

Dispersal of the endangered flightless beetle *Dorcadion fuliginator* (Coleoptera: Cerambycidae) in spatially realistic landscapes

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Received 24 September 2004; received in revised form 21 December 2004; accepted 30 December 2004

Abstract

Habitat destruction and degradation are the major causes for the decline of the endangered grass-feeding beetle *Dorcadion fuliginator* in Central Europe. In the southern part of the Upper Rhine valley (border region of Switzerland, Germany and France) the habitat suitable for this flightless beetle has been reduced to small remnants of extensively managed dry grassland, usually surrounded by intensively cultivated agricultural fields or settlements. Using a mark–release–resight technique we examined movement patterns in three *D. fuliginator* populations to obtain basic information on the dispersal ability and longevity of this beetle. Estimated daily survival rates ranged from 88.8% to 90.8% in the populations examined. This corresponds to a mean life span of 10.5 days. Distances moved by *D. fuliginator* differed among populations. The beetles walked the largest distances in the verges of a field track. Several beetles moved distances of 20–100 m along the track, with a maximum distance of 218 m (a male in 12 days). The shortest displacements were recorded in the bank of the river Rhine, a narrow habitat surrounded by tarmac roads. We also assessed the spatial arrangement of 12 patches with *D. fuliginator* populations in two regions and estimated the size of each population over 4 years. Data on dispersal, daily survival, population size and spatial arrangement of patches were used to simulate patch-specific migration rates. The simulations suggested that in both areas the beetles regularly moved between neighbouring patches separated by distances shorter than 100 m, whereas patches separated by distances exceeding 500 m are isolated.

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Keywords: Connectivity; Extinction; Habitat degradation; Isolation; Management plan; Spatially explicit dispersal model

1. Introduction

Natural and semi-natural areas throughout the world are becoming degraded and isolated, which is seen as a major threat to many species (Groombridge, 1992; Heywood, 1995). Much research in conservation biology has been focused on understanding processes that enable species to survive in fragmented landscapes (Hanski, 1999). Small populations that remain in fragmented areas are highly vulnerable to extinction as a result of

environmental, demographic and genetic stochasticity (Gilpin and Soulé, 1986). The metapopulation concept provides one explanation for how species can survive in fragmented landscapes. Movements of relatively few individuals between remnant, spatially separated populations ensure the survival of the metapopulation as a whole through recolonisation of patches where local populations have gone extinct (Hanski and Gilpin, 1997; Hanski, 2001). Therefore, studying animal movement and understanding the factors affecting it have become important issues in conservation biology and landscape management (Clobert et al., 2001; Goverde et al., 2002; Ng et al., 2004).

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Data on dispersal in endangered beetles are rare despite the great theoretical and practical importance. In a variety of flightless insects, dispersal results from small-scale movements made by individuals in their daily activity and/or from passive transportation (Wiens et al., 1995). The present study deals with dispersal in a highly endangered insect, the flightless beetle *Dorcadion (Iberodorcadion) fuliginator* (L.), which lives in different types of extensively managed dry grasslands (Baur et al., 2002).

D. fuliginator has a life cycle of 2 years (Baur et al., 1997). Females deposit their eggs in stems of grass, preferably *Bromus erectus*, their main larval host plant, in late March through May. The larvae hatch in May or June, feed on grass roots and pupate after 13.5–14.5 months (including one hibernation in a late larval stage). Adults (14–17 mm body length) emerge from the pupae after 2–3 weeks in July or August, but rest in the soil until the end of the second hibernation. Depending on weather conditions, adults emerge from the soil in March or April and are sexually active for c. 1 month.

The distribution of *D. fuliginator* extends from the Iberian Peninsula through Central Europe to Poland and from southern Holland to the northern border of Switzerland (Horion, 1974; Villiers, 1978; Vives, 1983; Althoff and Danilevsky, 1997). However, significant changes in land-use practices, combined with increasing levels of fragmentation decreased dramatically its abundance in the past 30 years (Horion, 1974; Klausnitzer and Sander, 1978; Coray et al., 2000). Owing to its rarity and endangerment the species is protected by law in Switzerland and Germany.

In the surroundings of Basel (Switzerland), several local populations of *D. fuliginator* have become extinct over the past few decades mainly as a result of habitat destruction (Coray et al., 2000; Baur et al., 2002). Currently, there are only two existing populations in North-western Switzerland (Coray et al., 2000). In the adjacent Upper Rhine valley north of Basel in France and Germany, there are still a few networks of *D. fuliginator* localities, which are threatened by gradual habitat deterioration (Baur et al., 2002). Information on the habitat requirements of *D. fuliginator* has been used to develop a management plan for the remaining localities in the German part of our study area (Hafner and Hofmann, 2002). However, essential knowledge for appropriate species recovery actions is still lacking. In particular, it is unknown whether migration between existing *D. fuliginator* populations occurs.

This paper has three aims: Firstly, we examined dispersal patterns and life span of *D. fuliginator* in three populations using a mark–release–resight technique. Secondly, we assessed the spatial arrangement of 12 local *D. fuliginator* populations in two areas and estimated the size of each population over 4 years. Thirdly, we

developed spatially explicit dispersal models to estimate migration rates among the existing local populations. The dispersal simulation allowed an examination of the degree of isolation of remnant populations. Our findings provide basic information to restore a network of suitable habitat patches that enables dispersal in this highly endangered species.

