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# Spatial population structure of the predatory ground beetle *Carabus yaconinus* (Coleoptera: Carabidae) in the mixed farmland-woodland satoyama landscape of Japan

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**Key words.** Coleoptera, Carabidae, *Carabus yaconinus*, adult movement, agroecosystem, conservation biological control, ecotone, forest edge, mark-recapture, natural enemy, sexual behaviour

**Abstract.** To conserve the predators and parasitoids of agricultural pests it is necessary to understand their population structure in a mixed landscape, and to consider the spatial and temporal changes in their distribution and movement of adults and larvae. We studied the distribution and movement of the ground beetle *Carabus yaconinus* (Coleoptera: Carabidae), which inhabits farmland-woodland landscapes. We placed a large number of pitfall traps along the border between a wood and an orchard and counted the number of *C. yaconinus* adults and larvae caught in the traps from 13 April to 28 June 2005. Some of the adults were marked before they were released. Adults were most abundant at the edge of the wood and the number caught gradually decreased when entering into the wood. In contrast, larvae were only found in the interior of the wood, although they moved closer to the edge of the wood as they matured. Adult females were collected within the wood and neighbouring orchards more frequently than adult males. It is likely that females enter woodlands in search of oviposition sites and leave woodlands in search of high-protein food sources to support reproduction. For sustaining populations of *C. yaconinus* it is necessary to have woodlands of at least 60 m in width adjacent to farmland. It is possible to design an appropriate landscape if the habitat requirements of the predatory arthropods are well understood.

## INTRODUCTION

Agricultural landscapes generally include farmland, such as fields or orchards and semi-natural habitats (non-crop vegetation), such as woodland, hedgerows, or grassland. In Japan, such a mixed rural landscape is called satoyama (Yamamoto, 2001; Takeuchi, 2003). The conservation of semi-natural habitats leads to an enhancement of the numbers of natural enemies present in fields and orchards (Landis et al., 2000; Altieri & Nicholls, 2004; Tscharntke et al., 2007), because many predatory invertebrates require a variety of habitats to complete their life cycle (Tucker, 1997; Delettre et al., 1998). As farmland is regularly disturbed by tilling, planting, pesticide and fertiliser application and harvesting the more stable semi-natural habitats can serve as temporal refuges for invertebrates (Gravesen & Toft, 1987; Bedford & Usher, 1994). Furthermore, semi-natural habitats are critical for the reproduction and overwintering of some natural enemies (Lyngby & Nielsen, 1981; Desender & Alderweireldt, 1988).

Ground beetles (Coleoptera: Carabidae) are considered to be beneficial arthropods as they are generalist natural enemies of various agricultural insect pests and have been studied intensively in Europe and North America (Thiele, 1977; Luff, 1987; Luff et al., 1992). They are ubiquitous in agricultural landscapes and prey on a great variety of pest insects (Sunderland, 2002). Semi-natural elements, such as hedgerows or woodland, are important overwintering habitats or temporary refuges for ground beetles (Thomas et al., 1991, 2000; Collins et al., 1996). However, most studies have focused on the distribution and movement of adult beetles (Landis et al., 2000; Lee et al., 2002; Altieri & Nicholls, 2004; Tscharntke et al., 2007) with little attention to habitat use by larvae. This is true not only for ground beetles, but also for many other predatory invertebrates (Altieri & Nicholls, 2004; Samways, 2005). In addition, differences in the movements of the adults of both sexes of predatory arthropods, especially those related to female oviposition, are rarely studied, although the importance of such studies is often stressed (Collins et al., 1996; Thomas et al., 2000; Altieri & Nicholls, 2004; Samways, 2005). Of importance for butterfly conservation is the observation of Dennis et al. (2003) that butterflies utilise different resources at different stages during their development. To conserve ground beetles, it is necessary to understand their population structure in a mixed landscape and consider the spatial and temporal changes in their distribution and the movements of adults of both sexes and of larvae.

