# Genetics and dynamics of a *Carabus auronitens* metapopulation in the Westphalian Lowlands (Coleoptera, Carabidae)

Franz-Josef Niehues, Peter Hockmann & Friedrich Weber

Niehues, F.-J., Hockmann, P. & Weber, F., Institut für Allgemeine Zoologie und Genetik der Universität Münster, Schlossplatz 5, D-48149 Münster, Germany

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In the Westphalian Lowlands (NW Germany), the carabid beetle Carabus auronitens inhabits forests and semi-natural (secondary) woods. Southwest of the city of Münster the frequencies of two alleles of an esterase-encoding gene (Est-1) change continuously by about 90% over a distance of 20 km. Within this cline several local populations, that are only a few hundred meters apart, differ significantly, suggesting that the evolution of the cline is a rather recent event. We propose the following hypotheses to explain these observations: (1) C. auronitens survived the period of nearly complete anthropogenic destruction of woodlands (during Middle Ages and early Modern Times) in the region southwest of Münster in a few small isolated populations; (2) in these refugia, the allele frequencies shifted by random drift in opposite direction (neutrality of the esterase genotypes against selection is supposed); (3) after semi-natural woods had regenerated and forests had grown up the refugial populations expanded and fused to a large metapopulation. We suggest that the cline observed in the Est-1 alleles reflects the continuous dynamics of the newly founded metapopulation. It is shown that in C. auronitens both population growth rates and individual dispersal ability seem to be high enough for an expansion over relatively large distances within a relatively short period.

# 1. Introduction

In Europe, ecological conditions changed several times during the postglacial epoch. Each major climate change left traces behind which still are recognizable in flora and fauna. The species pool was affected by both invasions and extinctions (Lindroth 1949, De Lattin 1967). Moreover, species ranges expanded and shrank. It is probable that during such events in many cases gene pools changed under the influence of selection or by random drift. Since human land use had intensified, anthropogenic effects also influenced the distribution and genetics of many species. For example, during Middle Ages and early Modern Times in Northwest Germany and in other regions of West and Middle-West Europe nearly all the woodlands, which had originally been protected as areas of natural resources, degenerated to heathes and brushwoods because of uncontrolled exploitation (Ellenberg 1978, Rothert 1981a pp. 432–434). The present island-like distribution of woodland species may be the consequence of this former woodland destruction (see Peterken 1993, for England; Assmann 1994, for Germany). Woodland destruction culminated in the Westphalian Lowlands in the 18th century (Hesmer & Schröder 1963, Rothert 1981b pp. 264–268, Pott & Hüppe 1991). During the first half of the 19th century semi-natural (secondary) woods began to regenerate, and forests were systematically planted.

In this article we show that the population genetics of the carabid beetle Carabus auronitens seem to reflect the history of woodland in the Westphalian Lowlands. Nowadays, most parts of the Westphalian Lowlands are covered by a mosaic of semi-natural woods, forests, meadows and arable fields (Westfälische Parklandschaft). Within this mosaic C. auronitens inhabits woods and forests. It seems that during the epoch of woodland destruction a few remaining populations experienced genetic drift (Wright 1931, Leberg 1992). Later, after woods had regenerated and forests had grown up, the ranges of this species expanded again permitting significant gene flow. We are interested in whether both population growth rates and individual dispersal ability are high enough in C. auronitens to allow expansion over relatively large distances within a relatively short period.

### 2. Material and methods

### 2.1. Population dynamics

We have studied the population dynamics of a local population of *C. auronitens* since 1982 in a forest near Münster (Forst Tinnen) (Althoff *et al.* 1992, 1994). On an area of 0.2 ha, 171 pitfall traps are opened twice a week during the activity seasons of the beetles. The beetles are individually marked at first capture and released again. From 1982 until 1992, the area of investigation was surrounded by a fence, which slowed down the exchange with the neighbouring areas. In summer 1992, a beetle-proof fence was erected (acryl glass, 25 cm below, 25 cm above the surface). Tightness is routinely controlled by pitfall trapping along the outside of the fence (64 pitfalls): beetles caught within the fenced area were never recaught outside, and, vice versa, beetles caught (and marked) outside the fence were never recaught inside the area. Abundances are estimated by the method of Jolly and Seber (using tables containing the catches from 2 and 3 seasons, respectively, cf. Althoff *et al.* 1992, 1994). Net reproduction (*B*) is calculated as ratio of "density of newly hatched individuals in the autumn season by density of females in the spring season". In order to examine the strength of the habitat preference of *C. auronitens* pitfall trapping was additionally carried out at the border of the Forst Tinnen to neighbouring arable fields and in a hedge and in a wooded mound (a *Landwehr*) nearby (Niehues 1995).

