5. The influence of radio transmitters on the movement behaviour of large ground beetles

Abstract - Telemetry is a great help for the observation of animal movement patterns in the field. Unfortunately, the usage of radio transmitters is confined to larger animals, which are capable of carrying such a device. Large ground beetles are at the threshold of the applicability of radio transmitters but a few field studies have already used radio transmitters to observe ground beetle movement patterns. A laboratory study was conducted to estimate the influence of radio transmitters on the movement behaviour of *Carabus nemoralis* Müller, 1764. Females of this comparably small *Carabus* species were observed in a laboratory arena with and without transmitters. Radio transmitters change not only the weight but also the body form of the beetles. Standardised obstacles were included to take altered body form into account. Tagged beetles moved straighter away from the release point than untagged ones. If tagged beetles had to move around an obstacle they compensated this deflection by turning to reassume the original direction after the obstacle. Tagged beetles shared these behavioural traits with fleeing beetles. In contrast, tagged beetles rested more than untagged ones, which contradicts fleeing behaviour. Thus, field studies can be affected by a potential behavioural bias through radio transmitters. High direction fidelity (directed walk) might be an artifact due to fleeing behaviour of the tagged beetles.

INTRODUCTION

Telemetric methods are valuable extensions for the study of movement behaviour and dispersal of animals. The disadvantages of mark-recapture studies, e.g. low recapture frequencies, limited spatial frame of the study due to the limited number of traps that can be handled, and random trapping success, can be overcome by tracking individual beetles. Historically, telemetric approaches for ground beetles began with radioactive marking of beetles (Baars 1979). Soon this method was replaced by less invasive methods, such as harmonic-radar systems and radio transmitters. Whereas the harmonic-radar system has been applied to a broad variety of ground beetles (e.g. *Abax parallelepipedus*: Charrier et al.1997; *Carabus hortensis*: Szyszko et al. 2004; *Poecilus cupreus*: Wallin and Ekbom 1994; *Pterostichus melanarius*: Wallin and Ekbom 1994; *Pterostichus niger*: Wallin and Ekbom 1994) radio transmitters were only applied to large ground beetles like those of the genus *Carabus* (Riecken and Raths 2000, Jopp 2003, Deichsel 2007). Despite the advantages of radio transmitters over harmonic-radar systems (Riecken and Raths 1996), such as greater transmission range and individual frequencies of different transmitters, the weight of the radio-transmitter is still a drawback for the application to smaller beetles. Riecken and Raths (2000) gave advice as to which *Carabus* species could be studied with radio transmitters, based on the transmitters available at that time. They did not give reasons for the threshold of beetle size they chose, but these authors excluded *Carabus nemoralis* Müller, 1764 from the species that were considered large enough for radio transmitter studies. In contrast, recent studies showed that *C. nemoralis* seems to be capable of carrying radio transmitters in the field (Deichsel 2007).

Despite technical progress in the development of lighter transmitters, they are still a heavy load for the beetles and this "backpack" might influence their behaviour (Hockmann et al. 1992, Reike 2004). In order to test this handicap, I conducted laboratory studies on beetles with and without transmitters, in order to estimate their effects on walking behaviour.

On a small scale I investigated whether there are behavioural differences between tagged and untagged beetles (speed, net displacement, and response to obstacles).

MATERIAL AND METHODS

Because *C. nemoralis* is a strictly nocturnal species, the laboratory experiments were done in a darkroom solely illuminated with subdued red light during the first half of the night. The beetles walked in a square glass arena (1m by 1m) carpeted with moisted paper towels (fig. 23). I used radio transmitters of the type LB-2N (Holohil Systems Ltd., Ontario Canada) temporarily attached to the beetles elytrae with double-faced tape. These transmitters weight 0.47g which is about 70%, approximately of the beetles' net weight (Hockmann 1992 and own data). Transmitters are not only an additional weight, but also a "backpack" that might alter the beetles' response to obstacles. In order to test this effect on walking behaviour, the laboratory arena was equipped with three kinds of standardised obstacles: (1) small walls that deflect the movement, (2) small ridges (6 mm high) as low hurdles, and (3) low open gateways to imitated branches lying near the ground. Only beetles without transmitters could pass the latter. Twenty-four females were used in the experiments. Females of the same species also have been observed in my field studies with the same species (Deichsel 2007), and were chosen for the experiments because they are larger than males and might carry the transmitter more easily.