*Carabus yaconinus* Bates, 1873 (Coleoptera: Carabidae) was selected as a model predator. This species is common in woodland, farmland and suburban areas throughout the lowlands of south western Japan (Yahiro et al., 2001). Its adults feed on the larvae of Lepidoptera and Diptera, as well as earthworms, and the larvae on

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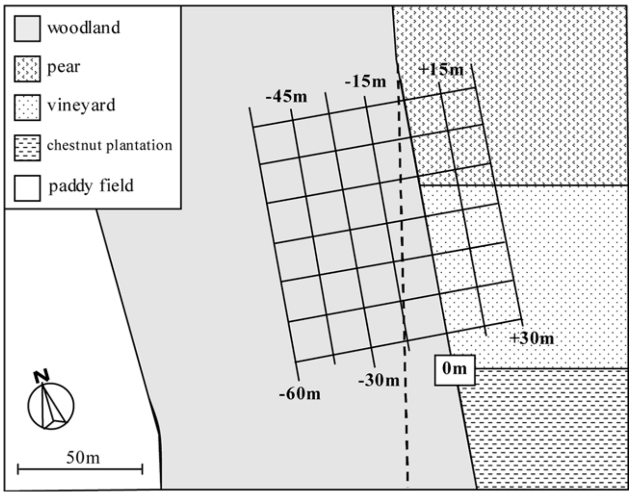


Fig. 1. Diagramme of the coppice woodland-orchard boundary area. The lattice indicates the arrangement of pitfall traps at the boundary; points of intersection indicate the locations of traps. A line of seven pitfall traps (0 m line) was placed along the woodland edge and other lines of traps at distances 15 m apart parallel to this line. In total, 49 traps were placed in a grid of 90 × 90 m. A path of approximately 3 m in width through the woodland is indicated by the broken line.

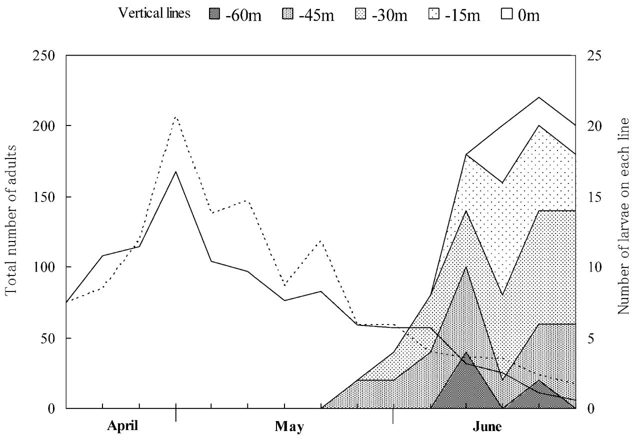


Fig. 2. Seasonal changes in the numbers of adults and larvae of *Carabus yaconinus* caught, females (broken line), males (solid line) and larvae (shaded areas). The distribution of larvae in the trap lines placed at different distances into the woodland is indicated on the right y axis.

earthworms (Sota, 1985a). Adults are often observed in open agricultural fields adjoining woodlands (Kagawa et al., 2008). The distribution and movement of *C. yaconinus* adults and larvae in a boundary area between coppice woodland and an orchard were recorded in order to address the following questions. (1) Do the adults and larvae have different habitat requirements? (2) Does the movement of male and female adults differ, and if so, why? (3) How should mixed farmland-woodland landscapes be managed in order to have a high abundance of natural enemies predatory arthropods that require a spatially heterogeneous habitat?

## MATERIAL AND METHODS

### Study site

The field study was done at the Food Resources Education and Research Centre of Kobe University (34°52′N, 134°51′E; 55–58 m a.s.l.) and in neighbouring woodland in Kasai, Hyogo Prefecture, Japan, in 2005. In this area the flat landscape consists of paddy fields, meadows, farm ponds, orchards and coppiced woodlands dominated by deciduous oak trees. In western lowland Japan, the succession of lightly coppiced deciduous broad-leaved woodland to dense and dark woodland with some evergreen trees is prevented by the farmers felling the trees for fuel and charcoal every 20 to 30 years (Yamamoto, 2001; Takeuchi, 2003). The woodland of the study area was still frequently coppiced and dominated by deciduous broad-leaved trees, but 30 years had elapsed since trees were felled so the canopy was mostly closed. This study was done in the border area between an orchard and woodland (Fig. 1). At the edge of the woodland the shrub layer was dominated by *Pleioblastus* sp. and *Quercus serrata* and *Q. acutissima* dominated the tree layer. In the interior of the woodland the tree layer was also dominated by *Q. serrata* and *Q. acutissima*, with some bamboo and *Carpinus spp*. Pear trees and vines were planted in the orchard. The orchard floor was thinly covered by fallen leaves and leaf mould and a few grasses and other weeds, which were more abundant around the bases of the pear trees and vines.

