

4. Influence of Habitat Corridors on the Movement Behaviour of *Carabus nemoralis* (Coleoptera: Carabidae) in an Urban Environment

Abstract - The effectiveness of habitat corridors for the connection of habitat fragments is still controversial. I studied the movement behaviour of *Carabus nemoralis*, a flightless ground beetle with limited dispersal ability, in urban habitat corridors. Radio-transmitters were used to study the behaviour of individuals in a roadside greenery strip. The movement rate equalled that of larger *Carabus*-species studied earlier. I found no evidence for directed walk components in the movement pattern. Thus, fleeing behaviour due to the experiment conditions and directed dispersal in corridors can be excluded. In addition, due to the lack of a guidance effect, the corridors might not enhance the dispersal speed between connected habitat fragments.

INTRODUCTION

Urban regions have been increasing in size and population worldwide (Alberti et al. 2003). The spatial organisation of a city is optimised to support its human activities such as transport, industry or habitation. As a consequence, in urban regions forests and other rural habitat types are reduced to remnants which are often highly isolated. The smaller habitat fragments can provide resources only for smaller subpopulations of organisms which, in addition, suffer from negative isolation effects such as inbreeding or lower probability of recolonization (MacArthur and Wilson 1967, Lande 1995). As a result locally increased extinction rates of organisms affect subpopulations which result in an alteration of the species communities of such habitats (Miyashita et al. 1989, Weller and Ganzhorn 2004, Deichsel 2006).

One possible nature conservation strategy to minimize the negative impact of habitat fragmentation is to connect isolated fragments with stepping stones or corridors (Wilson and Willis 1975, Saunders and Hobbs 1991). The exchange of individuals between subpopulations may reduce local extinctions in several ways: 1) demographic fluctuations of connected subpopulations are levelled (Den Boer 1981), 2) the re-colonisation rate of unoccupied fragments increases (Hanski and Gilpin 1997), and 3) the increased gene flow (Slatkin 1985, Coates 1991) decreases the inbreeding depression and keeps a high genetic diversity with a potentially adaptive value (Lande 1995). However, the effectiveness of corridors regarding a general increase of animal dispersal rates between habitat fragments is still controversial (Simberloff et al. 1992, Rosenberg et al. 1997), because species respond to corridors in different ways (Haddad 1999b). Several studies found a benefit of corridors for the dispersal of organisms between isolated habitat fragments (Petit 1994, Drees and Weber 2001, Haddad 1999a, Haddad et al. 2003), while other studies revealed no corridor effects (Bowne et al. 1999, Collinge 2000). The potential benefit of corridors depends on the way corridor structures influence the movement behaviour of the species (Haddad 1999b). However, only a few studies incorporated a behavioural approach, which

may provide the best opportunity to predict the use of corridors (Haddad 1999b, Berggren et al. 2002).

This study was part of the interdisciplinary postgraduate research and study programme “Perspectives on Urban Ecology - the Example of the European Metropolis of Berlin”. Different disciplines investigated the interrelations between abiotic and biotic environmental factors across a rural to urban gradient in southeastern Berlin. The research focused on the ecological significance of biodiversity in urban ecosystems and mechanisms to maintain it.

In urban environments linear fragments of vegetation, often called greenways (Little 1990), are part of an urban planning strategy which aims to mitigate for negative climatic effects of the sealed and built-up areas (Horbert 2000, Weber and Kuttler 2004) and to offer recreational space for the citizen with the opportunity to get in contact with nature (Platt et al. 1994). Greenways are also included in the urban nature conservation strategy of Berlin, the largest city of Germany. A habitat network planned by the local government (Lapro 2006) incorporates greenspaces along streets as dispersal corridors for different terrestrial organisms.

The objective of this study was to characterise the movement behaviour of a large flightless groundbeetle (*Carabus nemoralis*) in habitat corridors in an urban environment. This knowledge will help us understand the importance of such structures for the maintenance of dispersal in an urban habitat network.

The use of corridors depends on three main elements. The corridors must be found by the migrating organisms, they must be selected preferentially compared with the surrounding habitat (matrix habitat) and the migrants must traverse the corridor successfully (Rosenberg et al. 1997). My study focussed on the latter two elements.

Several studies revealed a behaviour change when beetles leave their preferred habitat and walk into a less suitable one either due to normal dispersal behaviour (Rijnsdorp 1980) or due to experimental manipulation (Riecken and Rath 2000). The normal movement behaviour with frequent turns of unpredictable angle, described as “random walk” (Baars 1979), changes to a more linear movement

with small turns. I used this difference in behavioural response as an indicator for the habitat quality of the habitat corridor.