2. Materials and methods

2.1. Study sites

A mark–release–resight study was carried out in three sites in the southern part of the Upper Rhine valley (border region of Switzerland, France and German; Figs 1 and 2(a) and (b)). In the city of Basel, *D. fuliginator* lives in a 391 m long and 2–10 m wide section of the bank (inclination 30–35°) of the river Rhine near the St. Johann Park at an altitude of 250 m a.s.l. (hereafter referred to as site A following Baur et al. (2002)). The east-exposed, unfertilized grassland strip is fragmented by two stone steps (each 1.9 m wide) and a 24 m-long

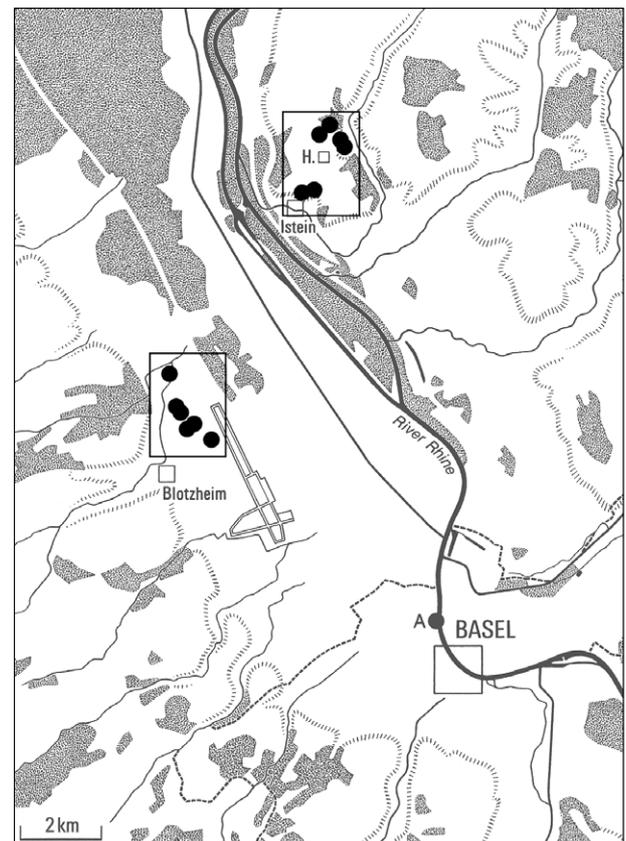


Fig. 1. Map of the southern part of the Upper Rhine valley showing the study site A in Basel (Switzerland), the study sites near Blotzheim (France; detailed map in Fig. 2(a)) and those near Istein-Huttingen (Istein-H., Germany; detailed map in Fig. 2(b)). Shaded areas indicate forest and hatching the slopes of the hills.



Fig. 2. Localities with *D. fuliginator* near Blotzheim, France (a), and Istein-Huttingen, Germany (b) in the southern part of the Upper Rhine valley. The habitat of locality M was destroyed in April 2001.

building. Several trees (*Tilla* sp.) at the upper edge shade the embankment and thus reduce the habitat quality for the beetle. The vegetation is mown twice a year. The vegetation of the study sites is described in detail in Baur et al. (2002).

Near the village Huttingen (Germany), the beetles inhabit the verges of a 2 m wide track at an altitude of 345 m (hereafter site Q; Fig. 2(b)). One verge consists of a south east-exposed embankment (inclination 10–20°, 2–3 m wide and 125 m long) covered with nutrient-poor grassland vegetation. The other verge is a flat, 1–2 m wide and 320 m long strip of grassland, bordered by arable land.

Near the village Istein (Germany), *D. fuliginator* lived in a meadow measuring 50 m × 70 m at an altitude of 335 m (hereafter site M; Fig. 2(b)). Tarmac roads (3.2 m wide) bordered two sides of the slightly inclined (5–10°), south-exposed meadow, intensively managed vineyards and farmhouses the other sides. The meadow was mown twice per year. For the mark-release-resight study an area of c. 700 m² along the roads was used. In April 2001, one year after the fieldwork of the present study, the meadow was converted into a vineyard, which resulted in the extinction of the entire population.

The three investigation sites differed in the shape of habitat suitable to *D. fuliginator*. Locality A was a long, narrow vegetation strip surrounded by tarmac roads. Locality Q also constituted a linear habitat to the beetle. Site M was a two-dimensional habitat. The localities Q

and M are situated 1.5 km apart and most probably represent remnants of a former metapopulation (Fig. 2(b)). Locality A is situated 12–13 km south of the localities M and Q.

The effect of the spatial arrangement of habitats on the metapopulation dynamics of *D. fuliginator* was examined in the region of Blotzheim (France) and in Istein-Huttingen (Germany) in 2001–2004. The two areas are known to support networks of remnant *D. fuliginator* populations (Baur et al., 2002). The localities near Blotzheim are spread over the flat, drained bottom of the Rhine valley at the western side of the airport Basel-Mulhouse. The investigation area (c. 2 km²) consists of a mosaic of arable fields (mainly maize) and patches of different intensively managed grassland (Fig. 2(a)). Istein-Huttingen is a hilly farmland area (c. 3.2 km²) consisting of intensively managed vineyards, arable fields, fertilized meadows, orchards, a few unfertilized grassland patches and some small forests (Fig. 2(b)). The two study areas are 6 km apart separated by the river Rhine and the Canal d'Alsace (Fig. 1). The labelling of localities follows Baur et al. (2002).

2.2. Mark-release-resight study

Searches for beetles were conducted only under meteorological conditions favourable for beetle activity (>15 °C and sunshine) between 1 April and 22 May

1988 (on 24 days at site A) and between 19 April and 7 June 2000 (on 21 days at site Q and on 27 days at site M). On these days the study sites were carefully searched for *D. fuliginator*.

We marked the beetles with three minute spots of nail varnish on their elytra and determined their sex. The use of four different colours and six defined positions on the elytra allowed an individual tagging (for details on the marking procedure see Baur et al., 1997). Marking was carried out in the field, and the beetles were put back to their original positions within 3 min. To minimize stress-induced movements due to handling, we placed each newly marked beetle in the vegetation under a dark plastic beaker and removed the beaker after 3–5 min. Each beetle found was checked for colour marks. In most cases the individual colour code of the beetle could be recognized without catching the animal. Untagged beetles were marked as described above.

We recorded the position of each beetle by measuring the distances to stakes or poles, which were established as a reference system at each study site. A computer program was used to transform field measurements into coordinates. Beetles of unknown sex (site A: 6 individuals, site Q: 4) and non-marked dead beetles were not considered in the data analysis. If a beetle was observed more than once on the same day, only the first observation was considered.

