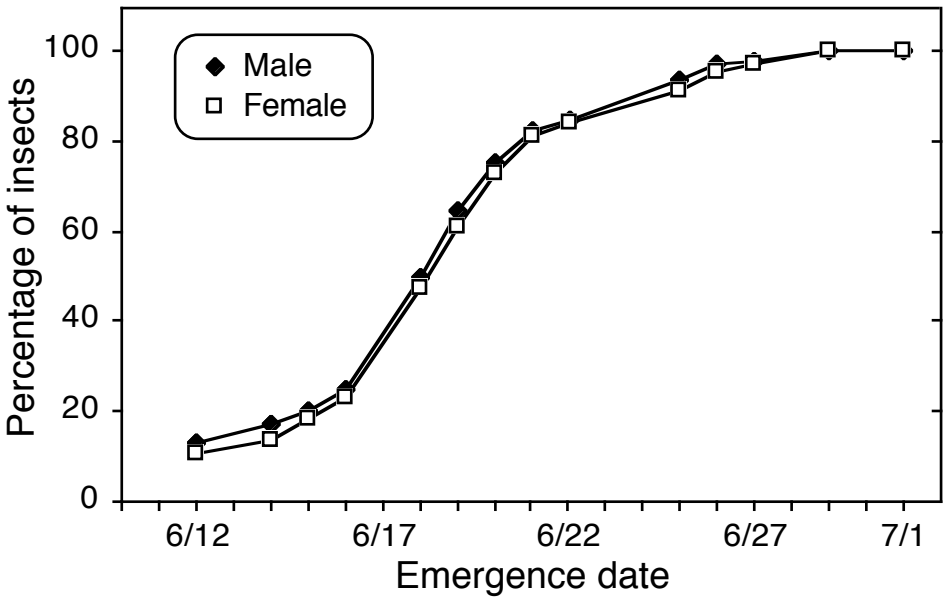

Figure 1. Cumulative emergence of adult *C. basicorne* from yellow starthistle roots collected in Turkey from 28 May to 3 June 2001 (sex ratio 53.9% female).