The type of movement patterns but also the behaviour at the habitat corridor boundaries are crucial for the speed of transition across the habitat corridors (Tischendorf and Wissel 1997, Haddad 1999b). Although the shape of the corridors is suited to steer individuals from one fragment to another, the effectiveness of the corridors depends on the transition speed in the habitat corridor compared to the speed through the surrounding landscape (Rosenberg et al. 1998).

In particular my research aimed to test the following assumptions.

1. Road side greenery is a suitable habitat for *Carabus nemoralis*, at least for dispersal. The beetles move according to the assumptions of a random walk model.
2. The shape of road side greenery influences the movements of *Carabus nemoralis*. In the case of elongated shape this alteration leads to a canalisation of the movement which results in an increased transition speed along the longitudinal axis of such a corridor.

MATERIALS AND METHODS

Study Area

The experiment was conducted in the inner city of Berlin (district: Neukölln). The observed area is a strip of street greenery which runs parallel to a water canal. The street greenery is divided into two strips of vegetation by a gravel path (4 m wide). A small street (11 m wide) with curbstones characterised by low traffic (less than 5000 vehicles per 24h, UEIS 2006) separates the observed area from a city park. Both parts of the greenery strip have a similar vegetation with

exotic (*Philadelphus coronarius*, *Spiraea* sp., *Symphoricarpos albus*) and native shrubs (*Crataegus monogyna*, *Prunus spinosa*) as well as some herbaceous species. The density of shrubs is higher in the part between the street and the gravel path. The border between the gravel path and the vegetation strip at the canal is characterised by some solitary trees (*Tilia* sp.) and a fence which did not hamper the movement of the beetles but kept dogs and humans from this part of the observed area, which had denser herbaceous vegetation but fewer shrubs (fig. 16).

Study Species

Carabus nemoralis is a night active, predatory species which cannot fly due to the reduction of hindwings (Turin 2000). The beetles are 18-28 mm long (Arndt and Trautner 2004). Main activity periods are the spring during the reproduction

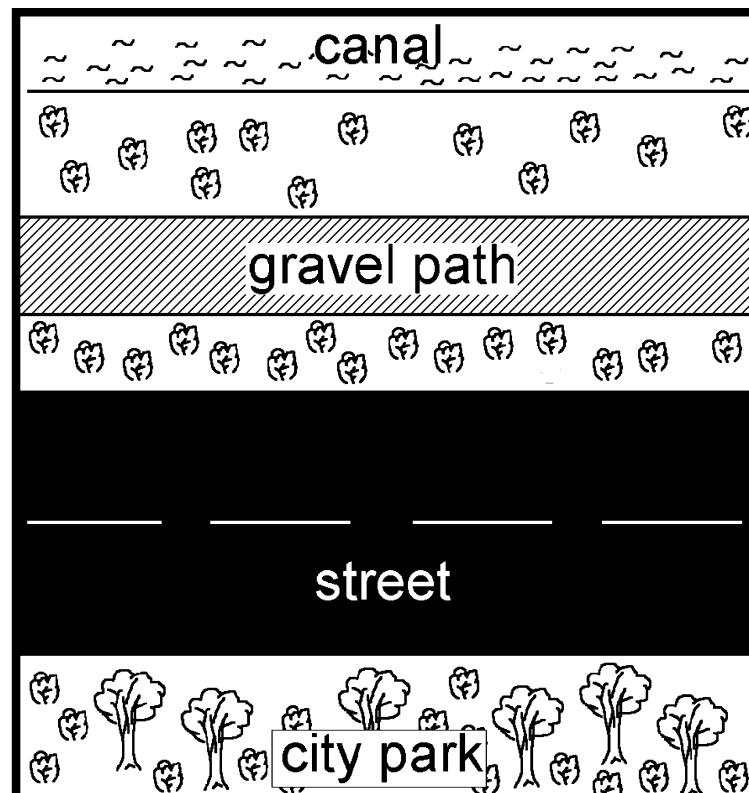


Figure 16. Study site close to the city park “Wildenbruchplatz” in Berlin. The street is 11m wide. Beetles were caught in the city park and released in the vegetation stripe between the gravel path and the street.

season and the early autumn when the new imagines hatch, but beetles can be caught in smaller number also throughout the summer. The field observations took place in May 2003 during the first activity peak. *Carabus nemoralis* and *Carabus granulatus* are the only large ground beetle species that can be found in wooded habitat fragments across a rural to urban gradient in Berlin, while other *Carabus* species of the rural woods do not infiltrate the urban habitat fragments (Deichsel 2006). *C. nemoralis* prefers wooded habitats, but it is not strictly confined to this habitat type (Thiele 1977, Kennedy 1994, Turin 2000).