2.3. Demographic parameters and number of individuals

Estimates of the daily population size and daily survival were obtained from mark–resight data using the Jolly–Seber model (Pollock et al., 1990). To estimate the total population size at each site, we calculated the total number of beetle-days by integrating the fluctuating estimated population size over the entire activity period and calculated the average life span of the beetles based on the estimated survival rates. The total population size at each site was then calculated by dividing the total number of beetle-days by the average life span of the beetles.

2.4. Analysis of movement patterns and dispersal

We computed the following dispersal parameters from the resighting positions of each beetle:

- (1) ‘Total time’ = number of days elapsed from marking until last resight.
- (2) ‘Total distance moved’ = the sum of linear distances between consecutive resightings.
- (3) ‘Net displacement’ = the distance between the first and last recorded position of the beetle.
- (4) ‘Daily displacement’ = displacement during one day.

We used two-way ANOVAs to determine the effects of locality and sex on these four dispersal parameters ($\log(x + 1)$ -transformed). The length of the observed ‘total distance moved’ depends on the frequency of resightings between the first and last position recorded of a beetle (if a beetle was recorded only twice, then total distance moved equals net displacement). To eliminate the influence of sex-specific differences in resighting frequency, we performed a rarefaction analysis. In this approach, we randomly omitted intermediate resightings of males from the data set until equal resighting frequencies were obtained for males and females at each site. The procedure of random omission of resightings was repeated 100 times. We considered the median *P*-value of these 100 ANOVAs as result of the rarefaction analysis.

In uncorrelated random movements, net displacement is expected to increase with the square root of time (Turchin, 1998). To assess daily displacement, we therefore divided the distance between two subsequent records by the square root of the time elapsed between the two sightings, provided that the time was less than 4 days. Observed movements over periods of more than 4 days were found to be influenced by the limits of the suitable habitat. The time elapsed was therefore restricted to less than 4 days. We used mean values per individual when the resight data of a beetle allowed two or more estimates of daily displacement.

2.5. Patch area and population size

In March–May 2001–2004, we searched for beetles under favourable weather conditions (see above) in each habitat patch in the two regions Blotzheim (Fig. 2(a)) and Istein–Huttingen (Fig. 2(b)) four to eight times. This resulted in a total searching effort of at least 4 h per patch and year. For each patch the relative population density was expressed as number of beetles recorded per hour searching (Table 3). For all populations we estimated the number of individuals on the basis of the observed relative population densities and the calculated population sizes at the localities Q and M in the year 2000. At locality Q, with an estimated total population size of 186 beetles, we found 2.86 beetles per hour net search time in an area of 1100 m² in 2000, indicating that each beetle observed per hour net search time corresponds to an average density of 0.059 beetles/m². Similarly, at locality M with an estimated total population size of 955 beetles, we found 5.97 beetles per hour search time in an area of 3500 m², indicating that each beetle observed per hour net search time is equivalent to an average density of 0.046 beetles/m². Thus we assumed that one beetle found per hour search time corresponds approximately to a density of 0.05 beetles/m². We used this factor and the relative densities obtained in the field

surveys to calculate the number of individuals in all populations in 2001–2004.

2.6. Modelling of dispersal in spatially realistic landscapes

We assumed the number of migrants to be related to the dispersal ability of *D. fuliginator*, the distance a beetle has to travel to reach another suitable patch (population), the probability of survival during dispersal, and the number of individuals in the source population. We did not consider any density-dependent effects, since no data on density-dependent dispersal were available and the density of beetles was low in most populations (Table 3).

2.6.1. Dispersal

We used four approaches to simulate dispersal of *D. fuliginator*. In the first approach we used observed daily displacements (including their directions) of beetles at the localities M and Q. From both localities, randomly chosen daily displacements were concatenated, and the net displacements were calculated for time intervals that increased from 1 to 45 days. The resulting dispersal probabilities (i.e. the probability that a beetle would disperse at least a certain distance) were averaged over the two localities.

The second approach was based on the observed daily dispersal at the localities M and Q. The distribution of distances covered per day was approximated by a log-distributed random variable. We used this distribution to simulate one-dimensional random movement with time steps of 1 day. The movement direction was randomly chosen for each day.

In the third and fourth approaches we also used one-dimensional random movement models. In contrast to the second approach, however, these approaches were based on video-recorded walking speed of *D. fuliginator* ($n = 5$ beetles; mean = 2.5 cm/s) moving along track verges at the localities N and Q in 2002. We assumed that a beetle moves during 4 h per day in a linear habitat. The movement direction was randomly chosen to be positive or negative after every 25 s (third approach) or after 600 s (fourth approach). The latter resulted in a more direct dispersal than the other approaches.

In all four approaches, the individually based simulations were repeated 10 million times.

2.6.2. Distance between populations

In the course of the fieldwork we observed a few migrating *D. fuliginator*. All of them walked along the verges of tracks or roads, and no beetle was observed to enter arable fields or forests. Consequently, we considered paths, tracks and roads as potential migration pathways. The localities O and Q were not connected by any track. In this case we measured the distance along the forest edge. Between each pair of populations

we listed all possible connections along the network of pathways. For each connection, we measured the length and the probability that a beetle would use this particular connection. This probability was calculated based on the assumption that a beetle is equally likely to choose any of the two to five pathways leading away from the source population and that it is also equally likely to choose any of the pathways at a junction, except the pathway from which it came.

2.6.3. Survival during dispersal

We used the daily survival rate of *D. fuliginator* estimated from mark–release–resight data of the localities A and Q (mean values). The Jolly–Seber model does not distinguish between marked animals that left the patch and those that died. Thus, both emigration and mortality of marked beetles decrease the estimate of daily survival. Consequently, our estimated daily survival rates were conservative. It is frequently assumed that migrating animals have a reduced survival (Charrier et al., 1997; Tischendorf and Fahrig, 2000). Since no information on the survival of migrating *D. fuliginator* is available, we used the mean of the conservative estimates of daily survival at the localities A and Q (90.5%; see results) for dispersing *D. fuliginator*.

