ACTIVITY PATTERNS OF *AMARA AULICA* (PANZER) (COL., CARABIDAE) IN A PATCHY BLACK KNAPWEED ENVIRONMENT

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ABSTRACT

We report observations on the behaviour and activity patterns of individually marked *Amara aulica* on Black Knapweed (*Centaurea nigra*) plants. Activity peaked in the early hours of the day, declined until about noon, with only low activity during the afternoon. The beetles fed on knapweed seeds, and flower heads were also used as mating sites. Some couples stayed *in copula* for at least six hours, and multiple copulations were recorded for both males and females. Beetles exhibited high site fidelity and moved only rarely to new knapweed patches. Some 10% of the flower heads in the study site were visited by beetles for feeding.

INTRODUCTION

In the course of a field study considering the insect community associated with the capitula of Black Knapweed, *Centaurea nigra* L., increasing numbers of adult *Amara aulica* (Panzer) forcing their way into the flower heads and feeding on the fresh seeds were observed towards the end of August 1993.

This carabid species is widely distributed in Europe and inhabits a broad range of habitats (Larsson, 1939, Lindroth, 1945, 1986). Although it occurs on many different soil types, the species' distribution is strongly influenced by vegetation type. In particular, the presence of plants of the family Compositae appears to favour the occurrence of the species (Lindroth, 1986), since *A. aulica* adults are phytophages with a preference for seeds of Compositae. In the vicinity of Prague, adults were abundant from July to September, with oviposition mainly in September and October (Hurka & Duchac, 1980). *A. aulica* has been previously reported to feed on Black Knapweed seeds (Lindroth, 1945) but the characteristics of the study site reported here with its experimentally introduced plants provided an opportunity to study some aspects of the ecology and dispersal behaviour of *A. aulica* in a semi-natural/semi-experimental environment.

In the present paper i) seasonal and daily activity patterns are described, ii) observations on general and dispersal behaviour of individually marked beetles are reported and, iii) the impact exerted by feeding beetles on the flower heads in the site is discussed.