### 2.2. Simulations

In order to test whether the assumption of high population growth rates during the supposed period of area expansion is reasonable, we simulated the historical fluctuations of abundance since 1853 (since this year meteorological data are available for Münster). The simulations are based on temperature dependent net reproduction rates (*B*). Further parameters are survival rates for young beetles (survival from autumn to spring:  $S_{a-s}$ ) and for old beetles (survival from spring to spring:  $S_{s-s}$ ). For old beetles belonging to different generations the same probability was assumed for survival from spring to spring. During the simulation runs the survival rates  $S_{a-s}$  and  $S_{s-s}$  were constant; however, simulations with different survival rates were performed. The abundance in year i is calculated as

$$N_i = N_{i-1} \times (0.5B_{i-1} \times S_{a-s} + S_{s-s}).$$
(1)

### 2.3. Genetics

For genetic analyses animals were collected during winter by hand. After drawing a drop of hemolymph they were released again. Electrophoretic methods are described by Terlutter (1990, 1991). The distribution of the local populations studied genetically is mapped in Fig. 1. Usually more than 30 animals were investigated per sampling site. Allele frequencies of females and males were tested for differences by the *G*-test (Sachs 1992). The frequencies of the genotypes in a sample were examined by the goodness-of-fit test for deviation from stochastic equilibrium. Allele frequencies between pairs of samples were tested for differences by the *G*-test (as a rule differences  $\ge 20\%$  are significant with p < 0.05).

### 2.4. Radar tracing

In order to examine the individual orientation behaviour radar tracing was carried out by the method of Mascanzoni and Wallin (1986). The application of this method to *C. auronitens* has been described by Hockmann *et al.* (1989). Beetles were tracked in a forest near an edge and on fallow land in front of a forest. On fallow land, the beetles were replaced to the start position, when they left the fallow land, and tracked again. Altogether 88 beetles have been traced up to one month (mean duration: 9.6 days).



Fig. 1. The sites of genetically investigated local populations southwest of Münster (Westphalia). The sectors correspond to the frequency of the allele slow (s, black) and fast (f, white) of an X-linked gene encoding a hemolymph esterase. The sites are numbered in the sequence of investigation (winter 1986/87–winter 1993/94). Sites nos. 1–18 were investigated by Terlutter (1991). Missing numbers correspond to sites outside this map. The size of the circles corresponds to the number of investigated animals. Small circles: 6–15 animals (6 samples), medium circles: 16–30 animals (38 samples), large circles: > 30 animals (85 samples). The Stever is a small stream lined by broad wet meadows. The canal (Dortmund-Ems-Kanal) was flooded in 1895.

### 2.5. Experiments in "orientation enclosures"

Rijnsdorp (1980) has shown that the orientation ability of carabid beetles can be studied in circular enclosures (see Hockmann *et al.* 1989, for the application of this method to *C. auronitens*). We investigated the behaviour of individually marked beetles in three enclosures ( $\emptyset$  20 m; height of the fence: 25 cm above the surface) on fallow land in front of a forest. Cultivation had been stopped one year before the experiments

started. Along the inner side of each fence 72 pitfalls were exposed. They were usually controlled several times per 24 h. The animals trapped were replaced to the middle of the fence. Circular statistics were carried out by Rao's spacing test, Rayleigh's test and the V-test (Batschelet 1981). From uninterrupted series of individual recatches, which distribution along the fence deviates from random ("orientation sequences"), the length (*a*) and the direction ( $\alpha$ ) of individual mean vectors were calculated. The method of angle duplicating was applied,

when the animals preferred opposite directions (Batschelet 1981). When in an enclosure experiment the individual mean vectors clustered around a distinct direction, the parameters of the overall mean vector of orientation were calculated. Moreover, we calculated the percentages of recatches belonging to "orientation sequences" (all recatches: 100%). If an animal is not caught and replaced to the middle of the enclosure, it would cover a "potential bee-line distance" of

$$d = r \times a \times n \tag{2}$$

(r = radius of the enclosure; a = mean vector; n = number of recatches within the orientation sequence; Batschelet 1981).