2.6.4. Number of beetles in the source population

In the simulations we considered two scenarios with different numbers of beetles in the source populations: scenario 1 with mean population sizes (average number of beetles estimated for each population over the years 2001–2004), and scenario 2 with peak population sizes (maximum number of beetles estimated for each population in 2001–2004).

2.6.5. Patchwise migration probability

For each of the four approaches to simulate dispersal we calculated the probability that a beetle would disperse at least a certain distance in its life. We used these dispersal probability distributions, the length of and the probability to use each connection between two patches (populations) to estimate the probability for a beetle to walk from one patch (population) to another along this particular connection. To estimate the number of migrants, we multiplied the cumulative probabilities of all connections between two patches with the number of beetles in the source population considering the two source population size scenarios presented above.

We repeated the entire procedure for each pair of populations in either migration direction within both areas. Scenario 1 (mean population size) may reveal a realistic estimate of migration among populations. Scenario 2 (peak population size) provides a very optimistic estimate, which may only occur in years with extremely large population sizes.

3. Results

3.1. Frequency of resightings

In total, 819 beetles were marked (Table 1). 273 (33.3%) of them were resighted once or several times (maximum 10 times, one beetle at locality M). The proportion of beetles resighted differed among localities (chi square = 23.90, $df = 2$, $P < 0.001$). In the linear habitat of locality Q, 49.0% of the marked *D. fuliginator* were resighted. Corresponding figures for the localities M and A were 36.8% and 24.8%, respectively. At all localities, more males were resighted than females (Fisher's exact test, locality A: $P < 0.001$; Q: $P = 0.009$; M: $P < 0.001$).

Marked beetles were resighted over periods of 7.2 days at locality A, 11.5 days at locality Q and 8.7 days at locality M (back-transformed mean values; Fig.

3(a)). However, maximum values of 29–38 days were recorded. Marked males and females did not differ in the number of days elapsed from marking to last resight (Table 2(a)). However, the total time over which marked beetles were resighted differed among the three localities (Table 2(a)).

3.2. Demographic parameters and population size

Estimated average daily survival rates were 90.2% at locality A, 90.8% at locality Q and 88.8% at locality M. Corresponding mean life spans were 10.2 days at locality A, 10.8 days at Q and 8.9 days at M. The observed lower life span at locality M was most probably due to both an increased traffic mortality on the adjacent roads and the fact that some marked beetles left the investigation area (both factors seemed to be less important at the localities A and Q). Thus, for further calculations we used

Table 1

Number of *D. fuliginator* marked, and frequency distributions of the number of resightings of the beetles of either sex at the three study sites

| Locality | Sex | Number of marked beetles | Number (percentage) of beetles resighted. . . | | | | |
|----------|--------|--------------------------|---|-----------|-----------|----------|----------|
| | | | Never | Once | Twice | 3 Times | ≥4 Times |
| A | Male | 211 | 145 (68.7) | 44 (20.9) | 16 (7.6) | 3 (1.4) | 3 (1.4) |
| | Female | 124 | 107 (86.3) | 16 (12.9) | 1 (0.8) | 0 (0.0) | 0 (0.0) |
| Q | Male | 67 | 28 (41.8) | 11 (16.4) | 12 (17.9) | 7 (10.4) | 9 (13.4) |
| | Female | 31 | 22 (71.0) | 5 (16.1) | 1 (3.2) | 3 (9.7) | 0 (0.0) |
| M | Male | 256 | 138 (53.9) | 65 (25.4) | 32 (12.5) | 11 (4.3) | 10 (3.9) |
| | Female | 130 | 106 (81.5) | 17 (13.1) | 4 (3.1) | 3 (2.3) | 0 (0.0) |

Numbers in parentheses indicate percentage.

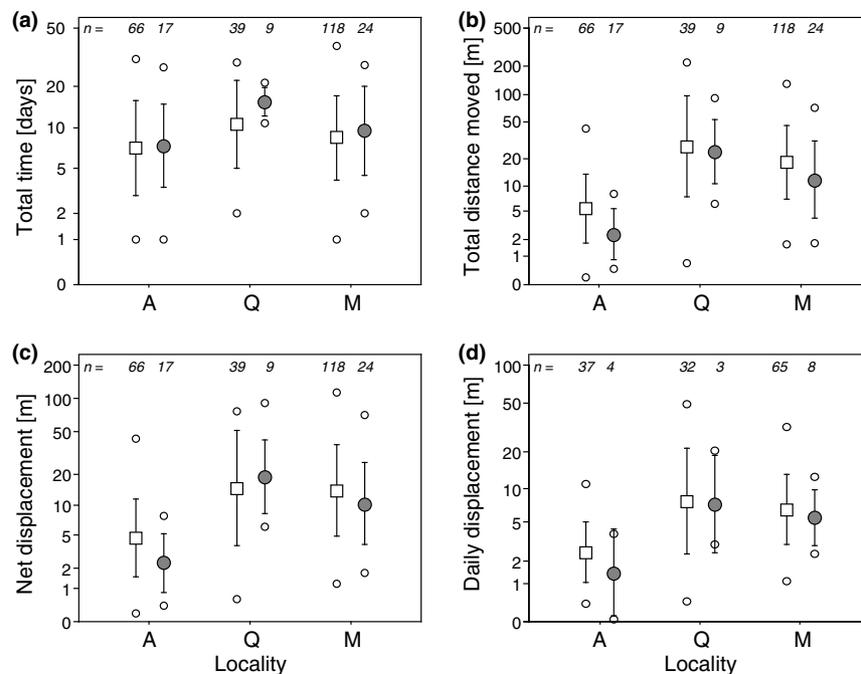


Fig. 3. Dispersal characteristics of male (□) and female (●) *D. fuliginator* (mean \pm 1 SD, minimum and maximum (○), $\log_{10}(x + 1)$ scale).