Field Study

The movement of the beetles was tracked using radio telemetry (Riecken and Rath 1996). Radio transmitters with different transmitting frequencies allow the individual tracking of several beetles simultaneously and the transmission range is greater than that of the harmonic-radar system (Mascanzoni and Wallin 1986), another telemetry system applicable to ground beetles.

The beetles for the experiment were caught with pitfall traps in a city park which was separated from the observed street greenery by a street (fig. 16). In the laboratory a transmitter (LB-2N, made by Holohil company) was glued on the elytrae of the beetles with an elastic silicone glue (Uniflex PU; Voss Chemie) after roughening the elytrae surface gently with sandpaper. The transmitter weighed 0.47 g and transmitted for approximately 14 days. I did not anaesthetise the beetles to avoid negative effects, such as hyperactivity, experienced in earlier studies (Riecken and Rath 1996, Jopp 2003). The beetles were transported back to the observation area and were released in the vegetation strip between the street and the gravel path. Capture, application of the transmitter and release were done within the same day. Beetle abundance in the city park was relatively low and I did not capture all individuals for the experiment during a single day. Therefore I could not release the beetles simultaneously, but capturing and releasing beetles on different days was preferable compared to an extended

laboratory captivity. Beetles release started in the evening at 8:30 pm, which was approximately the time of sunset. All individuals were released at the same point and tracked until the transmitter output got weaker. Beetles released on the same day, were released with a time-lag of 5 minutes. For the tracing I used the scanning receiver STABO X-1900, which was equipped with a removable YAGI-Antenna. The positions of the beetles could be determined to the nearest 5 cm without disturbing the tracked specimen. I measured the distances between the position of the beetle and two fix points, which were chosen from a row of fence posts along the vegetation stripe. I used trigonometric calculations to calculate x,y coordinates from these measurements. The position of the beetles was localised every morning at 8:30 am. Some individuals were observed during the night from 8:30 pm to 12:30 pm as well, to obtain information about short interval movements. Therefore the position was recorded once each hour during this time.

Females are bigger than males of *Carabus nemoralis* (Alibert et al. 2001). An additional weight such as a radio transmitter might influence females less than males because the ratio between body weight and additional weight is favourable. Therefore I used only females in this study. In addition I weighed the beetles before and after the experiment to evaluate the influence of the transmitters on the fitness of the beetles.

Statistical Analysis

The continuous path traversed by the individuals could not be recorded. Only points on this path were localised. As previous authors have done (Kareiva and Shigesada 1983, Wiens et al. 1993) I described the movement as a series of straight moves between the tracked positions. These are characterised by the move length as the direct distance, also called net displacement, between the successive locations and the direction of the move which can be related to the preceding move direction with the turning angle.

The maximum activity radius and dispersal range are robust estimators of dispersal (Samietz and Berger 1997) and were used to characterise the dispersal probability in the corridor. Maximum activity radius was measured as the maximal direct distance between the release point and subsequent positions and dispersal range was assessed as the maximal direct distance between any two observed positions. Both estimators were related to the observation time.

For the direction data circular statistics were applied. Watson-Williams test (Zar 1999) was used to test for differences between the different individuals regarding the directions chosen. Although this is a parametric test, it is robust to departures from the assumptions of conformity to von Mises distribution (the circular analog to the normal distribution) and homogenous angle dispersion (Zar 1999). Raleigh's test for circular uniformity was applied to test if the recorded directions are distributed uniformly around the circle (Zar 1999). The correlation between consecutive steps was tested using a circular analog of the Pearson's product moment correlation, implemented in the package "circular" (Lund and Agostinelli 2005) of the statistical software R (R Development Core Team 2006).