### 3. Results

#### 3.1. Seasonality and genetics

*C. auronitens* is a spring breeder. During March– June adults of several generations are active (Althoff *et al.* 1992, 1994). Preimaginal stages develop during 3–4 months in summer. Young beetles emerge asynchronously in late summer/early autumn ("autumn season"), they are active during 3–5 weeks (Klenner 1989). Catching probability is relatively low during autumn, and some young beetles are caught for the first time in the following spring season (Table 1). Surviving old beetles are dormant from the end of the spring season until the beginning of the next spring season.

Allozyme genetics of Westphalian populations of C. auronitens have been studied by Terlutter (1990, 1991), Assmann (1993), Assmann et al. (1994) and Niehues (1995). Two of 19 enzymes tested have been found to be polymorphic: glucose-6-phosphate isomerase (GPI) and a hemolymph esterase (EST-1). In some populations three rare GPI allozymes have been detected. For EST-1 two allozymes (S-, F-) have been found. Both allozymes are widely distributed with the slow variant usually more frequent. The Est-1 locus appears to be Xlinked, because heterozygotes have been detected only among females (cf. Weber 1966). In only two samples differences have been found between the allele frequencies of females and males (p < 0.05). In no case, the frequencies of female and male genotypes did deviate from the stochastical equilibrium of a bi-allelic, X-linked gene: the frequencies of the female genotypes did not differ from the Hardy-*Weinberg* equilibrium, and the frequencies of the male genotypes did not differ from the allele frequencies of the sample.

#### 3.2. The Est-1 allele frequency gradient

Southwest of Münster the frequencies of the Est-1 alleles change regularly (Fig. 1): in the Baumberge district and west of the village of Senden only the s-allele has been found, in the Davert and Hohe Ward districts, however, the f-allele prevails with frequencies around 90% (in site no. 15 the s-allele was even absent). In the middle of the cline local populations with allele frequencies around 50% have been found. The cline is rather steep: along a northwest - southeast transect of about 20 km (between the Baumberge and the Davert district) the frequencies change by 90%. Along a parallel transect southwest of Senden the cline is even steeper: over a distance of only 5 km the frequencies change by 80–90%.

Conspicuous changes of allele frequencies over short distances seem to be partly due to barriers to migration (Fig. 1). Especially the Stever, a small stream lined by wet meadows with dense vegetation (with a high Raumwiderstand), seems to be a barrier to gene flow. Moreover, genetic changes are more or less distinct along the entire length of the big canal (Dortmund-Ems-Kanal), which crosses the re-

Table 1. Age structure of the local population under observation in spring season 1995 (S '95). For each generation the table gives the number of individuals caught in successive seasons. For spring seasons also the percentages of surviving individuals are given in brackets. The beetles hatch during autumn; however, some young beetles were caught for the first time in the following spring season. In autumn 1993 and spring 1994, the investigations were carried out by A. van den Boom and B. Horstmann, in autumn 1994 by B. Horstmann, in spring 1995 by A. Bechtel and M. Landwehr. A: autumn season, S: spring season.

	A ´92	S ′93	A ′9	93	S ´94	A	´94	S ´95	Gene- ration
emales nales emales nales	147 113 1	113 (76.9% 85 (75.2% 13 6	6) 6)	63 50 7 10	(55.7 (58.8 (53.8 (62.5	'%) 5%) 5%) 5%)	27 22 3 3	(42.9%) (44.0%) (42.9%) (30.0%)	3rd
emales nales emales nales			202 162	15 122 61 60	(77.7 (75.3	'%) 8%)	103 90 35 39	(66.8%) (73.8%) (57.4%) (65.0%)	2nd
emales nales emales nales						18 10	32 134 35 102 21 22	(73.6%) (75.6%)	1st



Fig. 2. Correlation of the rate of net reproduction with mean meteorological temperature (°C) in May from 1982–1994. r = 0.79; p < 0.01. Linear regression: y = 0.33x - 2.95.

gion of investigation from SW to NE. In several cases, neighbouring local populations with significantly deviating allele frequencies are separated only by arable fields (for example nos. 61 and 62; 65 and 91; cf. arrows in Fig. 1). In one case even two forests, only ca. 250 m apart and connected by a mound stocked with trees, are inhabited by populations with different allele frequencies (sites nos. 112 and 118, cf. arrow in Fig. 1). Remarkably, *C. auronitens* has been found on this mound. Thus, present gene flow between these sites is probable (Niehues 1995).