Table 2
Summary of ANOVAs testing the effects of locality and sex on the dispersal characteristics of *D. fuliginator* (data $\log_{10}(x + 1)$ transformed)

| Source | df | MS | F | P |
|---------------------------------|-----|-------|-------|---------|
| <i>(a) Total time</i> | | | | |
| Locality | 2 | 0.489 | 5.87 | 0.0032 |
| Sex | 1 | 0.166 | 1.99 | 0.160 |
| Locality \times sex | 2 | 0.041 | 0.49 | 0.614 |
| Error | 267 | 0.083 | | |
| <i>(b) Total distance moved</i> | | | | |
| Locality | 2 | 6.984 | 43.56 | <0.0001 |
| Sex | 1 | 0.998 | 6.22 | 0.013 |
| Locality \times sex | 2 | 0.115 | 0.72 | 0.490 |
| Error | 267 | 0.160 | | |
| <i>(c) Net displacement</i> | | | | |
| Locality | 2 | 5.009 | 31.13 | <0.0001 |
| Sex | 1 | 0.213 | 1.32 | 0.251 |
| Locality \times sex | 2 | 0.244 | 1.51 | 0.222 |
| Error | 267 | 0.161 | | |
| <i>(d) Daily displacement</i> | | | | |
| Locality | 2 | 0.896 | 9.81 | <0.0001 |
| Sex | 1 | 0.075 | 0.82 | 0.366 |
| Locality \times sex | 2 | 0.016 | 0.18 | 0.840 |
| Error | 143 | 0.091 | | |

the average life span of the beetles at the localities A and Q of 10.5 days.

Based on the mark–resight data the estimated population sizes were 982 ± 168 (mean \pm SE) beetles for locality A (in 1988), 186 ± 25 individuals for Q and 955 ± 104 beetles for M (both in 2000).

3.3. Movement patterns and dispersal

Movement patterns of marked *D. fuliginator* at the localities A and Q are shown in Fig. 4. On the river bank of locality A, a habitat entirely enclosed by tarmac roads and fragmented by stone steps and a building, the

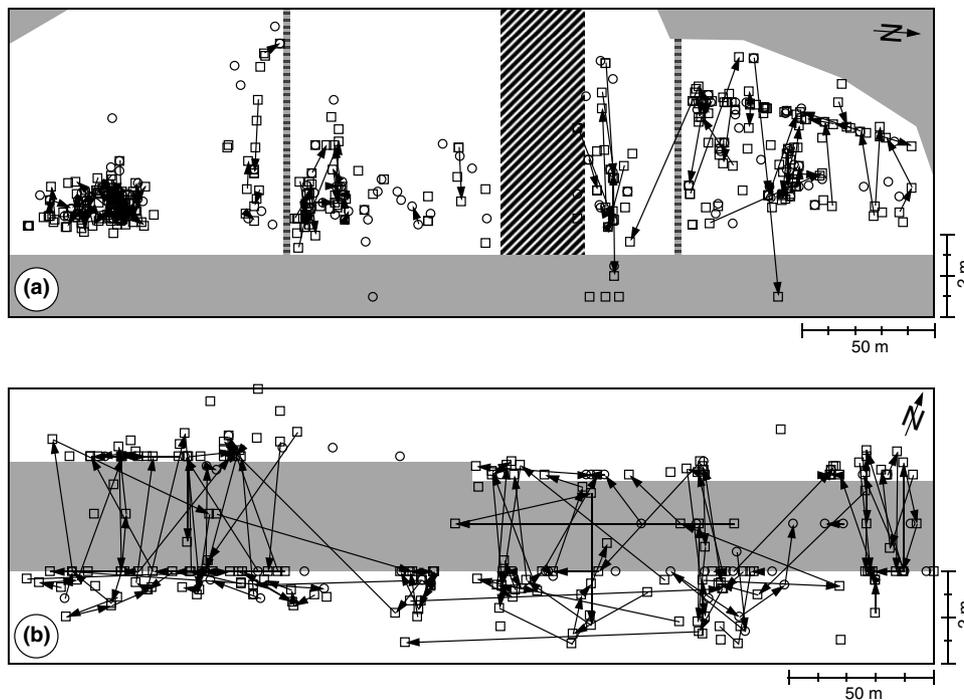


Fig. 4. Trajectories of marked male (\square) and female (\circ) *D. fuliginator* at the localities A (a) and Q (b). White areas denote grasslands and grey areas indicate roads (at locality A) or a track (at locality Q). Striped areas at locality A denote a building and two stone stairs.

beetles moved relatively short distances and did not leave the small vegetation patch (Fig. 4(a)). Only 1 out of 83 (1.2%) resighted individuals crossed a 1.9 m-wide stair. The 24 m-long building acted as dispersal barrier. Thus, the population appears to be sub-divided into several small sub-populations. At locality Q, *D. fuliginator* was found in both verges of the 2.0–2.5 m-wide field track. Several beetles moved distances of 20–100 m along the track. 33 out of 48 (68.7%) resighted *D. fuliginator* crossed the track at least once (Fig. 4(b)). Some beetles stayed for a shorter period in the grass strip in the middle of the track. No beetles were observed to enter the adjacent arable field.

D. fuliginator is capable of travelling total distances of up to 218.0 m (a male at locality Q in 12 days; Fig. 3(b)). The maximum net displacement recorded was 112.3 m (a male at locality M in 10 days; Fig. 3(c)). In general, males covered larger distances than females (Fig. 3(b) and Table 2(b)). The largest distances covered were recorded in the linear habitat of locality Q, the shortest in the entirely isolated locality A.

Net displacements differed among localities, but were not affected by the sex of the beetles (Fig. 3(c) and Table 2(c)). Net displacements were largest in the linear habitat of locality Q and shortest at locality A. Total distance moved differed among localities and was larger in males than in females (Table 2(b)). However, the difference between the sexes was partly due to a higher resighting frequency of males. When the resighting frequency of males was reduced to that of females using the rarefaction analysis, the difference was no longer significant ($P = 0.078$). The largest observed daily displacement of *D. fuliginator* was 49.2 m. Daily displacements differed among localities, but did not differ between sexes (Fig. 3(d) and Table

2(d)). Daily displacements were largest at the localities Q and M (7.7 and 6.4 m [backtransformed means]), and smallest at locality A (2.4 m).