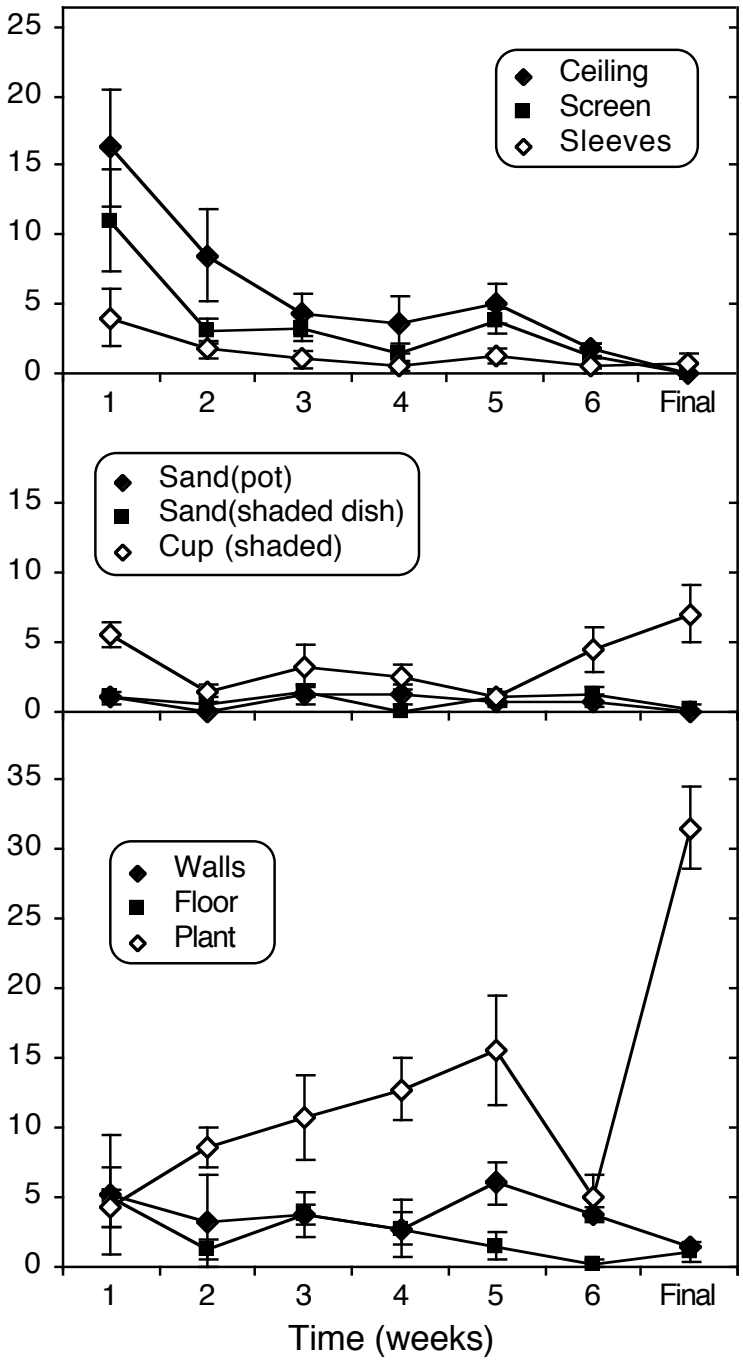

Figure 2. Location of newly emerged *C. basicorne* in a sleeve box in a greenhouse (ceiling - glass top, screen - window screen on back wall, sleeves - cloth sleeves sealing arm holes, sand(pot) - dry sand in flower pot, sand(dish) - dry sand in petri dish inside a shaded box, cup - cup lying on side containing a crumpled paper towel, walls - sides of sleeve box, floor - floor of sleeve box). During the first 6 weeks, insects were observed with minimal disturbance. The final observation was at the end of week 6 and included intensive sampling of all microhabitats. Mean $\pm$ SE of weekly sums of daily observations in 4 boxes, each containing 25 females and 25 males.