The behaviour of the beetles at the habitat corridor boundaries could not be observed directly due to the gaps in the observation. Thus, I used an indirect approach to evaluate the boundary effect. The directions of two successive moves should be independent if a random walking behaviour can be assumed. Considering the transition along the habitat corridor that means that each turning can result in a progression or a turning around equally. Theoretically, this random turning behaviour can change when the beetles encounter a habitat boundary. The beetles might use the habitat boundary as a guidance structure and they might move along the edge like a fish in a fish trap. Such a behavioural change would result in a biased turning and progression would increase in favour of turning around at the habitat boundary. I tested if the equilibrium between progression and turning around changed towards the habitat boundary. Therefore I subdivided the observed street greenery into strips of 2 m width and tested the ratio of progressions and instances of turning around for deviation from one using a χ^2 -test. All statistics except otherwise stated were calculated with STATISTICA (Statsoft 2001).

RESULTS

The mobility behaviour of 11 females could be recorded in the field. A high percentage of individuals could not be recovered (5 out of 11), presumably due to predation on the beetles or malfunction of the transmitters. In one case remnants of an individual could be recovered, because the predator left the elytrae with the transmitter untouched. Nonetheless, 139 position changes could be recorded. Two beetles gained weight, four beetles lost weight, and the other beetles were not recovered so no weights were recorded after the observation (tab. 7). The activity of the beetles increased towards midnight and was highest in the second half of the night (fig. 17).

Table 7. Tracked females of *Carabus nemoralis* in a street greenery in the city of Berlin. Weight development is given as weight loss or weight gain relative to the starting weight. The question mark stands for individuals that could not be recovered.

individual	Minimum distance covered [m]	release date	duration of tracking [d]	weight change	Number of days without position change
9	38.95	2.5.2003	9.1	?	2
10	20.90	2.5.2003	0.5	?	0
11	42.00	2.5.2003	6.1	-27%	3
12	20.15	3.5.2003	13.0	-7%	8
13	67.70	3.5.2003	14.1	+16%	3
14	145.55	9.5.2003	18.5	+9%	1
15	5.05	16.5.2003	3.1	?	2
16	64.60	16.5.2003	11.6	?	2
17	72.40	21.5.2003	13.5	-28%	2
19	13.35	27.5.2003	8.0	-31%	1
20	7.90	27.5.2003	5.0	?	2

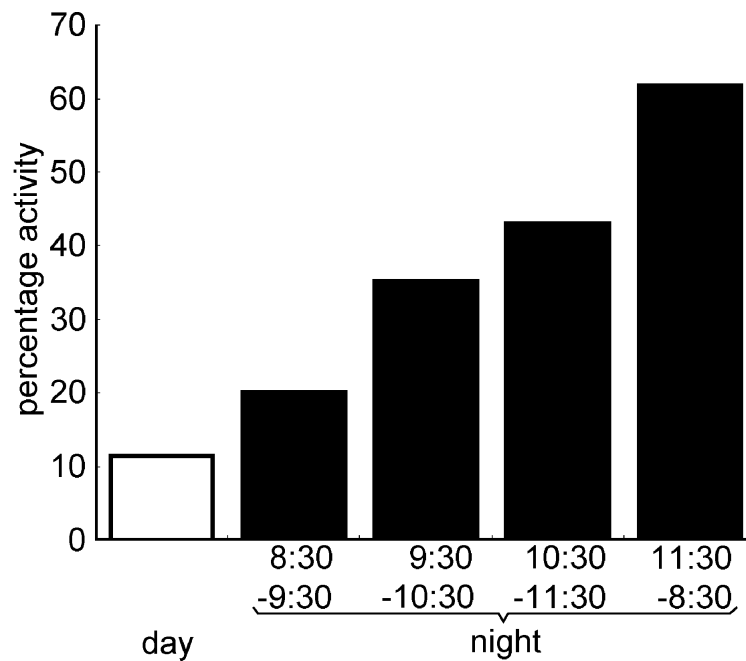


Figure 17. Percentage of movement activity of *Carabus nemoralis* females during different times of the day. Notice the longer time period of the last column.

The move length distributions for daily movement of the different individuals did not differ significantly (Kruskal-Wallis-test: $H=17.6$, $p=0.06$). Additionally, the Watson-Williams test revealed no significant differences regarding the directions of all moves of the different individuals (24h intervals, $p=0.05$, $F=0.44$, critical value=2.07). Therefore I pooled the results of all individuals for some of the following analyses.

The distribution of move length was left-skewed. Considering the distances between positions on two subsequent days 75% of the distances were shorter than 6.00 m, only 5% were longer than 16.00 m, and the median was 2.65 m (fig. 18).