3.4. Spatial arrangement and size of the populations

Near Blotzheim *D. fuliginator* was only found in a few patches of extensively managed grassland and in the verge of a main road. The matrix consisted exclusively of arable fields (Fig. 2(a)). In the Istein-Huttingen area, the beetle occurred in remnants of extensively managed dry grassland surrounded by intensively cultivated agricultural fields (Fig. 2(b)).

Interpatch distances ranged from 20 to 870 m in the Blotzheim area and from 10 to 1500 m in the Istein-Huttingen area. For example, the patches L and V are separated by a track in a hollow with hedges (distance along the connecting road: 10 m), and P and Q by an arable field and a fertilized meadow (distance along the forest edge: 40 m).

The estimated population sizes varied both among localities and years (Table 3). The population sizes ranged from 0 (very few) to 3000 beetles. In the Blotzheim area, the size of five of the six populations showed a pronounced parallel temporal fluctuation, whereas the size of population H was fairly constant. In the Istein-Huttingen area, all populations fluctuated strongly, with a tendency to have larger sizes in even than in odd years.

3.5. Simulated dispersal

The first three simulation approaches provided similar mean lifetime dispersal distances of 34.0, 28.1 and 32.9 m, respectively. In contrast, the fourth approach re-

Table 3

Area, mean number of beetles found per hour search and estimated total population size (in parentheses) of *D. fuliginator* at locality A (Basel, Switzerland), and in the regions of Blotzheim (France) and Istein-Huttingen (Germany) in 2001–2004

| Locality | Area (m ²) | 2001 | 2002 | 2003 | 2004 |
|--------------------------------------|------------------------|-------------|-------------|------------|-------------|
| <i>Basel</i> | | | | | |
| A | 2300 | 0.71 (80) | 0.70 (80) | 0.10 (10) | 0.00 (0) |
| <i>Blotzheim</i> | | | | | |
| H | 2300 | 1.75 (200) | 1.65 (200) | 1.62 (200) | 0.95 (100) |
| T | 4500 | 0.40 (90) | 2.12 (500) | 0.00 (0) | 2.56 (600) |
| I | 3800 | 1.29 (200) | 0.89 (200) | 0.00 (0) | 0.43 (80) |
| U | 9300 | 0.55 (300) | 0.50 (200) | 0.00 (0) | 1.65 (800) |
| G | 8500 | 1.51 (600) | 1.51 (600) | 0.00 (0) | 2.09 (900) |
| F | 15,000 | 0.55 (400) | 4.06 (3000) | 0.00 (0) | 4.46 (3000) |
| <i>Istein-Huttingen</i> ^a | | | | | |
| L | 2400 | 0.00 (0) | 0.25 (30) | 0.50 (60) | 0.75 (90) |
| V | 5600/5000 ^b | 0.68 (200) | 3.44 (900) | 0.22 (60) | 7.29 (2000) |
| N | 6000 | 0.46 (100) | 2.15 (600) | 0.00 (0) | 3.74 (1000) |
| O | 6000 | 3.17 (1000) | 1.72 (600) | 0.00 (0) | 0.47 (100) |
| Q | 1000/800 ^c | 0.98 (50) | 5.88 (300) | 0.25 (10) | 0.75 (30) |
| P | 2000 | 0.29 (30) | 0.50 (50) | 0.25 (30) | 0.00 (0) |

^a Locality M (area 3500 m²) was destroyed in April 2001.

^b Since 2002.

^c Since 2003.

vealed a much higher mean lifetime dispersal distance of 161.5 m. For further evaluations we used the first and fourth approach.

Scenario 1: Moderately direct dispersal and mean population size. This scenario combines the migration probability between pairs of patches in the first approach (dispersal estimated on the basis of daily displacements) with mean population size. Under these assumptions, beetles migrate among the four central populations (G, I, T and U) in the Blotzheim area (Fig. 5(a)) and between the two northernmost and the two southernmost

populations in the Istein-Huttingen area (Fig. 5(b)). The remaining populations are isolated. We consider this scenario to represent migration in a year with average population size.

Scenario 2: More direct dispersal and maximum population size. This scenario combines the migration probability between pairs of patches in the fourth approach (dispersal estimated on the basis of video recorded walking speed and a one-dimensional random movement model) with maximum population size. Under these assumptions, migration among populations increases