### Experimental design and sampling

Adults and larvae were sampled using pitfall traps (plastic cups 80 mm in diameter and 95 mm deep). Forty-nine pitfall traps were placed in a 90 m grid at the woodland–orchard border (Fig. 1). The lines of the grid either ran parallel to ("parallel lines") ("vertical lines") or perpendicular to the edge of the woodland ("perpendicular lines") ("horizontal lines"). Each trap had two or three drainage holes at the bottom; a plywood roof (12 × 12 cm) was placed above the trap to exclude sunlight and rainwater. The traps were operated dry and their rims were flush with the soil surface.

Carabid beetles were caught in the dry pitfall traps from 13 April to 28 June 2005. The traps were checked every 2–3 days and the number and sex (adults only) of *C. yaconinus* adults and larvae were recorded. Some of the adults were individually marked by using a hand drill (No. 28600, PROXXON) to carve a unique number on their elytra. About 30 individuals in total were marked per day from 13 April to 24 May. All the adults were released at the same location as they were captured. The trap location and date of recapture were recorded for each adult. We released a total of 377 marked adults (221 males and 156 females). Larvae were released without marking.

We also determined the density of earthworms at the edge of the woodland, in the orchard ~30 m from the edge and in the woodland ~30 m from the edge, from April to June 2004. In each area there were six plots 5 m apart parallel to the edge of the woodland. The number of earthworms in a quadrat of 1 m × 1 m × 5 cm depth in each plot was counted each month.

### Statistical analysis

The total numbers of *C. yaconinus* adult females, adult males and larvae caught in each pitfall trap were log transformed, if necessary, prior to analysis of variance (ANOVA). Variation in the numbers of adult males, adult females and larvae caught in the parallel, vertical and perpendicular, horizontal lines of traps was analysed using two-way factorial ANOVA without replication. Scheffé multiple comparisons of the catches of the vertical lines were also performed for each variable. The binominal test was used to test for a biased sex ratio (difference from 1 : 1) for catches in each line vertical to the edge of the woodland.

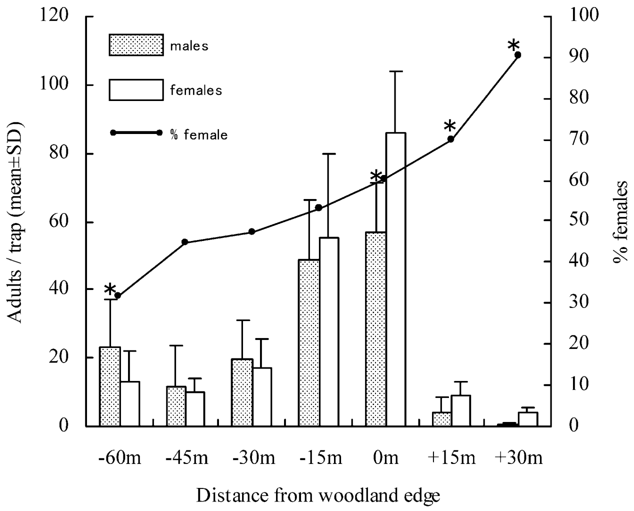


Fig. 3. Distribution of *Carabus yaconinus* adults caught in each vertical trap line and the percentage that were females. *P < 0.05 indicates a significant difference from an equal sex ratio (1 : 1), based on the binominal test.

The mean numbers of earthworms per m$^2$ in the three areas (i.e., woodland interior, woodland edge and orchard) in each of the three months (i.e., April, May, and June) were compared using repeated-measures ANOVA. Scheffé multiple comparisons were used to compare the areas.

The shortest distances between the release and recapture points for males and females was compared for periods of 1–10, 11–30 and >30 days after release using the Mann-Whitney U-test. We also calculated the coefficient of rank correlation between the shortest distance moved and the time in days since release for both males and females. All analyses were performed using SPSS 11.0 for Windows (SPSS Inc., Chicago, IL, USA).