MATERIALS AND METHODS

The study site, a rich unmown meadow dominated by ryegrass (*Lolium*

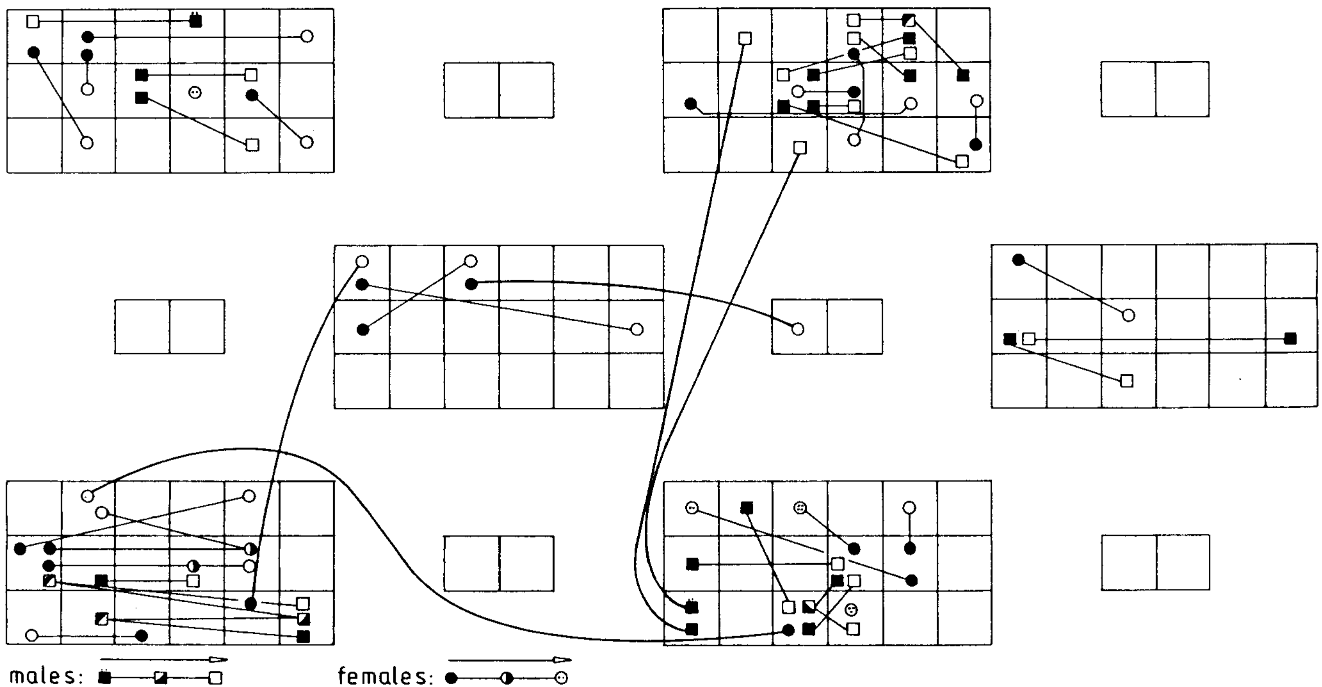

Fig. 1. — Arrangement of patches of Black Knapweed plants in the study site (not drawn to scale). Each square represents one plant. Distances between rows were about 7m, and between-patch distances within rows were about 5m. Movements of male and female *Amara aulica* within and between Black Knapweed patches are also shown. Dots added to symbols for males and females indicate the number of different days on which a single beetle was seen on the same plant.

perenne L.), is situated on the campus of Nottingham University. In February 1993, 12 patches of Black Knapweed were established in one part of the meadow. There were six patches with two plants and six patches containing 18 plants. Large and small patches were alternately arranged in three rows on an area 22m long and 19m wide (see fig. 1).

Observations were made on 14 days during a 22-day period starting on 24 August 1993. During each census (30–45 minutes), all Knapweed plants were inspected. Beetles were counted and the sex of each identified where this was possible without disturbing them. At first, censuses were made both in the mornings and in the afternoons but were later restricted to the time between 08:00 and 10:00 hours. Two additional censuses were made during the night.

A total of 119 beetles was individually marked using coloured model dope paint (Humbrol enamel) after anaesthetizing with CO_2. Beetles were marked on six days only in order to keep disturbance at a minimum (Southwood, 1978). Marked individuals were released on or close to the plants on which they had been caught. Both Knapweed plants and their flower heads had been labelled individually, so it was possible to record not only the presence of marked and unmarked beetles but also their exact location on the site.

All means given in the text are ±1 SE.

RESULTS

Seasonal and diurnal activity patterns

After the first few days of observation it became clear that beetles were more numerous in the mornings, while fewer individuals were seen on the plants in the afternoons (see figs 2 & 3). In view of this, the ideal time to start a census appeared to be early in the morning, when the sun was about to rise above the trees surrounding the study site (i.e. 8:00 to 9:00 a.m.). From these 'standard censuses', abundances were fairly constant during the first two weeks (40.2 ± 3.1 ind./census), but declined considerably in the final week (fig. 2). It is not known whether this decrease is due to *Amara* mortality, or to changes in the relative abundance of food resources: it is possible, for instance, that the number of fresh soft seeds was reduced in the course of time, thus rendering the knapweed heads less attractive.

Average numbers of beetles observed in particular time intervals were calculated across census days to reflect the diurnal activity pattern of *A. aulica* adults (fig. 3). Beetles tended to leave the plants by noon and censuses made after dusk (August 26) and before dawn (September 3) suggested that they climbed up again late at night.

Individual behaviour

A total of 42 clearly identifiable individuals was recorded for two or more times on different days. Mean differences between the day of

