# The Use of Harmonic Radar for Research on the Mobility of Small Invertebrates 

Berthold Janßen und Harald Plachter

## Synopsis

Information on mobility is an important condition for the development of individual based population models. Methods which provide high recapture rates of invertebrates are needed. Harmonic radar has the potential to solve some problems with tracking invertebrates and some aspects of the method are tested here.

The height above ground and the alignment of the radar tags in space have significant influence on the detection range: The achieved mean detection distance of 25 m in 60 cm height is three times the distance of radar tags located in 4 cm height (just above ground) with a mean of 8 m . The alignment tests led to the conclusion that a vertically hanging radar tag is optimal for the detection and would show no influence by the direction one approaches towards the animal. Additionally, the range of tags just above ground ( 4 cm ) is significantly higher in areas of low vegetation than in dense vegetation.

Choosing the land snail Cepaea nemoralis L. we selected an example of a species living close to the ground in dense vegetation. The method appeared to be effective in collecting a high density of recapture data. Therefore, evaluation of directional behaviour and short term distance distribution is possible. Furthermore the potential data density per specimen allows the investigation of individual differences.

## Dispersal, radar telemetry, movement behaviour, Cepaea nemoralis

## 1 Introduction

Studies on the mobility of animals are of interest for different reasons, i.e. to calculate probabilities for insect pest outbreaks in agriculture and forestry (RIESKE \& RAFFA 1990, WRATTEN \& THOMAS 1990), for the assessment of survival probabilities of endangered species (DEN BOER 1990, OPDAM 1990) and for the analysis of the connectivity of landscapes (MADER \& al. 1986).

Recent approaches in dispersal studies emphasize the modeling of the overall movements within populations (e.g. BAUR \& BAUR 1993). In all cases where
stochastic variables are of importance, deterministic models are only first steps to the problem (BERG \& KUHLMANN 1993). Conventional methods like mark and recapture may give estimates on spatial distribution but suffer in many cases from low recapture rates and therefore insufficient information on the movement behaviour. Therefore the requirements of individually based models (like data on frequency distributions of distances and directions, orientation abilities, landscape barriers, influence of abiotic factors like temperature and humidity) of single specimens are frequently not met by these methods. At present, radio telemetry, developed for vertebrates, can only be used for very large invertebrates (RIECKEN \& RATHS 1996), but radar telemetry (= harmonic radar) has the potential for the application with much smaller animals. The use of this method for ecological investigations (for carabid beetles) was first introduced by MASCANZONI \& WALLIN (1986), but only few applications were published since then (e.g. WALLIN \& EKBOM 1988, HOCKMANN \& al. 1989).

The evaluation of advantages and disadvantages and possible transfers to other taxa depends on the detail information available on this method. We therefore present data on features of radar telemetry that are still unpublished. Furthermore we show the practical applicability of the method in a study on dispersal of the snail Cepaea nemoralis L., which is very common in Central Europe. Snails are suitable for dispersal studies because of the mostly low range of motion and therefore limited research areas. On the other hand, there are some problems resulting from the ecology and behaviour of this taxon. Snails are often hidden in the vegetation and difficult to find. Such problems should be solved by this method, because of the possibility to search for individuals over distance and the expected high recovery rates.

## 2 Materials and methods

The investigations where conducted at the experimental farm of the Munich Research Association for Agricultural Ecosystems (FAM) in Scheyern about 40 km north of Munich ( $48^{\circ} 29^{\prime \prime} \mathrm{N}, 11^{\circ} 26^{\prime \prime} \mathrm{E}$ ), with a mean annual temperature of $7.4^{\circ} \mathrm{C}$ and a mean annual precipitation of 833 mm (see HANTSCHEL \& al. 1993 for further details).

### 2.1 Radar telemetry

Radar telemetry is based on harmonic radar: The signal of a microwave frequence (here: 917 Mhz ) sent by an emitter is received by a passive electronic device (Schottky diode) and this device is stimulated to emit the double frequency ( 1834 Mhz ). A receiver (built together with the emitter into one case) is tuned to this frequency and gives an audible sound in case of detection. In this study we used a radar detector of Recco, Sweden, that was constructed for the bearing of avalanche victims.