TABLE 1. The results of a two-way ANOVA of the numbers of adult males, adult females and larvae caught per trap.

| Factors | df | Mean square | F-value | p-value |
|---|---|---|---|---|
| Males[1] | | | | |
| Vertical line | 6 | 3.371 | 65.162 | <0.001 |
| Horizontal line | 6 | 0.143 | 2.754 | 0.056 |
| Residuals | 36 | | | |
| Females[1] | | | | |
| Vertical line | 6 | 3.219 | 68.131 | <0.001 |
| Horizontal line | 6 | 0.090 | 1.903 | 0.107 |
| Residuals | 36 | | | |
| Larvae | | | | |
| Vertical line | 4 | 3.871 | 15.093 | 0.008 |
| Horizontal line | 4 | 0.084 | 1.233 | 0.325 |
| Residuals | 16 | | | |

[1] Log-transformed number.

## RESULTS

### Spatial distribution of adults and larvae

In total 2235 adults (1213 females and 1022 males) were collected from April to June. There was a large peak in the numbers caught in late April (Fig. 2). The number of individuals caught per trap differed significantly among the vertical lines for both females and males, but not among the horizontal lines (Fig. 3, Table 1). Most females and males were caught in the traps in the 0 m line (boundary between the woodland and orchard) and the numbers caught differed significantly from those caught in any other vertical line, except for the –15 m line (in the woodland; Fig. 3, Table 2). In the interior of the woodland the number of adults caught per trap declined gradually with increase in distance from the edge of the woodland. Fewer adults were caught in the orchard than in the woodland (Fig. 3, Table 2). More females than males were caught in the traps in vertical lines 0 m, +15

TABLE 2. P-values for the Scheffé multiple comparisons test of the numbers of adult males, adult females and larvae caught per trap in the different vertical lines of traps.

| Males[1] | +15 m | 0 m | –15 m | –30 m | –45 m | –60 m |
|---|---|---|---|---|---|---|
| +30 m | 1.000 | < 0.001 | < 0.001 | < 0.001 | < 0.001 | < 0.001 |
| +15 m | – | < 0.001 | < 0.001 | < 0.001 | < 0.001 | < 0.001 |
| 0 m | – | – | < 0.001 | < 0.001 | < 0.001 | < 0.001 |
| –15 m | – | – | – | < 0.001 | < 0.001 | 0.111 |
| –30 m | – | – | – | – | 0.926 | 1.000 |
| –45 m | – | – | – | – | – | 0.172 |
| **Females[1]** | **+15 m** | **0 m** | **–15 m** | **–30 m** | **–45 m** | **–60 m** |
| +30 m | 1.000 | < 0.001 | < 0.001 | < 0.001 | < 0.001 | < 0.001 |
| +15 m | – | < 0.001 | < 0.001 | < 0.001 | < 0.001 | < 0.001 |
| 0 m | – | – | 1.000 | < 0.001 | < 0.001 | < 0.001 |
| –15 m | – | – | – | < 0.001 | < 0.001 | < 0.001 |
| –30 m | – | – | – | – | 1.000 | 1.000 |
| –45 m | – | – | – | – | – | 1.000 |
| **Larvae** | **–15 m** | **–30 m** | **–45 m** | **–60 m** | | |
| 0 m | 0.975 | 0.019 | 0.181 | 1.000 | | |
| –15 m | – | 1.000 | 1.000 | 0.371 | | |
| –30 m | – | – | 1.000 | 0.042 | | |
| –45 m | – | – | – | 0.057 | | |

[1] Log-transformed number.

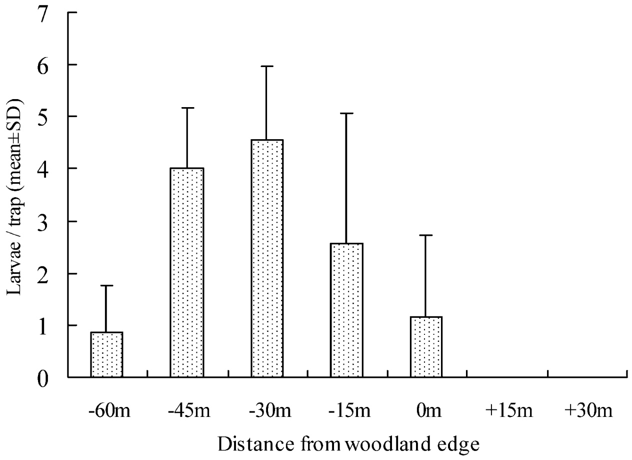


Fig. 4. Distribution of *Carabus yaconinus* larvae caught in each vertical trap line.

m and + 30 m. The percentage of females in the catches in the orchard gradually increased with distance from the edge of the woodland, indicating that females travelled further into the orchard than males.