The laboratory air temperature was 24°C during the experiments on June 4, 8, and 14, 2004. Before the start ,the specimens were transfered to a cylinder in the middle of the arena, where they could settle for a while (1 minute). When the cylinder was lifted, the walk could begin.

A digital camera (Canon Powershot A70, with video mode) mounted above the arena recorded the walks from the beginning until the specimen arrived at the
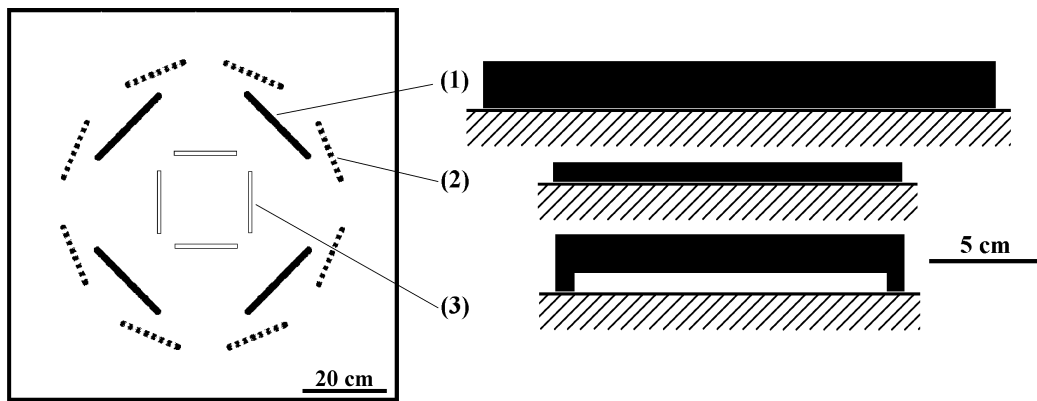
Figure 23. Scheme of a laboratory walking arena for beetle observation (birdseye view) on the left side, with a schematic front view of the obstacles used on the right side. Four small walls (solid lines), four gateways (lines white inside) and eight ridges (dotted lines) served as obstacles for the observed beetles. 10-cm-high walls around the arena stopped the beetles at the edges.

arena's edge. After that, the movement was not recorded further, because edge effects would have affected behaviour.

Upon release, some of the specimens tended to rest while others started to run immediately. To assure similar walking conditions, i.e. constant fleeing motivation, the beetles were tapped with a stick on the posterior abdomen whenever they rested in two of the four treatments (cf. Butterweck 1998). Each of 24 females had to complete several walks: (1) without transmitter or tapping, (2) without transmitter but with tapping, (3) with transmitter but without tapping and (4) with transmitter and tapping. Between the different walks the specimens had at least two hours to rest. After the mounting of the transmitters, they had at least four hours to settle.

The pathway of the individuals was digitalised using the video-analysing software Viana (Kersting et al. 2003). The position of the beetles was determined every 0.6 seconds and was measured to the nearest 0.5 cm. Length of the move between two subsequent points was used for the analysis. Because the chosen time interval is fairly short, the move length between two successive observation points could be used to calculate the walking speed of the beetles. If the time interval had been longer, the walking speed would be underestimated because the

actual circuitous path between two successive observation points is longer than the direct distance between these two points.

Additionally, the portions of resting phases in both of the non-tapping treatments were compared. The median values of move length were tested for significant differences with the Wilcoxon matched pairs signed rank test. It is necessary to use a statistical test for paired samples because the results of the different treatments for particular beetles were not independent of each other. In addition the Wilcoxon test is a nonparametric test based on rank sum comparision which requires no special data distribution (Sachs 1997).