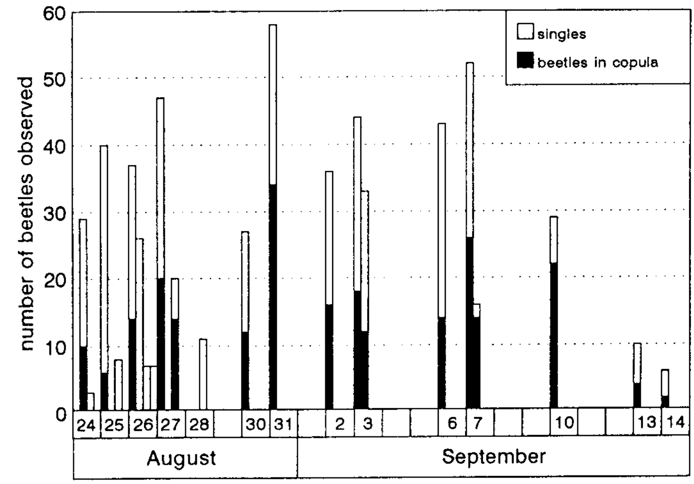

Fig. 2. — Numbers of *Amara aulica* adults seen during censuses in the study period (1993). For each date, columns positioned in the left and right half of the space available represent a.m. and p.m. censuses, respectively.

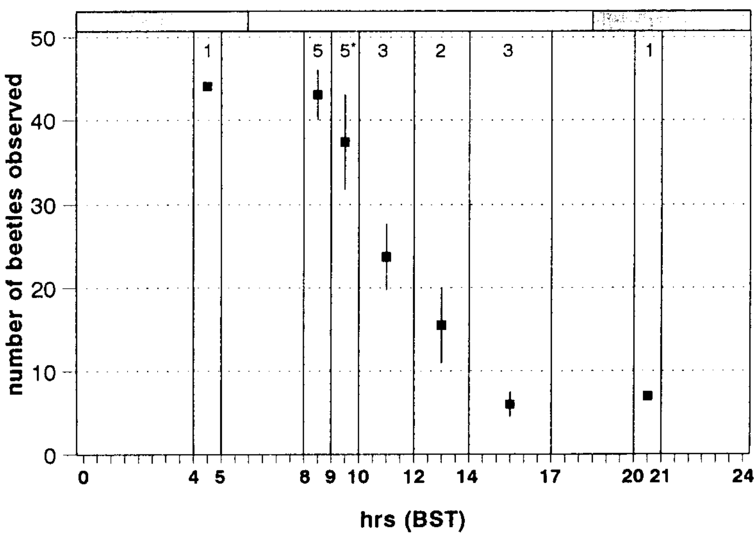

Fig. 3. — Mean numbers (±1 SE) of *Amara aulica* adults recorded on Black Knapweed plants at different times of day. Numbers of censuses per time interval are indicated; * = the final two censuses (September 13 and 14) were omitted, because overall numbers of *Amara* had declined substantially.

marking and the last observation date (fig. 4) were 4.0 ± 0.5d in females and 5.4 ± 0.7d in males, but these means did not differ significantly (one-way non-parametric ANOVA; $p > 0.05$).

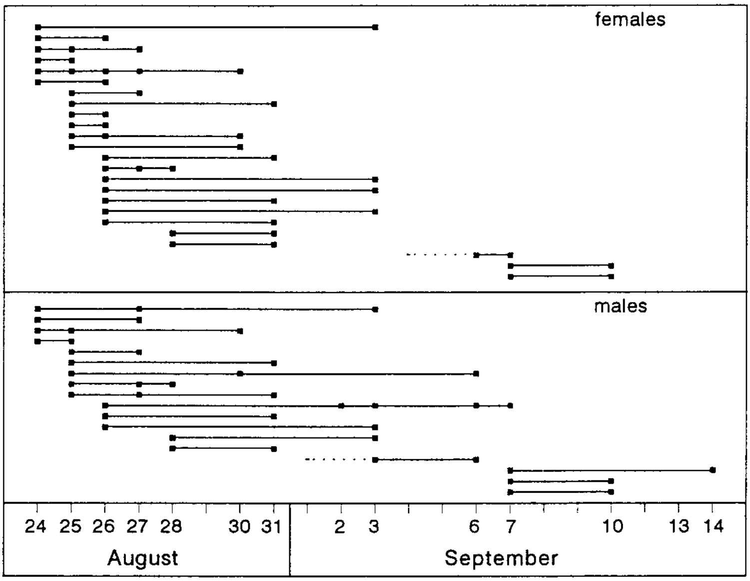

Fig. 4. — Time intervals between first date of observation and last date of recovery of individually marked *Amara aulica* adults in the course of the study period (1993).