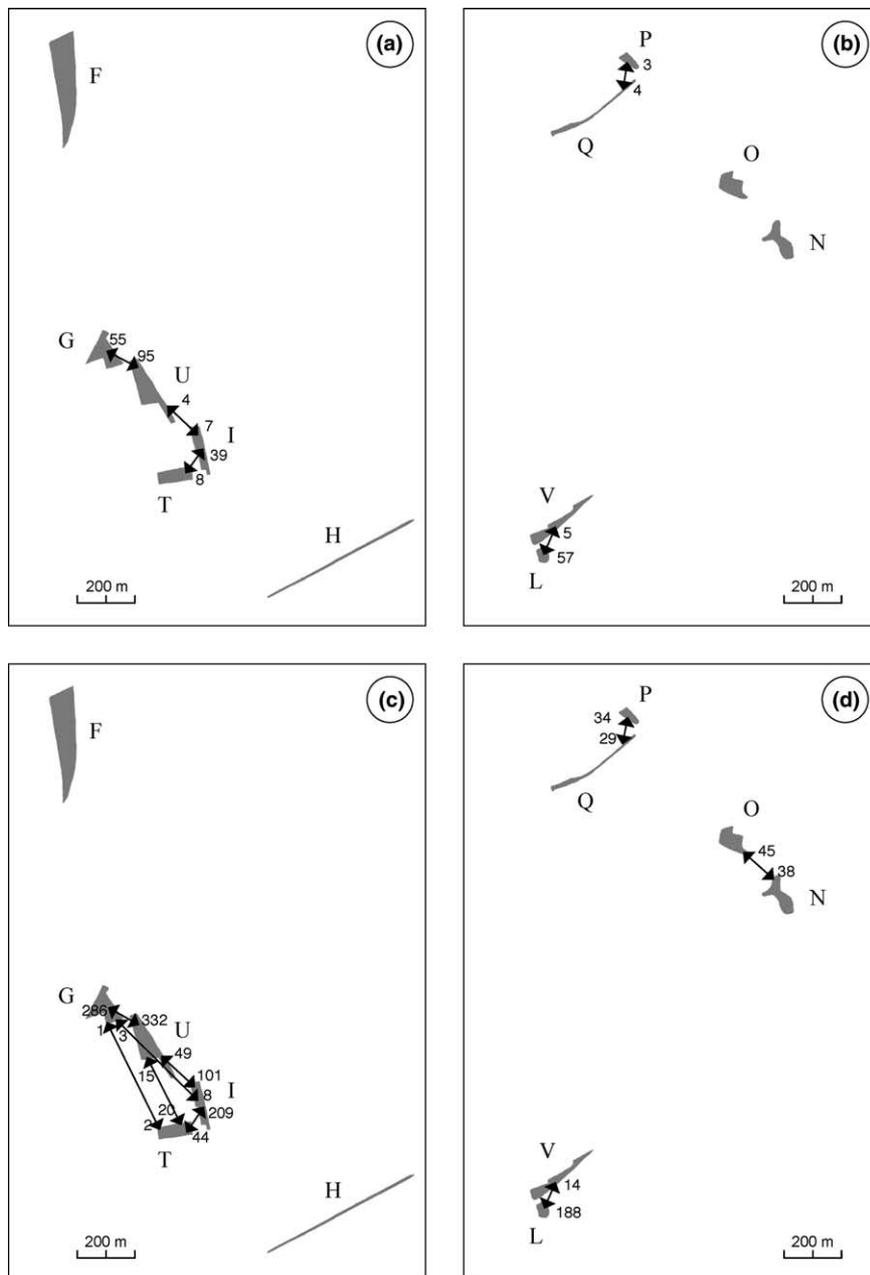


Fig. 5. Patchwise migration of *D. fuliginator* in the Blotzheim (a and c) and Istein-Huttingen area (b and d). Arrows with figures indicate the direction and number of migrating beetles between populations. (a and b) show the simulation results with a moderately direct dispersal and mean population size (scenario 1), and (c and d) those with more direct dispersal and maximum population size (scenario 2).

considerably in both areas. In the Blotzheim area, an increased number of beetles migrate among the four central populations (G, I, T and U) (Fig. 5(c)). However, the populations F and H remain isolated. In contrast to scenario 1, there is migration between the populations N and O in the Istein-Huttingen area (Fig. 5(d)). We consider this as a best case scenario.

4. Discussion

4.1. Spatially explicit dispersal model

Our results indicate that migration of *D. fuliginator* may only occur between closely situated patches. The simulations suggested that in both investigation areas the beetles moved between neighbouring patches separated by distances shorter than 100 m, whereas patches separated by distances exceeding 500 m were isolated.

The number of migrants among habitat patches is expected to decrease with increasing patch isolation because of the dilution effect associated with the spread of individuals in space (Ims, 1995), the mortality of dispersing individuals (Hanski, 1999), and the limited dispersal ability of the beetles. The lack of migration may have profound effects on the isolated populations. Predicting the effects of fragmentation and isolation on population viability is currently one of the main challenges in conservation biology. Metapopulation theory has been used widely to derive such predictions (Hanski and Gilpin, 1997; Hanski, 1998, 2001). A key parameter in a metapopulation is the dispersal rate. Sufficient dispersal among habitat patches is necessary for metapopulation persistence (Levins, 1969). Dispersal and gene flow among populations are important for the maintenance of local genetic variability and against loss caused by random genetic drift. Genetic variation is also important because it enables the populations to adapt to changing environmental conditions (Meffe and Carroll, 1997). The metapopulation concept stimulates conservation biologists to gather data that are critical for the development of effective conservation strategies for many species: movement rates between populations, reproduction and mortality rates that may vary among populations, population size-dependent extinction, and the like (Hanski et al., 2000).

In our study, field data and a spatially explicit simulation model were used to estimate migration between existing *D. fuliginator* populations. The data necessary for parameter quantification are often assumed to be insufficient, and criticism of spatially explicit dispersal models has emphasized problems associated with parameterizing dispersal processes (Ruckelshaus et al., 1997; Beissinger and Westphal, 1998). Monitoring of dispersal in small-sized, rare beetles presents formidable

problems in practice. In our study, most of the suitable patches supported only small populations; in some years the overall beetle density was extremely low. For instance, using a searching effort of more than 52 h, we observed only 13 beetles in the 13 localities examined in 2003 (Table 3).

We tackled parameter estimation by assessing dispersal at three localities with abundant *D. fuliginator* populations. *D. fuliginator* does not appear to occupy individual territories, but females may exhibit to some extent a site fidelity to *Bromus erectus* patches, their preferred oviposition sites. We do not know whether a high population density increases the dispersal rate in this beetle. Low population densities, however, may result in fewer mating opportunities, which can give rise to an Allee effect, possibly leading to a population decline or local extinction (Odum and Allee, 1954). Therefore, the Allee effect is expected to be an important factor influencing the population dynamics of rare and endangered species (Burgman et al., 1993). In sparse populations, individuals might be able to circumvent the lower probability of mate encounter by moving larger distances. In fact, evidence from a field experiment showed that individuals of the bush cricket *Metrioptera roeselii* can avoid an Allee effect by adjusting their movement behaviour in sparse populations (Kindvall et al., 1998).