In order to characterise the overall dispersal process, net displacement of the beetles from the starting point was calculated as the direct distance between the starting point and subsequent positions on the pathway. Most fleeing animals attempt to increase their distance from the point of disturbance as fast as possible (Wendler 1999). Fleeing beetles hardly change their direction, except for obstacles. Thus, the increase in net displacement would be more or less constant, assuming a constant speed of movement. Undisturbed animals that do not move away from a point as fast as possible but move according to a correlated random walk are not expected to show a linear increase of net displacement from an initial starting point (Kareiva and Shigesada 1983). The graphic analysis of net displacement rates is very illustrative compared to the quantitative approach of comparing expected and observed net squared displacement in the sense of Kareiva and Shigesada (1983). Considering my prevailing interest in qualitative differences between different treatments and the comparably small dataset, I prefered the former method.

The capability of the obstacles to deflect the beetles was tested for each type independently. For the obstacles that could be overcome, namely the small ridges (type 2, fig. 23) and the low gates (type 3, fig. 23) I calculated the direction change due to the obstacle by comparing the mean direction taken 5 cm before and 5 cm after the obstacle. These turns were compared pairwise with turns of the same individuals in a control section between the first and second obstacles (Fig. 24). A Wilcoxon test for paired samples was applied to test for significant differences.
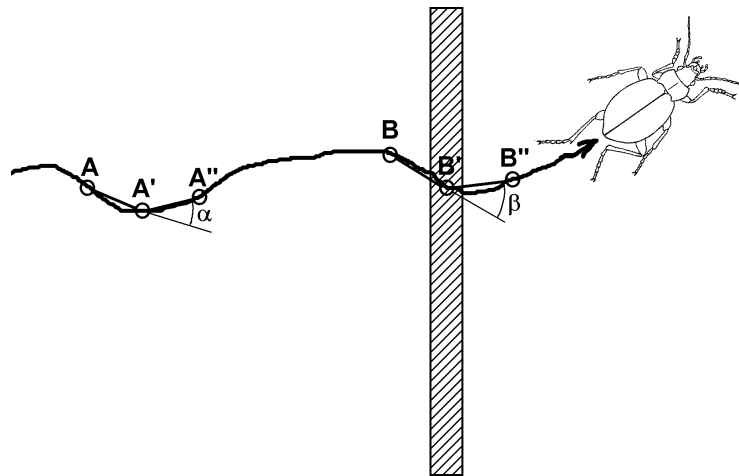
Figure 24. Scheme of the method allowing a comparison of deflection due to an obstacle that can be passed directly (angle β) and a control turning angle in an obstacle-free segment of the path (angle α). The segments A-A', A'-A'', B-B', B'-B'' are 5 cm each. The circuitous path between the different observation points is simplified to a straight line to measure the angle between the successive sections of the path. The shaded bar symbolises an obstacle that can be passed directly by the beetles, such as a low ridge.

While ridges and gates could be passed directly by the beetles, at least by those without transmitters, the wall-type of obstacle (type 1, fig. 23) could only be overcome by the beetles by walking around them.

In an earlier preliminary experiment, I observed that in some cases beetles tend to use the same direction before and after walls. To investigate this phenomenon, the deflection of the beetles due to the wall (angle γ) was measured (fig. 25). If the beetles attempt the same overall direction they should compensate for this deflection after leaving the wall, so I measured also this compensation turning angle (angle ε) and tested it for a correlation with the angle of deflection caused by the wall using Spearman rank correlation.
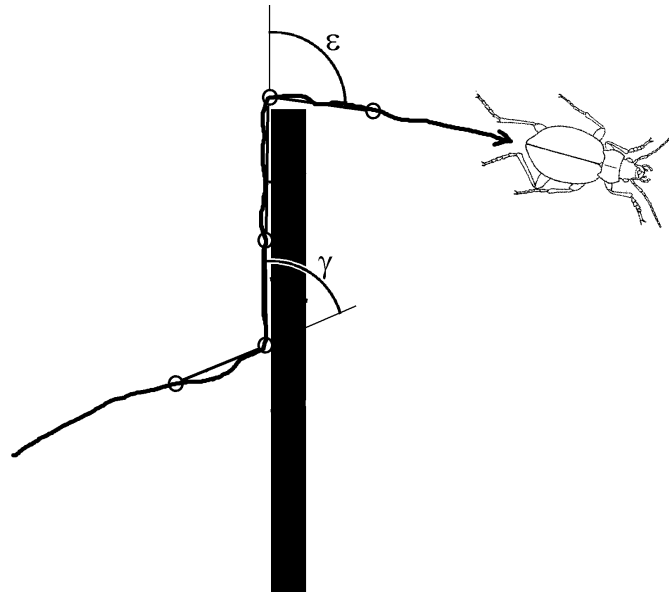
Figure 25. Scheme of the path of a beetle confronted with a wall obstacle (black bar). The wall forces the beetle to change its direction by the deflection angle γ. After the obstacle the beetle might compensate for this deflection by turning in the direction of angle ε.