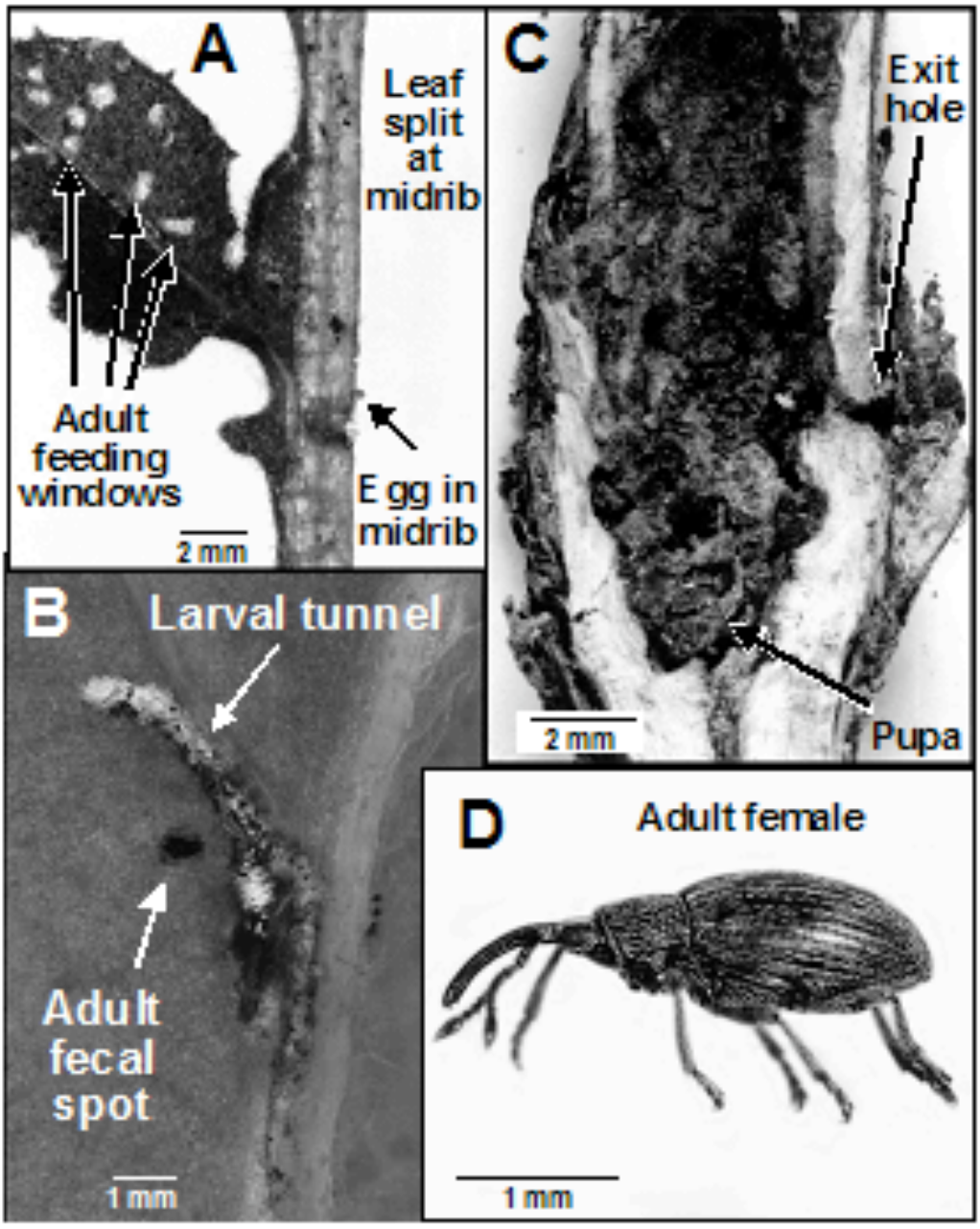

Figure. 3. A) Holes in leaves of yellow starthistle caused by adult feeding. Eggs are placed in narrow holes chewed in the leaf blade or midrib. B) Young larvae mine through the leaf blade to the midrib and down to the base of the petiole. Larvae from eggs placed in the midrib do not mine in the leaf blade. C) Damage to yellow starthistle root crown caused by many larvae. D) Adult female.

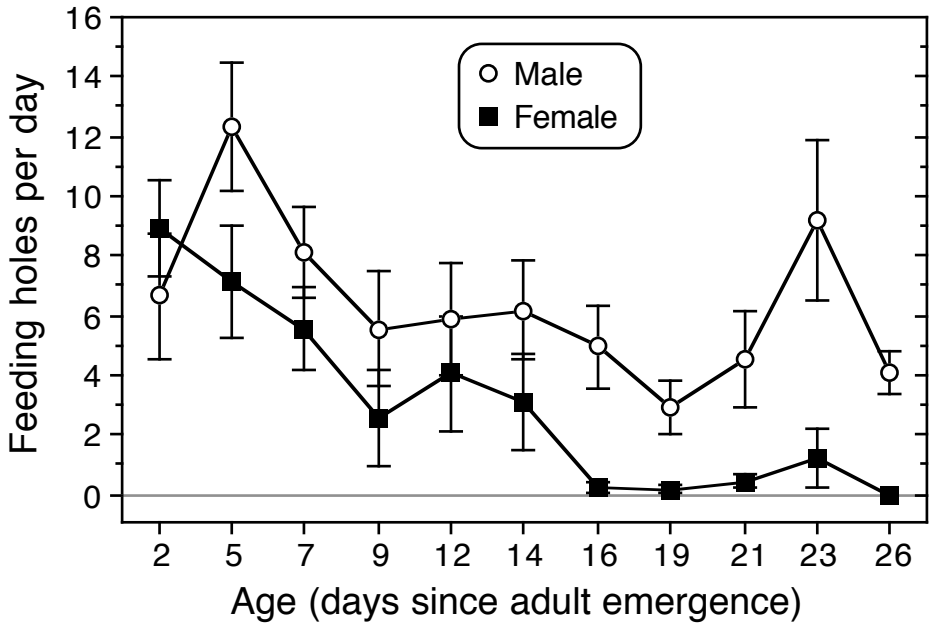

Figure 4. Feeding rate of newly emerged adult *C. basicorne* held individually on excised leaves of yellow starthistle in laboratory at 22°C day: 17°C night.