### 3.3. Temperature-dependent rates of net reproduction

From historical notices on the occurrence of *C. auronitens* in the Westphalian Lowlands we have to conclude that the cline evolved around 1900 within few decades (cf. chapter 4.3). Unlike in other *Carabus* species (for example in *C. irregularis*, *C. clathratus*, *C. auratus*: Horion 1941), in *C. auronitens* events of mass reproduction, sufficient for expansion into the presently occupied areas, have never been reported. The highest rate of net reproduction (*B*) measured since 1982 was 2.81, the lowest rate was B < 0.10. About 63% of the variability of the rate of net reproduction can be explained by the variability of the mean temperature of May (Fig. 2) (Althoff *et al.* 1992, 1994).

# **3.4.** Survival probabilities of the adults and age structure of the population

Since the beetle-proof fence has been erected, also the survival probabilities from season to season can



Fig. 3. Simulation of historical fluctuations of abundance (*N*) on the basis of the observed dependence of net reproduction (*B*) on mean May temperature (Fig. 2) and on  $S_{a:s} = 0.75$  for the survival from autumn to spring (young beetles) and on  $S_{s:s} = 0.55$  for the survival from spring to spring (old beetles) (cf. Table 1). The abundance declined until 1905 and then increased by the factor of about 100 until 1993.

be measured. The survival rates of young beetles (survival from autumn to spring) varied between 73.6% and 77.7%. For old beetles the following survival rates have been measured: 55.7% –73.8% for the first survival and 42.9%–44.0% for the second survival from spring to spring (Table 1). No differences have been found between females and males. In spring 1995, the enclosed population was composed mainly of three generations (Table 1). Ten females and 3 males were found, which hatched earlier than autumn 1992 (the oldest female hatched in autumn 1989, the oldest male in autumn 1990).

# **3.5.** Simulation of historical fluctuations of abundance

In order to examine whether a high increase in the number of individuals during the supposed colonization period could have been the consequence of favourable May temperatures we simulated the historical fluctuations of abundance since 1853. For the simulation experiment we calculated temperature-dependent values of *B* by the equation of the linear regression given in Fig. 2. The survival rate of the young beetles was varied between 0.70 and 0.80, the survival rate of the old beetles between 0.50 and 0.60.

With survival rates of 0.75 from autumn to spring and of 0.55 from spring to spring the simulated population decreased from 10 000 in 1853 to 300 in 1905; then, however, the trend turned, and the number of individuals increased again, up to 20 000 in 1993 (Fig. 3). During the 20th century temperature condi-

tions were obviously favourable for *C. auronitens*. With somewhat higher rates of survival the increase of individuals since 1905 was even more drastic. For example, with rates of 0.80 and 0.60, respectively, the abundance increased by the factor of 60 000 until 1993! On the other hand, with somewhat smaller survival rates the number of individuals stagnated since 1905 (for example with 0.725 and 0.525) or decreased even further (for example with 0.70 and 0.50). Thus, the results of these simulations do not provide strong evidence; however, they demonstrate that the temperature-dependent reproductive potential of *C. auronitens* could have been large enough to increase the number of individuals considerably during a rather short period.

# **3.6.** Radar tracing and experiments in orientation enclosures

Besides population growth, a high individual power of dispersal is a prerequisite for a fast expansion of

Table 2. Radar tracing in a forest near the edge and on a fallow land: lengths of linear distances covered per 24 h (in the forest the beetles were largely night-active, on fallow land they were also day-active).  $n_1$ : number of animals investigated;  $n_2$ : number of days without activity;  $n_3$ : number of days with activity; mean: mean length of the bee-line covered per 24 h (m); *S.D.*: standard deviation (m); max.: maximum bee-line (m).

	<i>n</i> <sub>1</sub>	<i>n</i> <sub>2</sub>	n <sub>3</sub>	mean	S.D.	max.
forest Sept. 1993						
males	11	8	84	6.4	9.3	64
females Oct. 1991	9	1	49	6.8	8.9	49
males	8	29	83	3.5	5.1	30
females May 1992	7	23	64	3.5	5.1	29
males	12	14	73	10.6	16.9	94
females June 1993	9	16	92	5.8	6.2	32
males	5	0	44	10.7	12.7	54
females	7	0	21	5.8	7.5	28
fallow land April 1993						
males	3	0	45	9.8	12.1	44
females June 1992	3	2	39	9.3	12.0	50
males	9	2	59	15.0	16.4	68
females	5	0	43	12.1	7.8	36





the occupied area. We know from pitfall trapping that in autumn newly hatched females are as active as males. In spring, however, females are usually less frequently recaught than males (with the exception of rather cold spring seasons; Althoff *et al.* 1992). Radar tracing in a forest near the edge confirms these results: in autumn the mean distance covered per 24 h was similar in both sexes, in spring the mean distance was longer in males. On fallow land, however, in spring the females covered nearly the same distances, as the males did (Table 2). Also, in enclosure experiments on fallow land, in spring the females were as frequently recaught as the males (data not shown).