The deflection at obstacles was only analysed under three different conditions: without transmitter and tapping, assumed to be undisturbed movement behaviour; without transmitter but with tapping, assumed to be forced fleeing behaviour; and with transmitter but without tapping, which I wanted to compare it with the others.

All statistical tests were calculated with the help of the computer program STATISTICA (StatSoft 2001)

RESULTS

Not all individuals moved in every treatment. Especially in the treatments without tapping many individuals rested for the whole duration of the experiment.

For the pairwise comparisons, I used only the beetles that had moved in both tests. The difference between median move length of females with and without transmitter (without tapping) was nearly significant (n=11; Z=1.96; p=0.0505;

fig. 26). In the tapping treatment, tagged individuals moved significantly shorter distances (n=21; Z=3.01; p<0.01; fig. 26). The median move length of the tagged and tapped beetles was 83 % of the tapped individuals without additional weight. The maximal velocity was 18 cm/s in the untagged, tapped beetles and 15 cm/s in the beetles that were neither tagged nor tapped.

Resting phases were significantly longer when the beetles had to carry a transmitter (n=11, Z=2.49, p=0.01).
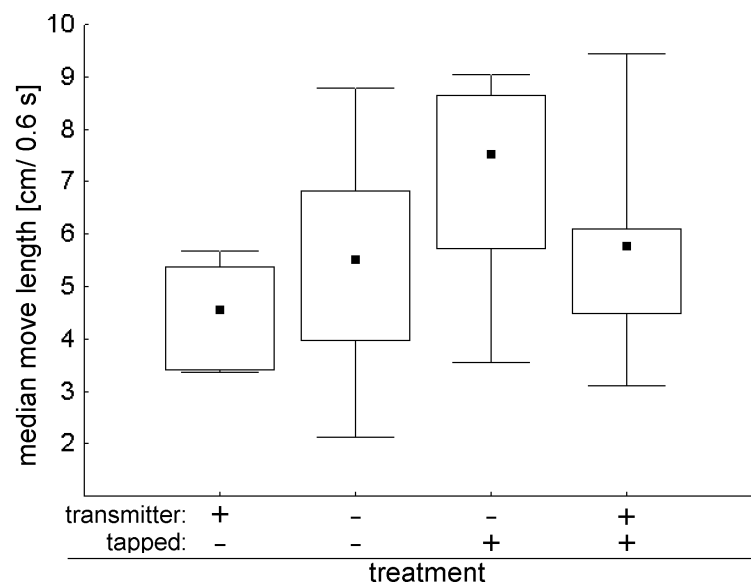

Figure 26. Median move length of female *Carabus nemoralis* in a laboratory experiment. The time between consecutive tracked positions was 0.6 s. The same beetles underwent four different treatments, indicated under the x-axis. Boxes display the interquartil distance; the whiskers, the minimal and maximal values; and the central square, the median.
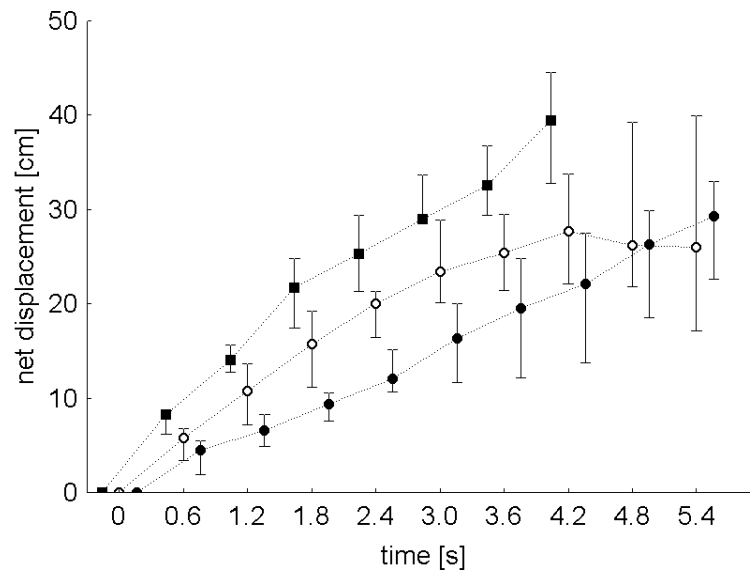
Figure 27. Net displacement (median and interquartil) of female *Carabus nemoralis* in a laboratory experiment. In the first run, the beetles walked without transmitter and were not tapped (open circles). In a second run, beetles without a transmitter were forced to flee by tapping them with a stick (squares). During the third run, the beetles were equipped with a transmitter, but were not tapped (full circle).