The gravel path in the tracking area was crossed 11 times by 6 individuals at least once. The street between the park area, where the beetles were caught and the observed green bed where the beetles were released was never crossed. The daily move length was significantly greater when the beetles crossed the gravel path (Mann-Whitney U-test; $p<0.001$).

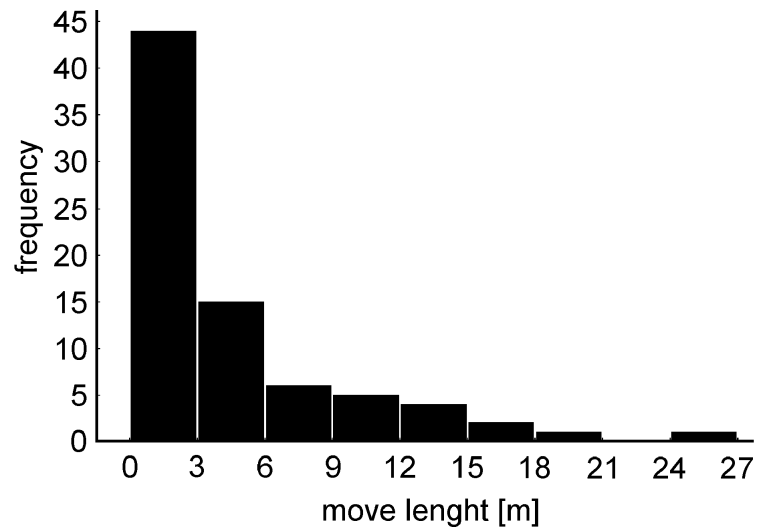


Figure 18. Frequency distribution of direct distances (move length) covered by female *Carabus nemoralis* during periods of 24 h.

Maximum activity range and dispersal range increased with the observation time. Both values increased approximately linearly during the observation period of 12 days (fig. 19).

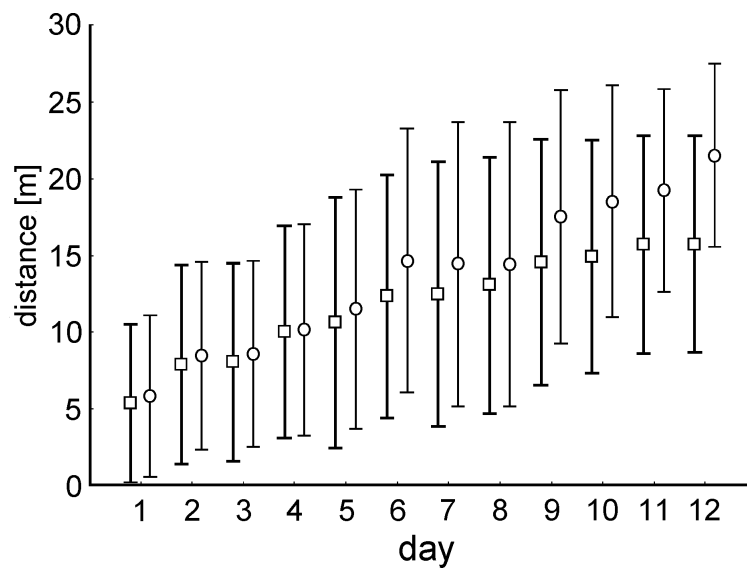


Figure 19. Increase in maximal activity range (squares) and dispersal range (circles) of female *Carabus nemoralis* in an urban habitat corridor. The figure shows the mean values and standard deviation of five individuals.

The directions of consecutive moves were uncorrelated, neither by analysing 24 h intervals ($n=55$, $r=-0.079$, $p=0,5641$) nor by analysing 1h intervals ($n=24$, $r=0.094$, $p=0.623$). Small turning angles were not necessarily associated with long successive moves (fig. 20). Small turning angles connected only very short moves in most cases. Only one female (no. 9) showed long moves on two successive days and did not changed the direction (fig. 21).

The directions of the moves during the 1h intervals were distributed uniformly around the circle (Raleigh's $z=0.223$, critical value=2.983). However, the moves during the 24h interval showed a preference direction along an axis which was almost parallel to the longitudinal axis of the observed street greenery (Raleigh's $z=3.131$, $p<0.05$). The difference was only 14° .