Throughout the period of investigation 95 larvae were caught in the woodland. The first larva was caught on 20 May and the number peaked in mid-June (Fig. 2). The number of larvae caught differed significantly among the vertical lines (Tables 1 and 2) and was greatest in the –30 m line (within the woodland; Fig. 4). Few were caught at the edge of the woodland and well into the woodland (–60 m line). Larvae were only caught in the interior of the woodland in late May, but more were caught near or at the edge of the woodland edge in mid-June (Fig. 2).

**Abundance of earthworms**

The number of earthworms per $m^2$ (mean ± SD) was 4.80 ± 1.17, 7.83 ± 4.83, and 29.80 ± 8.73, in the interior of the woodland, at the edge of the woodland, and in the orchard, respectively. The number of earthworms differed significantly among areas, but not among months (Table 3). There were significantly greater numbers of earthworms in the orchard (Scheffé test, $p < 0.001$) than in the interior of the woodland and at the edge of the woodland, where the numbers were similar (Scheffé test, $p = 0.576$).

**Movement of adult beetles**

Of the 377 adult beetles (221 males and 156 females) that we marked and released, 61 males and 49 females were recaptured. The shortest distance from their release points to where they were recaptured 10 days later differed significantly between males and females (Table 4), but not after this period. The shortest distance from the release point to the recapture point increased significantly with time in days from when they were released for males (Fig. 5A), but for females it did not appear to increase after the first few days (Fig. 5B). For those that were recaptured within 10 days of release, most of the males moved along the woodland edge, whereas females most frequently moved between the edge and the interior of the woodland (Fig. 6).

TABLE 3. The results of a repeated-measures ANOVA of the log-transformed numbers of earthworms.

| Factors | df | Mean square | F-value | p-value |
|---|---|---|---|---|
| Location | 2 | 3.298 | 58.762 | <0.001 |
| Month | 2 | 0.042 | 0.751 | 0.478 |
| Location × Month | 4 | 0.016 | 0.288 | 0.884 |
| Residuals | 45 | 0.056 | | |

**DISCUSSION**

We examined the spatial population structure of a predatory ground beetle in the mixed farmland-woodland satoyama landscape in Japan (Takeuchi, 2003) and considered not only the static distribution of adult beetles, but also the movements of males and females and the changing distribution of larvae. Adult *C. yaconinus* aggregated at the edge of the woodland, from which many, particularly females, entered the adjoining farmland. In contrast, the larvae were mainly caught in the woodland.

Woodland edges generally support a rich fauna because it is an ecotone between woodland and open fields (Lewis, 1969; Fagan et al., 1999; Holland & Fahrig, 2000). There are some reports that there are more ground beetles in such habitats (Kotze & Samways, 1999; Hori, 2001; Ewers & Didham, 2008), which was confirmed by this study. An abundance of herbivore prey at the edge of the woodland may have supported the high abundance of carnivorous *C. yaconinus* adults, but physical conditions may also be important. In particular the microclimate (Matlack, 1993; Chen et al., 1995), with the greater abundance of shrubs and weeds at the edge of the woodland providing the light, humidity and temperature conditions most suitable for *C. yaconinus* adults. In addition, beetles may more easily hide from predators, such as small mammals and birds, in the thick undergrowth present at the edges of woodland. In old rural landscapes, forest edges were very common and formed a matrix of connections between a fine mosaic vegetation. Populations of *Carabus yaconinus* are sustained by such edge-related heterogeneous habitats (woodland-edge – open land). However, recently there has been an increase in monotonous rural landscapes in Japan and *C. yaconinus* may be losing the edge-related habitats it needs.