The net displacement of beetles carrying transmitters increased nearly linearly with the observation time (fig. 27), as was the case with beetles forced to flee by tapping them. The net displacement rate of the tapped beetles was higher.

In contrast, the net displacement of the beetles without transmitter increased directly after the start - more than that of undisturbed beetles with a transmitter - but the rate dropped with time although the beetles had not yet reached the margins of the arena (at 50 cm).

Beetles with a transmitter did not seem to regard the gates as obstacles. While they immediately changed directions at the wall-obstacles, they tried to walk beneath the gate. Some individuals fell to one side accidentally and could pass the obstacle in this position; others moved around the gates. For those that walked around the obstacle, I measured the direction change as the difference in direction before arriving at the gate and the direction after the obstacle. Compared with an obstacle-free walk, neither the gates (fig. 28) nor the ridges (fig. 29) induced a significant direction change, regardless of the beetle treatment.
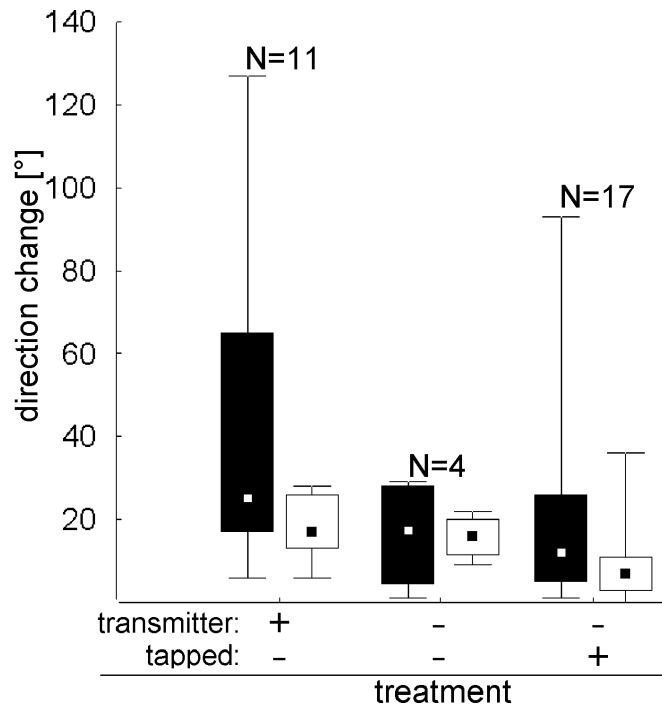
Figure 28. Direction changes of female *Carabus nemoralis* at gate obstacles in a laboratory situation (black boxes). Reference turnings in the absence of an obstacle are given by the open boxes. For each treatment, median (squares), interquartil (boxes), range (whiskers) and the number of replicates are given.
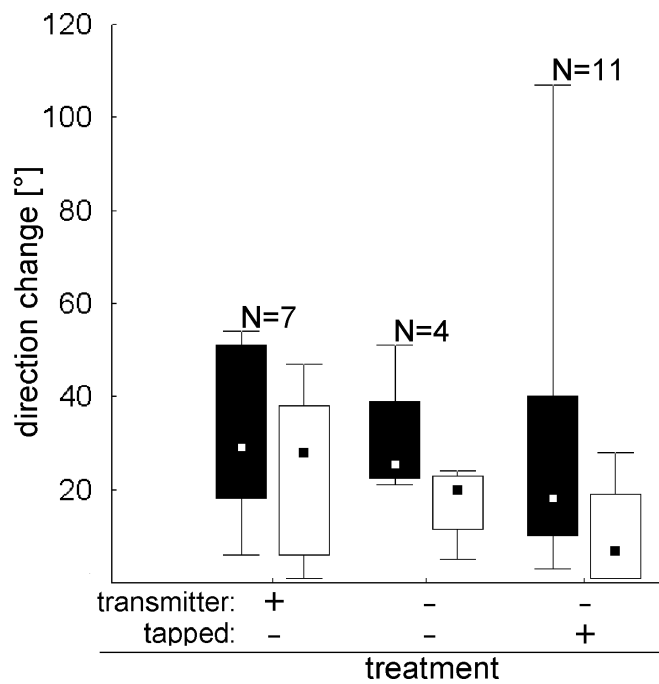