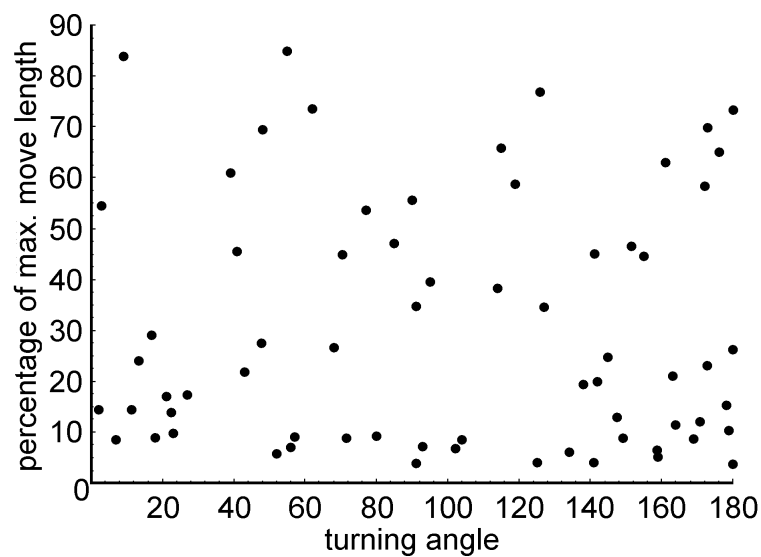


Figure 20. Turning angles between successive moves of *Carabus nemoralis* applying a 24-h-interval in relation to the summed lengths of the moves expressed as percentage of the maximal move length.

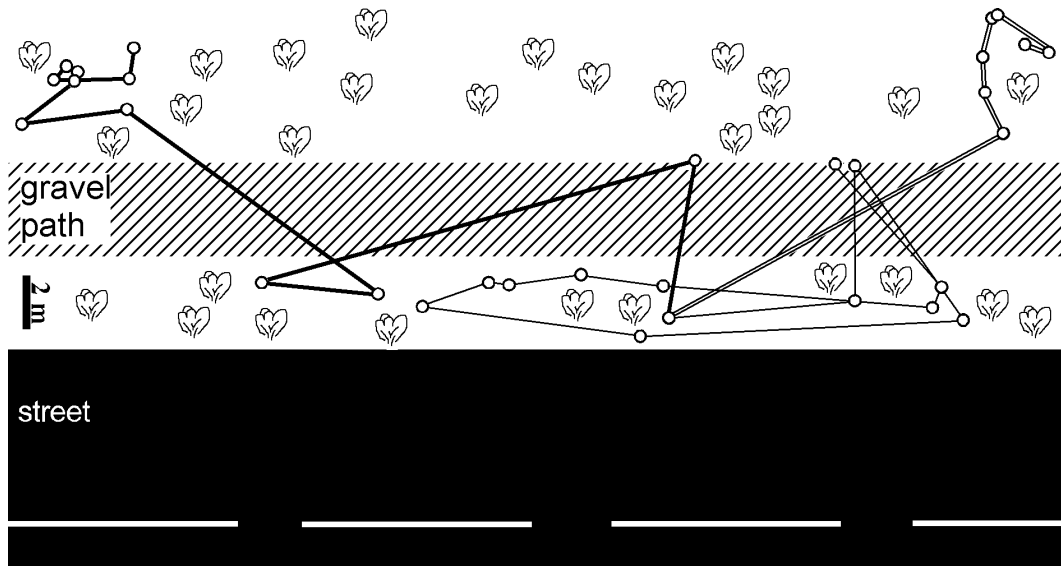


Figure 21. Tracked positions (interval=24h) on movement paths of *Carabus nemoralis* (female no. 1 with double line, no. 5 with thick line and no. 9 with thin line) in a street greenery divided by a gravel path.

The analysis of the turning behaviour in relation to the distance from the habitat boundary revealed no biased turning. Although I found more cases of progression than turning back close to the boundary, this difference was not supported statistically (fig. 22).