The detection range of a given radar device is mainly determined by the electric quality of the antenna fixed to the diode. In this study we used a dipol antenna of varnished copper ( 0.1 mm diameter) with a lenght of the antenna arms of 4.1 cm (wavelength $\lambda / 8$ ). These two essential components where accomplished by an silicone encapsulation of the diode and its soldered joint for a better physical endurance. The radar tags had an average weight of $39.2 \mathrm{mg}( \pm$ SD 5.7 mg$)$ and were glued to the shell. The glue and an individual mark on the shell by a numbered label of opalith together had a weight of $14 \mathrm{mg}( \pm$ SD 2.5 mg ).

### 2.2 Detection range

The detection range was investigated with regards to three variables: height in vegetation, alignment in space and vegetation type. The measures were taken in a fallow land and in a recently mowed meadow (Tab. 1).

To test the influence of height above ground on the detection range fifteen radar tags were fixed to the vegetation with sticky tape so that the diodes were located in 4,30 and 60 cm height. While slowly approaching the tags along a straight line, the distance was measured in intervals of 50 cm when a signal was first registered. For each height and each
radar tag three approaches were made and the median was used for further calculation.

To assess the effect of the alignment in space ten radar tags were tested for three different alignments: along the direction of detection, at right angles horizontally and at right angles vertically (see Fig. 2 for explanation). The tags were fixed to the vegetation in 4 cm height, thus the end of the lower antenna touched the ground. The mode of measurement was the same as with heights.

To compare the influence of the two vegetation types the data of the vertically aligned radar tags in the meadow and the 4 cm data (also vertically aligned) of the height test in fallow land were used.

### 2.3 Mobility of Cepaea nemoralis L.

To investigate average and maximum movement ranges and directional behaviour, 30 adult specimen of C. nemoralis where captured in a nettle stand ( $U r$ tica dioica) in about 30 km distance from the experimental farm on June 16th 1997. The snails were marked the day after their capture and released on June 18th 1997 in an $8 \times 8 \mathrm{~m}$ grid in a fallow on the experimental farm. They weighed between 1.860 and $3.984 \mathrm{~g}(\bar{x}=2.851 \mathrm{~g})$, thus the weight of the transponders equaled 1.0 to $3.8 \%$ of their body weight (shell included). The fallow land was bordered by a forest in the south and by a small creek in the north.

Every second day the snails were searched by the aid of the radar device and the location of the individual animal was marked by a plastic stick with its number. The direction and the distance from the former place were taken by tape and a compass, respectively. On average 6 minutes were necessary for localization and measurement of one snail. When a snail could not be found in the close surrounding of its last location, the search was extended to a circle with a diameter of 30 m . Due to losses of radar tags by snails only 19 animals were recaptured after 10

Table 1
Vegetation parameters of the areas where the detection ranges of the radar tags were tested.

|  | Fallow land | Meadow |
| :--- | :---: | :---: |
| Maximum height of vegetation | 160 cm | 15 cm |
| Median of maximum heights | $110 \mathrm{~cm}(\mathrm{n}=20)$ | $12.5 \mathrm{~cm}(\mathrm{n}=10)$ |
| Median of average heights | $60 \mathrm{~cm}(\mathrm{n}=20)$ | $12.5 \mathrm{~cm}(\mathrm{n}=10)$ |
| Plant cover | $95-100 \%$ | $95-100 \%$ |
| Use in height test | X |  |
| Use in alignment test | X | x |
| Comparison of vegetation types | x |  |

days and for a detailed valuation of the method it was distinguished between the location rate of tags and the recapture rate of animals. The first is the proportion of radar tags that could be located - with or without adhering snail - of all tags in the field at that moment, whereas the latter gives the proportion of snails that were recaptured of all snails in the field at that moment.