Copulations lasted for several hours: identical couples were recorded 2 to 6 hours after first being observed. Three females and five males were recorded *in copula* with two different partners; intervals between the two observations were 3 to 6 days and 2 to 4 days for females and males, respectively. Copulating with a second partner might be more likely in males than in females but again the difference between sexes was not significant. The typical posture of copulating pairs was with the male sitting on the female's back, while her head was sunk into the flower head, probably for feeding. Couples like this were observed in 108 cases (216 individuals).

Males feeding as singles were recorded in 36 instances and there were 34 records of non-feeding males roving on the stems and leaves. The figures for females were 73 and 14, respectively. Thus males and females differed significantly in their utilization of food resources (chi-squared test, $p < 0.001$). This finding agrees with the assumption that feeding should be more important in females, which are likely to convert seed biomass to egg biomass.

Individual marking further allowed description of the movements of *A. aulica* adults within and between knapweed patches. Generally, both males and females seen on two or more different days had stayed in the knapweed patch in which they had been encountered first (fig. 1). Within the patches, the mean distances between two plants on which the beetles were observed on different census dates was 115.2 ± 19.2cm (n = 28) for females and 148.6 ± 19.9cm (n = 25) for males. Average within-patch distances covered per day were 81.6 ± 20.7cm/d for females and 67.4 ± 16.2cm/d for males. Only three females and two males were found to change patches (fig. 1), so the overall ratio between within- and inter-patch movements was 53 to 5. Thus, both sexes tended not to change patches.

DISCUSSION

Luff (1978) described the diurnal activity pattern of *A. aulica* based on pitfall trap catches made in a field of heather and found the species to be nocturnal. Activity patterns of beetles moving on the ground may differ from the patterns exhibited by individuals who are feeding, searching for mates and copulating on knapweed plants. Luff's findings do agree with our assumption that knapweed heads are entered around midnight, but in contradiction to Luff's results, the present study showed that a large proportion of the population remained active on the heads until about noon.

Movements of predacious carabid beetles have often been studied, and their ability to (re-)colonize arable fields has been emphasized (e.g. Knaust, 1990; Baars, 1979; Welling, 1990). Predacious ground beetles of a size similar to *A. aulica* can cover some 2 to 4m/d (Welling, 1990; Assmann, 1995), and thus movements within the knapweed patches were rather slow. *A. aulica* adults should, however, disperse little after having arrived at such a favourable habitat.

Adults of *A. aulica* entered the heads of Black Knapweed to feed on the seeds. Both sexes were observed feeding, but female feeding was more common. The proportion of males and females seen feeding as singles was 36 : 73. However, in copulating pairs the female can also be assumed to feed or to have been feeding, and therefore the ratio changes to 36 : 182; we conclude that females fed about five times more often than males.

Van Huisen (1977) reported that *A. plebeja* switched from feeding on grass to seed feeding during the reproductive period. According to Larsson (1939), *A. aulica* is an autumn-breeding species, and this is also indicated by the high number of copulations recorded during the present study. Thus the observations reported here can be interpreted as consequences of the large food demands of females: nutrients obtained from the seeds are probably allocated to reproductive effort.

The present study was conducted in connection with studies considering the fauna of Black Knapweed heads. The knapweed plants had been planted in February 1993, hence the *Amara* population was offered a food resource entirely new to the site, but readily attacked and exploited. How big was the impact of feeding by *A. aulica*?

We should first consider beetle abundance. Unfortunately, marking individuals was not always successful since the paint used did not always dry before the beetles resumed activity, obscuring the colour pattern: thus in some cases, marked beetles could not be identified individually. It was therefore not possible to use the Jolly-Seber method of population estimation (which would have been the more appropriate statistic in this situation), and hence we give only a very tentative estimate of the population size of *A. aulica* based on the Lincoln-index (see Southwood, 1978). The median value of population sizes estimated for the 'standard censuses' was 365 individuals during the first two weeks of the study period (this estimate was based on those censuses where marked beetles accounted for more than 10% of all beetles observed). It is not known whether the decline in numbers of recoveries of beetles marked early during the study period (fig. 4) is due to mortality or to reduced food demands; the latter would have led them to be recorded only rarely on the plants. It seems likely that some beetles observed early in the study period were replaced by other individuals emerging later in the year, or taking longer to arrive at the knapweed patches.