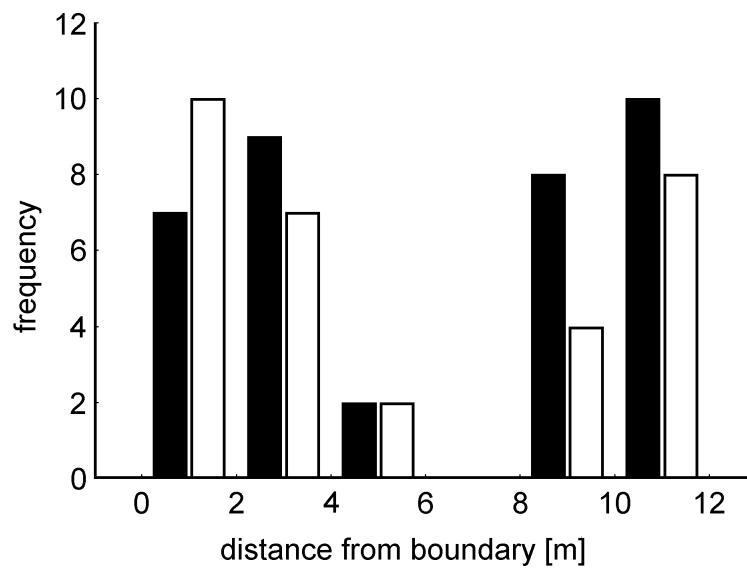


Figure 22. Number of turns that resulted in a progression (white bars) or turning back (black bars) relative to the longitudinal axis of a habitat corridor in relation to the distance of the turning point from the habitat corridor boundary (distance class width=2m).

DISCUSSION

Carabus nemoralis seems to have a high dispersal ability: in North America, where it was introduced by the European settlers at the east and at the west coast it has now reached almost the centre of the continent. In Canada only Manitoba and the northern districts are not settled today (CBIF 2006). Of course, it is difficult to differentiate the portion of anthropogenic transport and the active movement of the beetles themselves.

C. nemoralis is the smallest *Carabus* species that was tracked with radio transmitters up to now. Larger ground beetles often move faster than smaller ground beetles (Mossakowski and Stier 1983, Klazenga and De Vries 1994). However, the movement rate of *C. nemoralis* equals that of other larger *Carabus* species approximately. *Carabus clathratus* (body length: 20-36 mm; Arndt and Trautner 2004), a *Carabus* species of wetlands, was tracked in a meadow and walked 2.5 m/day (interquartil 0.9 to 5.8 m/day; median and interquartil from Jopp 2003). I obtained a similar value for *C. nemoralis* with 2.6 m/day (interquartil 1.0 to 5.5 m/day). Comparing *Carabus coriaceus* the largest ground beetle of central Europe (body length: 30-42 mm; Arndt and Trautner 2004) with *C. nemoralis* (4.5 ± 4.9 m/12 h) the former has a higher movement rate in forest (11.74 ± 12.12 m/12 h) but a comparable movement rate in meadows (4.6 ± 4.8 m/12 h). Earlier mark-recapture-studies on *C. nemoralis* reported a maximal net displacement of a single individual which covered a distance of 50 m in 24 h on arable fields (Welling 1990). This is about twice as far as the biggest move length in my data set. But most of the animals recaptured by Welling (1990) were slower. Six of 14 recaptured beetles covered a distance of 10 m and needed (6.0 ± 4.1) days for this distance. Although this velocity did not differ from my data, the mentioned maximal speed indicates that the beetles might move faster on arable land. These results were corroborated by Kennedy (1994) who traced *C. nemoralis* in different habitats and found the velocity of male *C. nemoralis* in arable fields nine times higher than in other habitats such as rough grassland or a river bank. This can be explained by the very low local

spatial resistance in an arable field which affects the dispersal power of beetles positively (Heydemann 1957, Butterweck 1998, Jopp and Reuter 2005).

Earlier studies found several reasons that lead to a change of movement patterns in carabid beetles, such as foraging behaviour at different prey densities (Baars 1979, Wallin and Ekblom 1994), dispersal (Rijnsdorp 1980), and escape from unfavourable habitats (Niehues et al. 1996, Riecken and Rath 1996). While the change in movement patterns due to foraging can differ due to varying hunger level and prey densities (Wallin and Ekblom 1994) dispersal and escape movements are uniformly characterised by long moves, little turning and therefore a high degree of correlation between successive moves, a movement behaviour commonly known as directed walk (Baars 1979).

My study revealed no evidence for a directed walk of *Carabus nemoralis* in the observed habitat corridor. The lack of escaping behaviour leads me to the assumption that the beetles accept street greenery as a possible habitat. But it also means that the beetles did not switch their movement behaviour to dispersal in the habitat corridor. Wallin and Ekblom (1988) characterized the walking behaviour of *C. nemoralis* as a correlated random walk, corroborating my results. In contrast to this, Hockmann et al. (1992) observed directed walk in almost all individuals of *C. nemoralis* which they observed in fenced circles. Considering the frequently disruption associated with the experiment design of fenced circles with pitfall traps at the fences, the high ratio of observed directed movement might have been a result of fleeing motivation influencing the behaviour of the beetles.