The directions of 2 -day movements were tested for differences from a uniform distribution by the Rayleigh test (for further information on circular statistics see BATSCHELET 1981). To investigate a possible influence of the adjacent forest on the snails' orientation, for every 2 -day movement event the snail's distance from the forest border before the move was calculated (range: $12.2-63.3 \mathrm{~m}$ ) and related to the chosen direction. For different distances from the forest ( $25-50 \mathrm{~m}$ in 5 m steps) the chosen directions below the respective distance were compared to those above by the chi-squared test. The data of the lowest ( $\leq 20 \mathrm{~m}$ versus $>20 \mathrm{~m}$ ) and highest distance classes ( $\leq 55 \mathrm{~m}$ vers. $>55 \mathrm{~m}$ and above) did not meet the requirements for the chi-squared tests and were omitted. To analyse the individual behaviour all animals with at least 3 recaptures were tested for differences from an uniform distribution of directions.

Distances between animal locations were determined as moved distance per 2 day interval ( 27 animals with a total of 115 movements) and as maximum distance from the release point in the 10 day interval ( 19 animals that were recaptured after 10 days). The latter is a measure of dispersal power whereas the first gives information on movement behaviour in general.


Fig. 1
Median and range of the distance of detection in dependence on the height of the radar tags in the vegetation. All differences statistically significant (Mann-Whitney U-test, p << 0.001).

## 3 Results

### 3.1 Detection range

Heights of radar tags in the vegetation and alignment in space have significant influence on the detection range (Fig. 1, 2). The mean detection range of radar tags in 30 cm height (median 16.5 m ) is more than double the distance of radar tags in 4 cm height (median 8 m ). When tagged animals climb up in vegetation to 60 cm above ground, they may be detected in a distance of 25 m (all differences significant with $p<0.001$, Mann-Whitney U-test). This indicates a high potential for the use with invertebrate groups with such climbing behaviour, as many locusts and grashoppers might be examples for. The high detection distance enables the researcher to walk through an investigation area in parallel lines keeping great distances to each other, which means a low disturbance effect by the investigation itself.

This is limited by the impact of the alignment of radar tags in space (Fig. 2). It is smaller than that of height, but nevertheless of statistically significant influence (Mann-Whitney U-test, $p<0.01$ and $p<0.001$, respectively). The radar tags - only 4 cm above ground - could be detected from 11.8 m (median) when their axis was vertically aligned. Lower distances were investigated for horizontally alignment $(10.0 \mathrm{~m})$ and alignment along the direction of detection ( 8.5 m ). Thus the probability to detect animals is not equal for all potential exposure directions of the tag. In the worst case (minimum of »along«: 5.5 m ) only $39 \%$ of the range of the best case (maximum of »vertically": 14 m ) is reached.


Fig. 2
Median and range of the distance of detection in relation to the alignment of the radar tags in space. Test of 10 radar tags, each of which in different alignments. Arrows indicate direction of detection. All differences statistically significant (Mann-Whitney U-test, * : $\mathrm{p}=0.0099$; ** : $\mathrm{p}=0.0008$ ).

The comparison of detection ranges under different vegetation types (cut meadow versus fallow land) demonstrate a higher detectable distance in the low vegetation stand. While there was a considerable overlapping of the ranges (meadow: $10-14 \mathrm{~m}$; fallow land: $7-11 \mathrm{~m}$ ), the median value for the meadow $(11.8 \mathrm{~m})$ is significant higher than that on the fallow land ( 8 m, Mann-Whitney U-test, $\mathrm{p}<0.001$ ). It must be concluded that the lowering influence of vegetation on the radiation is not neglectable, especially if the tagged animals are close to the ground.

### 3.2 Recapture data

### 3.2.1 Recapture and location rate

The loss of radar tags by snails led to lower recapture rates (mean $90.6 \pm 5.8 \%$ ) than location rates (mean $95.9 \pm 4.0 \%$ ). This problem is mainly due to the thinness of the antenna $(0.1 \mathrm{~mm})$ and the movement behaviour of the snails, because crawling on grass leaves in acute angles leads to kinks in the wire which may break after a while. The location rate of 95.9\% indicates that not all radar tags that were expected could be detected (see discussion for possible reasons).