Daily displacements in *D. fuliginator* were similar to those of larger flightless carabid species with a high dispersal power (Baars, 1979; Wallin and Ekblom, 1988). However, *D. fuliginator* has a much shorter adult life span than large sized carabid beetles. Movement among habitat patches is not simply a function of an organism itself, but also depends on the type of substrate, the vegetation structure at different spatial scales of heterogeneity, and the landscape through which it moves (Crist et al., 1992; Wiens et al., 1995). Modelling studies showed that assumptions about movement among habitat patches greatly influence the predictions of such models (e.g. Fahrig and Paloheimo, 1988; Lindenmayer and Possingham, 1996; Henein et al., 1998). Spatially explicit dispersal models may be especially sensitive to errors in the estimate of dispersal rates and survival (Ruckelshaus et al., 1997). To determine the estimation errors in dispersal parameters or to assess how dispersal patterns are affected by landscape structure, we need more empirical studies on how organisms disperse under various conditions (Wiens, 2001).

For our simulation model we used dispersal rates assessed in suitable habitat. This is a simplifying but unavoidable assumption because only a few observations on the movement behaviour of *D. fuliginator* have been made in unsuitable habitat. At the localities examined, *D. fuliginator* moved rapidly and more or less linearly along track verges (e.g. in the localities M and Q), whereas the beetles moved more slowly in grass patches

(Baur, B., unpublished data). Occasionally, we observed single beetles migrating between two patches. For example, one beetle was found walking along the field track between the localities G and U in May 2004. The beetles showed an attraction to habitat edges, which therefore acted to some extent as corridors. However, the response by beetles to novel and unfavourable habitats (arable fields, forest), which they encounter when dispersing between fragmented local populations, is unknown.

Movement of individuals in the matrix is frequently supposed to be random or linear, but at least homogeneous across a landscape (Wiens, 2001). In general, the Euclidean distance between suitable habitat patches and the species-specific dispersal capacity are assumed to determine colonisation probability (Hanski, 1999). We considered the beetles' point of view by using the actual length of the track and road verges as interpatch distance. Detailed knowledge of movement rules could be used in improved simulation models to generate more accurate predictions on species-specific dispersal capacity and patchwise migration rates in complex landscapes. Furthermore, the use of genetic markers may confirm the findings from mark–release–resight studies.

We used different approaches to estimate dispersal parameters in the simulation models. Approaches 1–3 revealed similar dispersal estimates, whereas approach 4 resulted in considerably longer dispersal distances. This difference allowed the simulation of two scenarios. For scenario 1 we considered mean population size and moderately direct dispersal, for scenario 2 maximum population size and more direct dispersal, i.e. a higher dispersal rate. The first scenario may represent the patch-specific migration that can be expected under 'average conditions', whereas the second scenario illustrates possible patch-specific migration under optimal conditions. Populations with no exchange of individuals under scenario 2 can be considered to be isolated. In the Blotzheim area, the populations T, I, U and G form a metapopulation with a regular exchange of individuals. In the Istein-Huttlingen area, the two patches V and L are closely connected to each other, with the expected number of beetles immigrating into patch L approaching the mean population size of that patch. These two patches may therefore harbour a single population.

4.2. Longevity and population size

The resight data of marked beetles allowed an estimation of daily survival and of mean life span of adult *D. fuliginator*. No demographic data were so far available for this endangered beetle. The estimated population size is the cumulative number of beetles emerging in a patch over one season (c. 6 weeks).

Early emerging individuals may die before later emerging beetles appear (mean life span of 10.5 days). This fact reduces further the probability of encountering mating partners in patches with low population sizes.

The localities differed considerably in population size. The differences in population size between patches could partly be explained by differences in habitat quality and patch management, and partly by patch size. Due to its 2-year life cycle one would expect less variation in population size between odd years and between even years. A part of the among-year variation in population size can be explained by the prevailing weather conditions in a particular year. Deviations in population size from the general pattern indicate local habitat degradation, e.g. at locality Q in 2003 (Table 3).

Based on the results of our mark–release–resight study, we can estimate total population size of other *D. fuliginator* populations living in similar habitats. If the area of a suitable patch is known, and this area is searched evenly for *D. fuliginator* under favourable weather conditions for at least 4 h (as done in the present study), then the total size of that population can be estimated by multiplying the number of beetles found per hour search time with the area (in m²) and the factor 0.05.

4.3. Implications for conservation and management

Our results indicate that in both study areas several *D. fuliginator* populations are out of reach of neighbouring populations and therefore isolated. The landscape in the Upper Rhine valley is dominated by intensively cultivated fields and fragmented by highways, numerous roads with high traffic density and railways. The majority of the known *D. fuliginator* localities are too isolated to become connected by the establishment of corridors. An appropriate management of the existing man-made habitats including mowing (1–2 times/year) or lightly grazing is the most important task and a prerequisite for potential later, farther-reaching conservation measures.

The remnants of extensively used grasslands are vulnerable as they are easily converted into other habitats no longer suitable for the focal species, as a result of agricultural intensification or abandonment (Baur et al., 1996). In the Upper Rhine valley, *D. fuliginator* habitats partly overlap with the Xerobromion community, which is also inhabited by numerous threatened relic species including butterflies (Herrmann et al., 2000), grasshoppers (Coray, 2000) and plants (Moor, 1962). Appropriate management of such grasslands is essential for maintaining the focal plant species and/or thermophilous conditions that they require, while also conserving a range of more common grasshoppers and other insects (Morris, 2000).

Our study shows that individual-based, spatially explicit dispersal models can be applied to management problems even if data are sparse. This gives clear management directives for the restoration of grassland patches, which may serve as stepping stones and thus facilitate migration among existing populations.

Acknowledgements

We thank Max Balmer, Anette Baur, Martin Baur, Nadine Cueni, Monika Keller, Michel Wurtz and several students for help in the field. Georg Armbruster, Anette Baur, Hans-Peter Rusterholz, Peter Stoll and two anonymous reviewers provided constructive comments on the manuscript. We also thank the 'Naturschutzbehörde des Regierungspräsidiums Freiburg', Germany, for permission to work with this protected species. Financial support was received from the Christoph Merian Stiftung, the Basler Stiftung für Biologische Forschung, Pro Natura Basel-Stadt and the Fachstelle für Naturschutz Basel-Stadt.

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