335 heads were seen visited by beetles during this study, but this is only a minimum value. It is not likely that many heads were visited on those days on which no censuses were made, because these days were usually cold and/or wet. However, beetles may switch between heads during a single night. The total number of knapweed heads which set seeds is not known exactly, but 3,000 to 4,000 heads is a reasonable estimate. Thus, feeding by *A. aulica* adults should affect approximately 10% of Black Knapweed heads.

The damage done, i.e. the number of seeds taken, is not known. Johnson & Cameron (1969) fed different types of grass seeds to various North American carabid species and recorded feeding rates of between 3 and 20 seeds per individual per night. *A. aulica* is about four times larger than the *Amara* species considered in their study, but knapweed seeds are probably larger too, although the difference cannot be quantified exactly: the biomass values given by Johnson & Cameron (1969) are supposedly fresh weight data, while only dry weights are available for knapweed seeds. On the other hand, 23 heads were recorded as visited by beetles on two different days, and there was one head which was visited on three different days, suggesting that the seeds are not fully exploited during one single feeding bout.

Overall, reproduction of Black Knapweed appeared thus to be affected by seed feeding *Amara aulica* to a moderate degree; whether feeding by the beetles also inflicts mortality on the insect fauna of Black Knapweed flower heads deserves further study.

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Further observations on Tribolium castaneum (Herbst) (Col., Tenebrionidae), especially in arboreal contexts. — On 2.vi.1998, whilst examining small exfoliated bark platelets 35cms from the ground on the trunk of a 22 year old apple tree, *Malus* "Flanders Pippin", at Little Comberton, Worcestershire (SO 94), I caught sight of an ostensible *Tribolium*. Removing a number of the bark platelets, I eventually located 16 imagines of *Tribolium castaneum* (Hbst), 48 *Cryptolestes ferrugineus* (Ste.) (Col., Cucujidae) and 1 *Cis bilamellatus* Wood (Col., Ciidae).

In addition, *T. castaneum* was noted higher up the trunk, at a height of about 200cms, clustered in threes and fours, also around exfoliating bark platelets. The beetles were nearly all on the southern aspect of the trunk, and were associated with fairly dry, powdery, necrotic, but not visibly fungoid, tissue between the outer bark and cambium. On 22.vi.1998, the same association of *Tribolium castaneum* and *Cryptolestes ferrugineus* was observed in pits of necrotic tissue (like minor non-proliferating canker-lesions) under thin bark flakes of an intact but senile apple tree, *Malus* "Cox's Orange Pippin", planted in 1944, also at Little Comberton. This is apparently the first evidence of *T. castaneum* occurring in numbers on trees in Britain, and may well be a further instance of "habitat reversion" following the recent episode of climatic warming, as discussed elsewhere by Whitehead (1991, *Entomologist's Rec. J. Var.*, **103**: 139–140; 1997, *Biologia, Bratislava.*, **52**(2): 147–152) and Alexander (1998, *Coleopterist*, 7(1): 21), and previously by Allen (1965, *Entomologist's mon. Mag.*, **101**: 115). This notion is given further support by examples of *T. castaneum* knocked from the dead branches of large ash (*Fraxinus excelsior* L.) trees in open country at Dumbleton, Gloucestershire (SP 03, 130m alt.) on 25.vi.1998, and at Stanton, Gloucestershire (SP 03, 200m alt.) on 3.vii.1998. This latter specimen appears to have been associated with necrotic areas close to ash canker bark lesions, a highly distinctive niche of considerable significance for a beetle which had previously been regarded as strongly anthropocentric in Britain.

Finally, when a number of reports reached me of nocturnal insects accompanying people asleep in bed in the Pershore area of Worcestershire during June 1998, I was able to confirm that these were also *Tribolium castaneum*. Their objectives remain a matter of speculation. — P.F. WHITEHEAD, Moor Leys, Little Comberton, Pershore, Worcestershire, WR10 3EH: *July 9th*, 1998.