### 3.2.2 Analysis of dispersal in Cepaea nemoralis

 The analysis of the chosen directions of all 2-day movements shows a significant difference from an equal distribution (Rayleigh-Test, $\mathrm{p}=0.0038$ ) with a mean vector at $208^{\circ}\left( \pm 100^{\circ}\right)$ (Fig. 3). Snails within a low distance ( $\leq 25 \mathrm{~m}$ ) from the forest border have a different distribution of directions compared to those

Fig. 3
Frequency distribution of directions of 2-day movements of Cepaea nemoralis based on $5^{\circ}$-classes. Mean vector and $95 \%$ confidence interval are shown, the distribution is significantly different from a uniform distribution (Rayleigh test, $\mathrm{p}=0.0038$ ).
within a higher distance (chi-squared test, $\mathrm{p}=$ $0.0498)$. For other distances this comparison exhibited no significant differences ( $0.336<\mathrm{p}<0.716$ ). The mean vector of the snails within low distance from the forest was at $185^{\circ}\left( \pm 74^{\circ}\right)$ and the distribution is significantly different from a uniform distribution (Rayleigh-Test, $\mathrm{p}=0.0052$ ). Thus the forest obviously has an influence on the snails orientation.

The median of the moved distances per 2 days ( $\mathrm{n}=115$ ) was 1.85 m (1 $1^{\text {st }}$ quartile: $1.15 \mathrm{~m}, 3^{\text {rd }}$ quartile: 2.75 m ), whereas a maximum of 7.0 m was achieved (s. Fig. 4). This maximum is more than the 2.5 fold of the third quartile and raises the question whether there are individual differences in movement behaviour.

After 10 days, 19 animals were recaptured. Their maximum distance from the release point ranged from 2.5 to 17.9 m (median: 5.4 m ). Eighteen of them were continuously recaptured in 2 -day intervals, the one with the highest distance was not found for two times. For the three animals with the highest and with the lowest dispersed distance, respectively, from the release point the movement patterns are shown in Fig. 5. The comparison of dispersal distances and means of moved distances per 2 days for those 6 animals reveals a relation between these factors (Tab. 2). The strong correlation ( $\mathrm{r}=0.915$; $p<0.001$ ) indicates a higher resulting distance with higher 2 day movements. This is not self-evident, because only directed movement will lead to effective higher distances. Two animals chose directions that differed significantly from an uniform distribution (Rayleigh test, $\mathrm{p}=0.038$ in both cases), one of which was the snail with the highest dispersal distance.


Fig. 4
Frequency distribution of distances (2-day intervals) of Cepaea nemoralis in $50-\mathrm{cm}$ classes (median $=185 \mathrm{~cm}$ ).

Table 2
Dispersal distances and mean distance moved per two days
for the three most and least dispersing snails. The medians of all snails are given for comparison.

|  | Snails with highest <br> dispersal distances |  |  | All snails <br> (median) | Snails with lowest <br> dispersal distances |  |  |
| :--- | :---: | ---: | ---: | :---: | :---: | ---: | :---: |
| Maximum distance from release point (m) | 17.90 | 11.80 | 11.20 | 5.35 | 2.55 | 2.55 |  |
| Mean of moved distances per 2 days $(\mathrm{m})$ | $3.65^{1)}$ | 3.55 | 3.35 | 1.85 | 1.15 | 1.40 |  |

${ }^{1)}$ This snail was not recaptured on two consecutive recapture days. To give a mean of five 2 day movements, the distance for six days ( 10.6 m ) was divided by 3 .

## 4 Discussion

### 4.1 Missing radar tags

The missing of radar tags can be due to predation of snails by mice (Apodemus sp.) or by birds, namely the song thrush (Turdus philomelos) (WILLIAMSON \& al. 1977). In the first case the tags are transported into the ground, which reduces the range dramatically, because electromagnetic waves of the used wavelenght are strongly absorbed by the soil. In the latter case the tags may be transported out of the detection range. Besides predation, dispersal of snails out of the searched area might occur. In this case the animal would have to crawl a distance of at least 15 m from the last location, more than twice the highest distance recorded for a two day movement in this study. A fourth possibility is that the snail buried itself for a resting period. Only one snail was recaptured after beeing missed for 2 searching events, indicating that


Fig. 5
Movement patterns of animals with a) high and b) low dispersal distances in 10 days.
this animal might have been buried or out of the searching area.