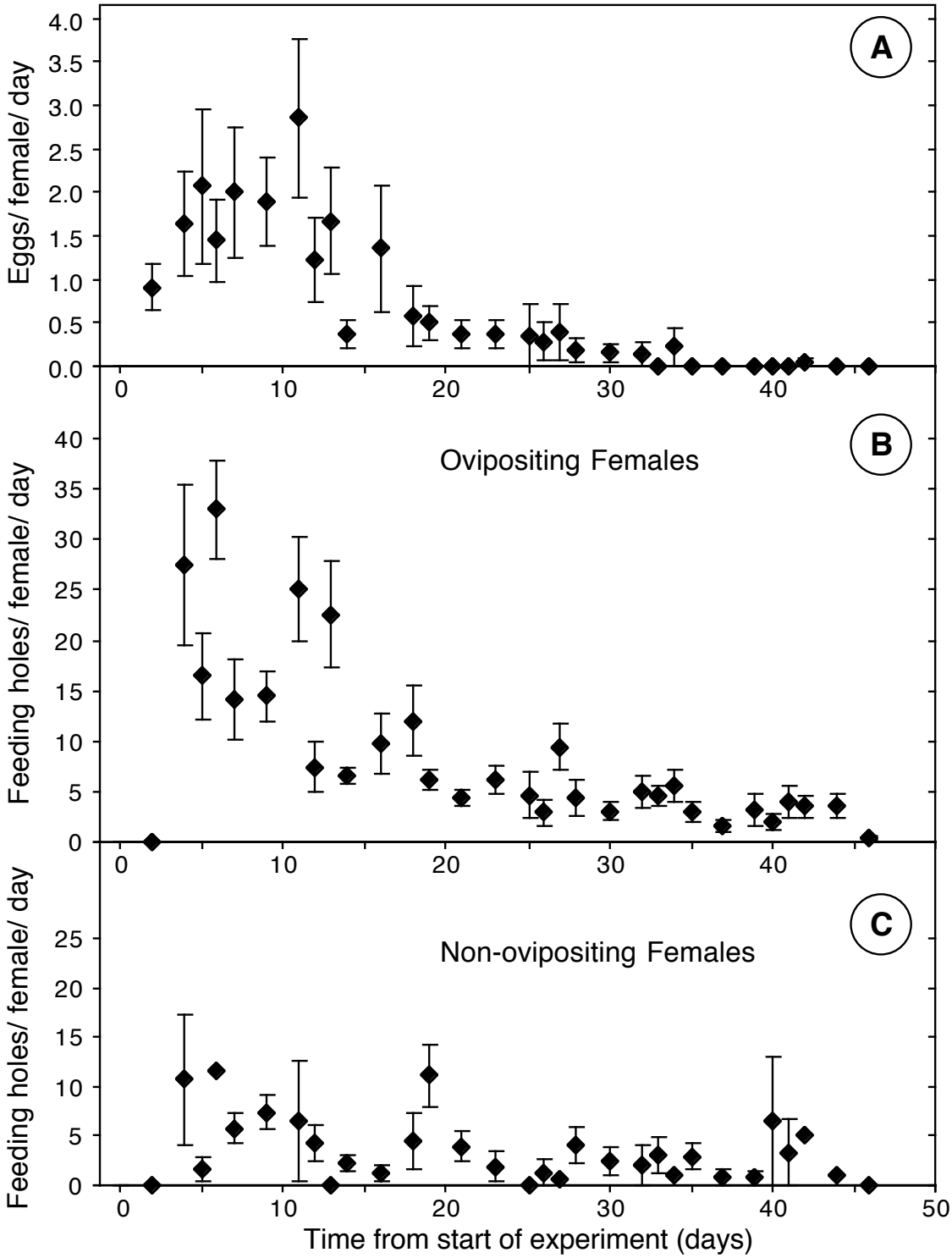

Figure 5. A) daily fecundity of *C. basicorne*, B) feeding rate of ovipositing females, C) feeding rate of non-ovipositing females, measured by counting number of feeding holes in foliage. Observations began when the insects were removed from hibernal conditions.

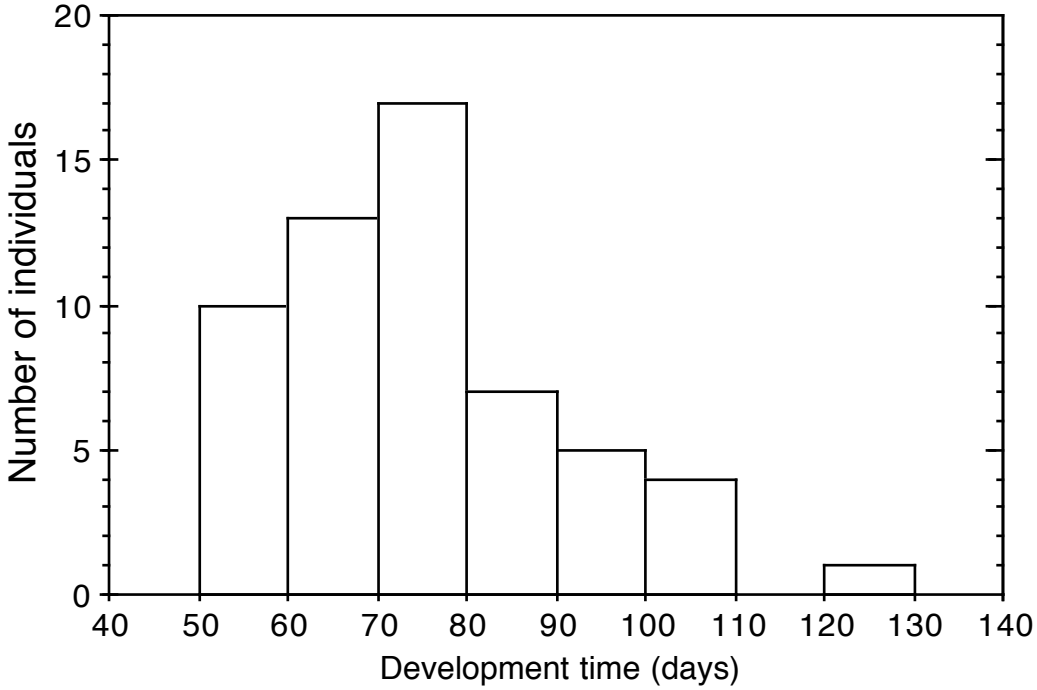

Figure 6. Frequency distribution of development time from oviposition to adult emergence of *C. basicorne* at about 19°C.