TABLE 4. Comparison of the shortest distances (m) moved by males and females.

| Days after release | Shortest distance (mean ± SD) | | Significance[1] |
|---|---|---|---|
| | Males | Females | |
| 1~10 | 10.2 ± 11.0 (n = 28) | 28.4 ± 22.3 (n = 19) | U = 140, p = 0.004 |
| 11~30 | 27.3 ± 12.2 (n = 16) | 31.6 ± 22.0 (n = 14) | U = 107, p = 0.851 |
| 31~ | 43.7 ± 23.3 (n = 7) | 55.4 ± 21.3 (n = 8) | U = 18, p = 0.274 |

[1] Mann-Whitney U-test.

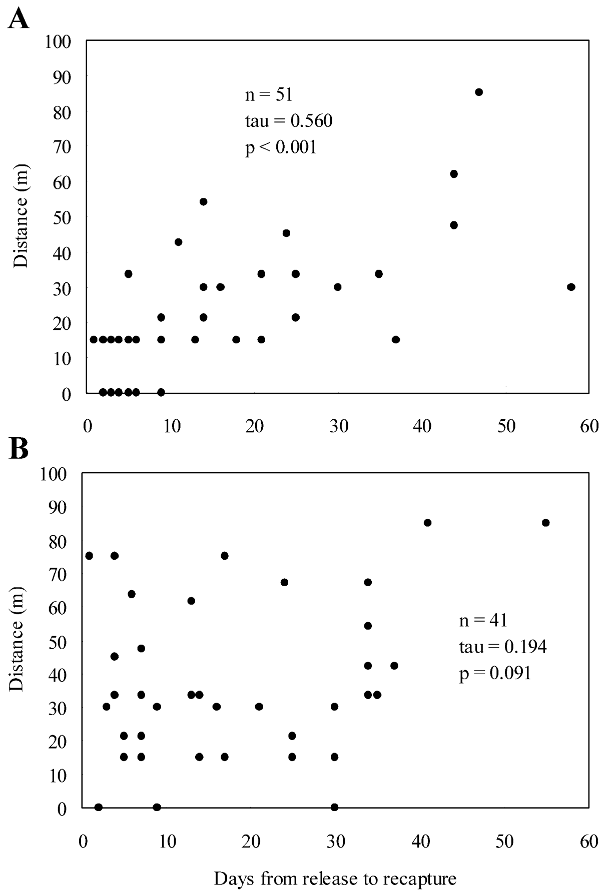


Fig. 5. Relationship between the shortest distance moved and the number of days from release for (A) adult males and (B) adult females of *Carabus yaconinus*.

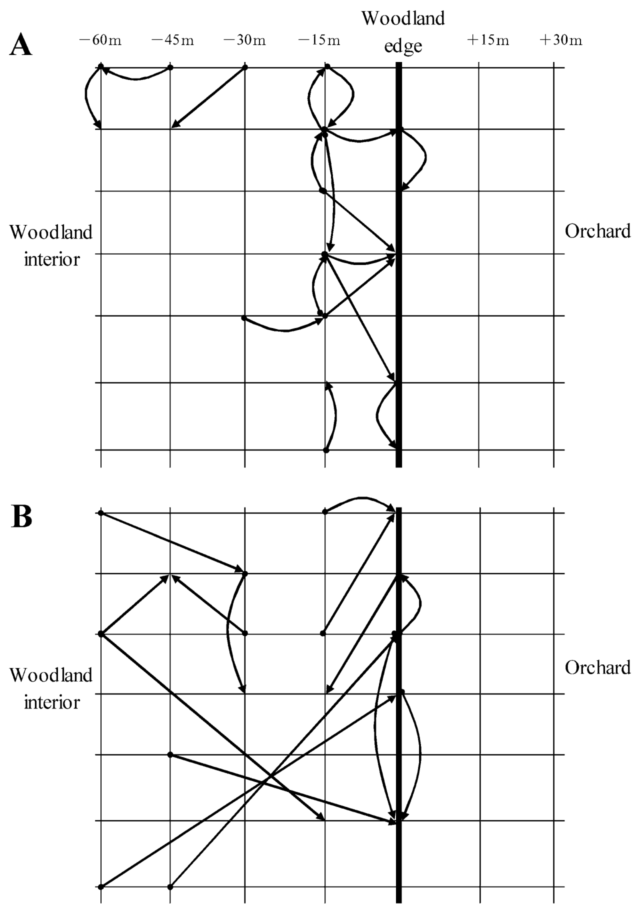


Fig. 6. Shortest distances moved by adults that were recaptured 10 days after release. (A) males (n = 17) and (B) females (n = 14). Each point of intersection of the grid indicates the position of a trap; the bold line indicates the woodland-orchard boundary. The points of release (●) and recapture (arrowhead) are indicated.