These examples valid for most land snails indicate some disadvantages of the method. First, animals that temporarly live in the soil (e.g. for resting periods) will be found with a lower probability. Secondly, if travelled distances significantly exceed the expected range, those specimens may easily leave the searched area because of the relatively low detection range.

### 4.2 Detection range and use of radar telemetry

In general, the detection range of a telemetric method should be as high as possible. In this study we prove that the attainable range depends on the height at which the tagged animals are located, the vegetation type of the area and the alignment of the tag in space.

With species that ususally stay in a height of 60 cm or more above ground in the vegetation and with the described devices a detection range of 25 m can be realized. The limit of the range is partly due to the transportability of the radar detector, and the renunciation of transportability leads to much higher ranges of up to 250 m (RILEY \& al. 1996). Another reason for the limitation of range is the restriction of the antenna's size, due to size and shape of the animal. The fixing of the tag to the animal is also important for the detection range: If the species is often vertically aligned on stems of herbs or grasses, fixing the tag at right angles to this direction is of disadvantage whereas a vertical alignment along the body axis of the animal gives best results.

Sparse vegetation should have the same effect as low vegetation: a lowering of the radiation by water containing plant bodies does hardly appear in this case. Some unsystematic tests in a forest showed a nearly total absorbance of the radiation by trees. Thus the application of the method in forests will probably be limited (but see HOCKMANN \& al. 1989).

The obvious potential of the method with regard to flying insects has been realized for bees and bumble bees (RILEY \& al. 1996), tachinid and sarcophagid flies and butterflies (ROLAND \& al. 1996). But also in cases when ground dwelling species were investigated, the use of radar telemetry resulted in valid data (MASCANZONI \& WALLIN 1986, WALLIN \& EKBOM 1988, HOCKMANN \& al. 1989). MASCANZONI \& WALLIN (1986) stated that the animals have to be at least $\approx 1 \mathrm{~cm}$ of body size but the tags ROLAND \& al. (1996) take use of ( $<0.5 \mathrm{mg}$ ) are suitable for flies with a weight of $55-75 \mathrm{mg}$.

In the present study on the land snail Cepaea nemoralis, although the coincidence of unfavourable circumstances (snails live few centimeters above ground, the vegetation of the fallow land was high and dense, all kinds of alignment of radar tags occured) the method worked fine. BAUR \& BAUR (1993) state that in mark and recapture studies with snails a reduced recovery must be accepted if the vegetation shall not be damaged. Radar telemetry is a way to avoid this problem by receiving a high density of recapture data while vegetation damage remains low.

The discrepancy between the recapture rate and the location rate was mainly due to antenna breaks, which led to locations of radar tags with a half antenna and without a snail. The problem might be solved by embedding the antenna into a thin layer of silicone or else. The mean recapture rate of more than $90 \%$ is much higher than in a comparable investigation without use of telemetry (BAUR \& BAUR 1993: average of $47.5 \%$ for Arianta arbustorum).

### 4.3 Dispersal distances and directions

Activity and movement of Cepaea nemoralis are influenced by several environmental factors (e.g. height of vegetation, CAIN \& CURREY 1968, or olfactorious signals, GOODFRIEND 1983). Knowledge on orientation is sparse: C. nemoralis can move towards a shelter with high humidity from more than one meter distance (ROLLO \& WELLINGTON 1981) and positive anemotaxis (moving upwinds) is also proved (GOODFRIEND 1983). In the present study the analysis of moving directions reveals a tendency of the snails to move towards a nearby forest. Since the study was not planned to investigate this question, further research on the kind of perception and the spatial range of this orientation ability are required. Due to the fact that $C$. nemoralis climbs up trees and shrubs (JAREMOVIC \& ROLLO 1979), it seems reasonable to expect the capability to orientate towards these habitat elements.