Figure 29. Direction changes of female *Carabus nemoralis* at ridge-shaped obstacles in a laboratory situation (black boxes). Reference turnings in the absence of an obstacle are given by the open boxes. For each treatment, median (squares), interquartil (boxes), range (whiskers) and the number of replicates are given.

The deflection of untreated beetles (no transmitter, not tapped) due to the wall obstacles was not correlated with the turn when the beetles left the obstacle (N=6, p=0.544). Some individuals didn't even walk along the whole wall, but moved away from it before they reached the end of the obstacle. In contrast, fleeing beetles (tapped) and beetles that carried a transmitter compensated the deflection. The deflection angles were correlated significantly with the compensation turning angle after the obstacle both in the treatment without tapping but with a transmitter (N=9, R=0.83, p<0.001) and in the tapping treatment (N=12, R=0.70, p<0.05). Although the deflection angles and the compensation turning angles after the wall are highly correlated in the treatment with the transmitter, they deviate from the theoretical expectation that compensation turn is exactly as large as the initial deflection (fig. 30). If the forced turn was comparably small than the compensation turn was too small to compensate the forced turn completely.
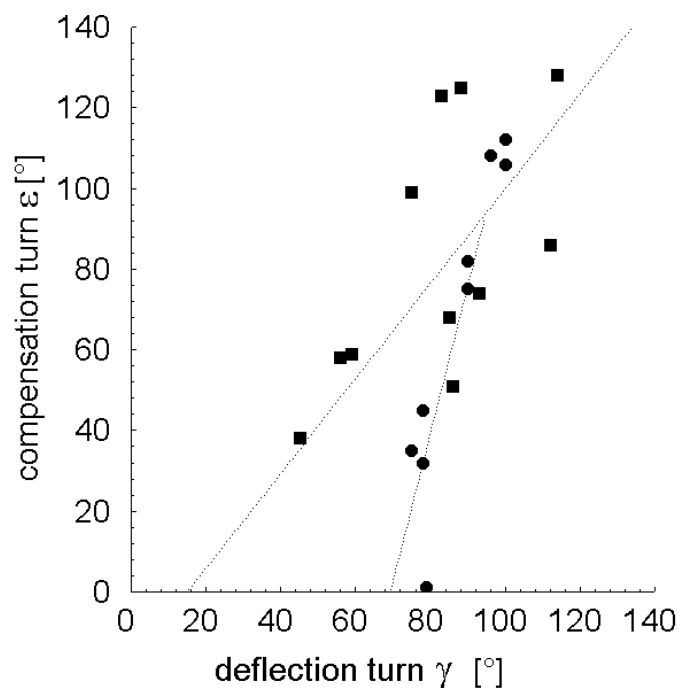

Figure 30. Turning behaviour of female *Carabus nemoralis* at wall obstacles in a laboratory experiment. In one treatment, beetles were forced to flee by tapping them with a stick (squares) and in another treatment, they were not tapped but had to carry a transmitter (circles).