An alternative explanation for the missing of directed walking might be that a distinct dispersal period occurs in the life cycle of *Carabus nemoralis* like Rijnsdorp (1980) observed for *Carabus problematicus*. This dispersal period might have been not included in my observation time. The species has a distinct peak of activity during the reproduction period from April to May but stay active during the summer and has a little peak again in autumn (October) when the juveniles emerge (Rietze 2001). Whether this autumn activity peak indicates the dispersal period remains uncertain. However, for a species with a comparable life

cycle, *Carabus auronitens*, the main dispersal events occurred within the reproduction period in the spring (Drees and Weber 2001).

Several studies revealed that ground beetles cover greater distances per time unit in their home habitat than in comparably narrow habitat corridors (Zerbe 1989, Vermeulen 1994, Charrier et al. 1997). Computer simulation studies (Tischendorf and Wissel 1997, Jopp and Reuter 2005) revealed that movement behaviour, namely the difference between random walk and directed walk, might be most important for the determination of the transition speed along habitat corridors. Considering that *Carabus nemoralis* did not show directed walk in a habitat corridor it might not move very effectively through habitat corridors.

Another determinant of the corridor efficiency is the behaviour at the corridor boundaries (Tischendorf and Wissel 1997, Haddad 1999b). Theoretically, a random choice of a new direction when beetles reach a boundary might decrease the guidance function of a habitat corridor. Furthermore, both theoretical (Jopp and Reuter 2005) and experimental studies (Haddad 1999b) revealed that habitat corridors did not enhance the dispersal compared to a situation without habitat corridors if the animals do not return at habitat boundaries constantly but leave the habitat frequently and move also through the surrounding matrix habitat. In the present study *Carabus nemoralis* females did not change their random turning behaviour near the boundaries but the beetle returned constantly at the habitat boundaries and never crossed the street. Very low street crossing ratios were also revealed in a mark-recapture study with more individuals by Mader (1979).

Both the lack of directed walk and the missing of a guidance effect of the habitat corridor suggest that the dispersal efficiency of habitat corridors for *Carabus nemoralis* is low. In addition, the efficiency of habitat corridors might be decreased by an effect observed by Baum et al. (2004) for a planthopper species. In their study the effectiveness of habitat corridors and stepping stones depended on the kind of the surrounding matrix habitat. The connecting structures were less effective if they lead through a high-resistance matrix habitat, which hampers dispersal intensively. Nonetheless *C. nemoralis* can use street greenery as a dispersal corridor. Both the preference for directions along

the longitudinal axis of the corridor if long-interval moves are considered as well as the constant increase in dispersal range with the observation time support this conclusion. In a rural landscape this beetle species might not need habitat corridors for the connection of subpopulations due to the ability of survival in open-habitat structures (Turin 2000), but in an urban environment, with its high degree of surface sealing and traffic, man-made habitat corridors might be the only possible landscape structures that preserve some connectivity between the urban forest remnants for flightless ground beetles. The distances that can be covered by the beetles during their lifetime can be extrapolated from the short-term data I obtained, but this can estimate the real values only very roughly, because temporal and scale dependent changes affecting the movement behaviour are not included. Assuming a linear increase of the dispersal range with the time as revealed by my data and a high movement activity in April, May, July and October (Rietze 2001) the possible dispersal range would be 150-250 m/year. Maximal dispersal distances of this range are also corroborated by the results of earlier mark-recapture studies (Reike 2004). However, distances between urban forest fragments are often much greater. Although it is known that *C. nemoralis* can survive longer than one year (Hockmann et al. 1992) it is necessary that the beetles can also reproduce in habitat corridors or similar structures like small habitat patches (“stepping stones”) to bridge the distance between habitat fragments step by step. This necessity might be a reason why other *Carabus* species, that are more specialised in forest habitats, might not profit from urban green corridors. Their habitat quality is generally too low to support even small temporary populations of true forest specialists.

Although my study revealed evidence for a high isolation by sealed surface in the urban landscape especially streets the ability of beetles to cross such gaps can not be excluded. Narrow asphalted lanes in rural environments without curbstones were crossed by *C. nemoralis* infrequently (Mader 1979, Welling 1990). During traversing streets or other matrix habitat space a higher mortality must be assumed for the beetles. However, the beetles might be able to compensate this increased mortality with a higher movement speed in such habitats (Rosenberg 1998). The high movement speed which was observed when

the beetles crossed the gravel path in the experiment, which was also a plain surface without any vegetation, supports this interpretation.