Although the meaning of individual differences has already been discussed 40 years ago (WELLING-

TON 1957), individual differences rarely have been taken in account as an important factor in population ecology. For Arianta arbustorum, BAUR \& GOSTELI (1986) found individual differences in geotactic reponses of snails to artificial inclination. They stress the possible advantages of a risk spreading tactics for snails in unstable habitats, like different offspring movement behaviour, when some specimens stay close to their shelter place and others disperse to find new suitable habitats.

The present study indicates individual differences in dispersal patterns of $C$. nemoralis. The frequency distribution of distances moved in 2 days is exponentially declining as found for other snails (BAKER 1988, BAUR 1993). The comparison of individual movement patterns and the correlation of achieved maximum distances with the mean of short term distances lead to the assumption that not all animals of a population are involved in dispersal processes in the same way, and that the probability for a higher distance move is not equal for all snails. Further studies are necessary to quantify different movement types and to assess the influence of genetic differences and environmental impacts (including intraspecific interactions) on dispersal patterns, respectively.

The analysis of movement data for individual differences in distances and directions as well as the development of stochastically based dispersal models require detailed and high resoluted information on single specimen. In many habitat types a sufficient density of data cannot be realized by conventional searching for marked animals but radar telemetry might solve this problem. Furthermore, a fast and non destroying search for animals living in dense veg. etation is possible by this technique.

## 5 Acknowledgements

The scientific activities of the research network , Forschungsverbund Agrarökosysteme Münchens (Munich Research Association for Agricultural Ecosystems; FAM) are financially supported by the Federal Ministry of Science, Education, Research and Technology (BMBF 0339370). Rent and operating expenses of the experimental farm in Scheyern are paid by the Bavarian State Ministry for Education and Culture, Science and Art. Parvis Fallaturi (University of Kassel) introduced us to the radar technique and Ulrich Müller from the Developmental Laboratories for Electronics (University of Marburg) gave important hints on the construction of the radar tags. Thomas Neßlauer was a good assistant during field work and Volker Homes and Antje Burgard served us with valuable advice on improving the manuscript.

## References

BAKER, G. H., 1988: The dispersal of Cernuella virgata (Mollusca: Helicidae). - Austral. J. Zool. 36: 513-520
BATSCHELET, E., 1981: Circular statistics in biology. - Academic Press, London; 372 p .

BAUR, A. \& BAUR, B., 1993: Daily movement patterns and dispersal in the land snail Arianta arbustorum. - Malacologia 35: 89-98
BAUR, B. \& GOSTELI, M., 1986: Between and within population differences in geotactic response in the land snail Arianta arbustorum (L.) (Helicidae). - Behaviour 97: 147-160
BAUR, B., 1993: Population structure, density, dispersal and neighbourhood size in Arianta arbustorum (Linnaeus, 1758) (Pulmonata: Helicidae). - Ann. Naturhist. Mus. Wien, Ser. B, Bot. Zool. 94-95: 307-321
BERG, E. \& KUHLMANN, F., 1993: Systemanalyse und Simulation. - Ulmer, Stuttgart; 344 p.
CAIN, A. J. \& CURREY, J. D., 1968: Studies on Cepaea. III. Ecogenetics of a population of Cepaea nemoralis (L.) subject to strong area effects. - Philosoph. Transact. Roy. Soc. London 253: 447-485
DEN BOER, J. P., 1990: The survival value of dispersal in terrestrial arthropods. - Biol. Conservation 54: 175-192
GOODFRIEND, G. A., 1983: Anemotaxis and its relation to migration in the land snail Cepaea nemoralis. - Am. Midl. Nat. 109: 414-415
HANTSCHEL, R. E., LENZ, R. J. M., KAINZ, M. \& BEESE, F., 1993: Ziele, Hypothesen und Arbeitsschritte des Forschungsverbundes Agrarökosysteme München. - FAM-Bericht 3: 1-12
HOCKMANN, P., SCHLOMBERG, P., WALLIN, H. \& WEBER, F., 1989: Bewegungsmuster und Orientierung des Laufkäfers Carabus auronitens in einem westfälischen Eichen-Hainbuchen-Wald (Radarbeobachtungen und Rückfangexperimente). Abh. Westf. Mus. Naturkunde 51: 1-71
JAREMOVIC, R. \& ROLLO, C. D., 1979: Tree climbing by the snail Cepaea nemoralis - a possible method for regulating temperature and hydration. - Can. J. Zool. 57: 1010-1014
MADER, H.J., KLÜPPEL, R. \& OVERMEYER, H., 1986: Experimente zum Biotopverbundsystem tierökologische Untersuchungen an einer Anpflanzung. - Schriftenr. Landschaftspfl. Naturschutz 27, 136 S.
MASCANZONI, D. \& WALLIN, H., 1986: The harmonic radar: a new method of tracing insects in the field. - Ecol. Entomol. 11: 387-390
OPDAM, P., 1990: Dispersal in fragmented populations: the key to survival. - in: BUNCE, R. G. H. \& HOWARD, D. C. (eds.): Species Dispersal in