*Carabus yaconinus* larvae hatched in the interior of the woodland and moved toward the edge of the woodland as they developed (Fig. 2), but were never caught in the neighbouring orchard. Why were they restricted to the woodland? According to Sota (2000), *C. yaconinus* larvae mainly feed on earthworms. However, the abundance of earthworms cannot be the only factor affecting larval habitat choice, because earthworms were less numerous within the woodland than in the orchard, where no larvae were caught. Thus, the distribution of *C. yaconinus* larvae may depend more on soil and leaf litter conditions. In general, carabid larvae require soft humid soil and deep leaf litter (Thiele, 1977; Luff, 1987).

The landscape structure of farmland often plays a key role in determining the abundance, diversity and dispersion of arthropods (Fry, 1995). This is more important when the sexes use the habitats differently. Adult females of *Carabus yaconinus* not only moved more widely within the woodland they also entered the neighbouring orchard more frequently than did males. Egg production by carabid beetles is positively correlated with food supply (Baas & Van Dijk, 1984; Van Dijk, 1994). Rijnsdorp (1980) showed that females of *Carabus problematicus* Herbst, 1786 (Coleoptera: Carabidae) were more active than males during the reproductive period. Therefore, it is likely that females enter the woodland to search for oviposition sites and leave the woodland to search for high-protein food sources to support reproduction. Sota (1985b) reports that the number of eggs laid by females of *Carabus yaconinus* in the laboratory depends on the amount of minced beef eaten. There was an abundance of earthworms in the orchard and *C. yaconinus* adults were also often observed eating noctuid larvae there (unpubl. data). In contrast, males most likely remain at or near the inner edge of the woodland and wait for females with which to mate. The differences in the quantity of animal protein required by the sexes can account for their different patterns of movement. For *Leptocarabus kumagaii* (Coleoptera: Carabidae) plant material is unsuitable for egg production but sufficient for the survival of both male and female adults (Sota, 1984).

Many studies indicate a positive relationship between forest size and the species richness of ground beetles (Niemela et al., 1988; Niemela, 2001; Hori, 2003; Boulton et al., 2008; Fujita et al., 2008). Mader (1984) suggests that forest patches of <0.5 ha that lack an undisturbed central area have no forest-interior species. Even though *C. yaconinus* is a forest generalist and not a forest-interior species, it cannot live in a patch of woodland in an urban landscape of <0.4 ha (Fujita et al., 2008). Our results indicate that this may be because small fragments of woodland lack a suitable forest-interior habitat for larvae. For the conservation of this predatory ground beetle it is necessary to have woodlands of at least 60 m in width (i.e., 30 m from both woodland edges) close to farmland.

Carabid and staphylinid adults disperse from field boundaries up to 200 m into cereal fields (Coombes & Sotherton, 1986). Various predators and parasitoids enter crop fields from adjoining hedgerows and woodland (Topham & Beardsley, 1975; Wratten, 1987; Landis & Haas, 1992; Thies & Tscharntke, 1999). In Switzerland, greenbelts that are composed of several types of non-crop plants are planted between fields (Nentwig et al., 1998). These weed strips are habitats for many spiders and ground beetles, which disperse throughout the fields (Nyffeler & Benz, 1987; Richert & Bishop, 1990; Yano, 2002). *Carabus yaconinus* adults can move at least 60 m from the edge of woodland into an orchard (Kagawa et al., 2008), but artificial green corridors, such as weed strips, might help guide the beetles further into the farmland. In the traditional satoyama landscapes of Japan (Takeuchi, 2003), the network of coppices and shrubs near farmland may provide habitat corridors for beetles and other natural enemies.

In conclusion, it is possible to design a landscape consisting of suitable habitats and corridors for predatory arthropods as well as fields if one understands the ecology of these beneficial insects. Thus, it is important to study in detail the main predatory arthropods in order to promote conservation biological control.

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