DISCUSSION

Unfortunately, active transmitters like the ones I used are still very heavy in relation to the weight of the beetles and are likely to influence the behaviour of the tagged beetles. Earlier approaches to estimate the influence of such backpacks on the movement behaviour were confined to the weight development of the beetles. The weight development of the tagged beetles is one opportunity to estimate the fitness of the beetle, although it reveals no detailed information about the possible alteration of movement patterns. No weight loss during the observation with a radio transmitter was found for the larger *Carabus*-species *C. coriaceus* (Riecken and Ries 1992) and *C. clatratus* (Jopp 2003). For the smaller *C. hortensis*, Reike (2004) found a weight loss when he used radio transmitters, but they put on weight with lighter radar diodes. Unfortunately, he did his observations only with a small number of individuals and did not use both methods at the same time. During a field experiment with *C. nemoralis*, some individuals gained weight whereas others lost weight (Deichsel 2007). Considering these data alone, conclusions about the influence of transmitters on beetle movement remain ambiguous.

To estimate the bias of radio transmitters on the results of mobility studies it is necessary to add information about the behavioural changes that can be observed.

A clear difference in velocity between beetles with and without transmitter were only observed when the beetles were forced to flee by tapping them. The physical conditions during a movement with increased mass but constant muscular strength (likely the beetles run with "full power" during fleeing) must result in a decreased speed. Not-tapped beetles walked with a moderate velocity, and no difference between tagged and untagged beetles could be found. In this case, the tagged beetles seem to be able to compensate for their weight handicap.

Hockmann et al. (1992) observed an increased recapture rate of *Carabus nemoralis* individuals that carried a weight (47-101% of the beetles' own weight) in experiments with fenced circles, which was interpreted as a possible result of fleeing behaviour. In contrast, in my study tagged beetles rested more than untagged ones.

It was shown for other arthropods, they flee in a nearly straight line away from a disturbance and make few turns (Wendler 1999). This would be reflected in a linear increase in net displacement from the point of disturbance. While the linear increase of net displacement in tagged individuals as well as fleeing beetles that had been tapped implies a constant movement away from the starting point, the leveling of the untagged beetles curve indicates a less directed movement. Although the untagged beetles started with a higher net displacement, likely due to a higher movement speed, the mean net displacement was not higher than that of tagged beetles at the end of the analysed walking sequence.

In addition, beetles that were forced to flee and tagged beetles shared another common behaviour at wall obstacles. Instead of choosing a random walking direction after contacting the obstacle, like the untagged individuals, they walked along the obstacle until they reached its end and then turned in the direction that they had walked before the obstacle. Direction compensation behaviour would make sense if the beetles try to keep a constant direction, e.g. to flee from a certain point. There is also empirical evidence for such a compensation behaviour in other beetles such as *Tenebrio molitor* (Wendler 1999) and other arthropod taxa (Dingle 1961, Burger 1971). These are able to perceive the turns that they make with the help of mechanoreceptors at the joints of their exosceleton and they can compensate for such turns even without external orientation cues. This behaviour is also a possible explanation for the increased recaptures of tagged individuals in fenced circles (Hockmann et al. 1992). When the beetles reach a fence they try to walk around this obstacle and fall right into the next pitfall trap. In contrast, untagged beetles might leave the fence, choosing a random direction, and thus, decrease their chance of recapture.

However, the compensation turning of the tagged beetles was not perfect. Instead of choosing exactly the same compensation angle compared with the angle of deflection due to the wall, their compensation was too weak, especially when the deflection was comparably small. As an explanation for this phenomenon I suggest that the perception of the turning might be adjusted to the normal weight of the beetles and that the increased weight due to the added transmitter contribute to this shift.

The behaviour at the other obstacle types, ridges and gates (type 2 and 3, fig. 23) revealed no difference between tagged and untagged beetles. The deflection angles due to the obstacles did not differ from those in a comparable, obstacle-free walking situation, whether the beetles were tagged or not.

Concluding, my findings suggest a behavioural change in tagged beetles compared to untagged ones. Some behavioural parameters, namely compensation turning after wall obstacles and linear increase in mean net displacement of the tagged beetles indicated a fleeing behaviour. Only the increased resting periods of tagged beetles contradict a fleeing behaviour. Considering the artificial laboratory situation and the limited dataset the transfer of this observation to the field situation might be limited to some extent. However, in field studies this possible bias should be kept in mind. Movement behaviour characterised by directed walk components (Baars 1979) might be a result of an unusual fleeing behaviour of tagged beetles instead of naturally-occuring dispersal processes.