Agricultural Habitats. Belhaven Press, London: 3-17
RIECKEN, U. \& RATHS, U., 1996: Use of radio telemetry for studying dispersal and habitat use of Carabus coriaceus L. - Ann. Zool. Fenn. 33: 109-116
RIESKE, L. K. \& RAFFA, K. F., 1990: Dispersal pattern and mark-and-recapture estimates of two pine root weevil species, Hylobius pales and Pachylobius picivorus (Coleoptera: Curculionidae), in Christmas tree plantations. - Environ. Entomol. 19: 1829-1836
RILEY, J. R., SMITH, A. D., REYNOLDS, D. R., EDWARDS, A. S., OSBORNE, J. L., WILLIAMS, I. H., CARRECK, N. L. \& POPPY, G. M., 1996: Tracking bees with harmonic radar. - Nature 379: 29-30
ROLAND, J., MCKINNON, G., BACKHOUSE, C. \& TAYLOR, P. D., 1996: Even smaller radar tags on insects. - Nature 381: 120
ROLLO, C. D. \& WELLINGTON, W. G., 1981: Environmental orientation by terrestrial Mollusca with particular reference to homing behaviour. Can. J. Zool. 59: 225-239
WALLIN, H. \& EKBOM, B., 1988: Movements of carabid beetles (Coleoptera: Carabidae) inhabiting cereal fields: a field tracing study. - Oecologia 77: 39-43
WELLINGTON, W. G., 1957: Individual differences as a factor in population dynamics. - Can. J. Zool. 35: 293-323
WILLIAMSON, P., CAMERON, R. A. D. \& CARTER, M. A., 1977: Population dynamics of the landsnail Cepaea nemoralis L.: A six-year study. - J. Anim. Ecol. 46: 181-194
WRATTEN, S. D. \& THOMAS, C. F. G., 1990: Farmscale spatial dynamics of predators and parasitoids in agricultural landscapes. - in: Bunce, R.G.H. \& Howard, D.C. (eds.): Species dispersal in Agricultural Habitats. Belhaven Press, London, New York: 219-237

## Address

Dipl. Biol. Berthold Janßen
Prof. Dr. Harald Plachter
Fachbereich Biologie, Fachgebiet Naturschutz
Philipps-Universität Marburg
Karl von Frisch-Straße
35032 Marburg

## ZOBODAT - www.zobodat.at

Zoologisch-Botanische Datenbank/Zoological-Botanical Database
Digitale Literatur/Digital Literature
Zeitschrift/Journal: Verhandlungen der Gesellschaft für Ökologie
Jahr/Year: 1997
Band/Volume: 28_1997
Autor(en)/Author(s): Janßen Berthold, Plachter Harald
Artikel/Article: The Use of Harmonic Radar for Research on the Mobility of Small Invertebrates 217-223