Radar tracing experiments revealed that the beetles avoid leaving the forest (Fig. 4 a and b). Frequently, movements more or less parallel to the edge were observed (Table 3). In spring, the maximum distance covered along the edge was 40 m during 5 days in a female and 330 m during 8 days in a male. Beetles released on fallow land < 30 m from the forest frequently took the shortest way towards the forest (for example female No. 21 in Fig. 5; Table 4). Animals released > 30 m from the forest mostly did not orient towards the forest, but some beetles probably showed a behaviour described as "directed

Table 3. Radar tracing in a forest near the edge of the forest: directions of bee-lines covered during a night. Seven classes of directions of the bee-lines relatively to the edge, and three classes of distances of the evening start points from the edge are distinguished. Line vertical to the edge:  $0^{\circ}$  direction; opposite into the forest: 180°; parallel to the edge:  $90^{\circ}$ . Only bee-lines larger than 3 m are considered. Observations from males (n = 36) and females (n = 32), and observations in autum (1991 and 1993) and spring (1992 and 1993) are pooled. Statistics: goodness-of-fit test for random distribution of directions.

direction	distance of the	e start points	from the edge
of bee-lines	s < 5 r	n 5–15	5 m > 15 m
0°–15°	2	9	1
15°–45°	5	22	10
45°–75°	7	20	10
75° –105°	22	19	13
105°–135°	16	24	14
135°–165°	11	13	14
165°–180°	0	14	6
p	< 0.001	n.s.	n.s.

movement" (for example male No. 24 in Fig. 5). During a period of directed movement an animal keeps a constant direction without using local orientation stimuli (it has been speculated that the geomagnetic field is used; Baars 1979).

Both orientation towards the silhouette of a forest and directed movement were also observed in enclosure experiments. Fig. 5 and 6 summarize the behaviour of the females (males showed a similar behaviour). In autumn, the mean individual vectors clustered around distinct directions (Fig. 6; one exception: in enclosure C the mean vectors of the males were randomly distributed). It was evident that most females and males tended to the forest from a distance of 15 m (enclosure A; some females preferred the opposite direction). In spring, the individual preferred directions of females were axially distributed in enclosure C (Fig. 5). In the other cases the individual mean vectors were randomly distributed indicating that many animals showed directed movements as described by Baars (1979). Nevertheless, the preferred directions were as distinct as in autumn (cf. the length of individual mean vectors and the percentages of recatches belonging to orientation

Table 4. Radar tracing on a fallow land in front of a forest (April 1993, June 1992): circular statistics of the vectors of linear distances covered per 24 h. Three classes of distances of the evening start points from the forest are distinguished. For the experiments with distances of 0–15 m and 15–30 m the same animals were used (cf. Table 2). Expected orientation: vertical towards the forest (0° direction); *n*: the number of linear distances covered per 24 h; Rayleigh's test:  $\alpha$  direction of the mean vector; *a* length of the mean vector, *p*<sub>R</sub> significance of the clustering of the single directions around the mean vector; *V*-test: *p*<sub>V</sub> significance of conformity between the direction of the mean vector  $\alpha$  and the expected direction of orientation (0°).

	п	α	а	$p_{\scriptscriptstyle \mathrm{R}}$	$p_{\rm V}$
0–15 m males ( <i>n</i> = 9) females ( <i>n</i> = 5)	17 13	0° 0°	0.61 0.71	< 0.001 < 0.001	< 0.001 < 0.001
15–30 m males ( <i>n</i> = 9) females ( <i>n</i> = 5)	42 30	- 32° - 5°	0.20 0.48	<i>n.s.</i> < 0.001	<i>n.s.</i> < 0.001
> 30 m males ( <i>n</i> = 3) females ( <i>n</i> = 3)	39 39	– 173° 158°	0.21 0.49	<i>n.s.</i> < 0.001	n.s. n.s.



Fig. 5. The site of experiments on fallow land. From the radar tracing experiments on this site the tracks of two animals are shown. The animals were replaced to the start position, when they left the fallow land, and tracked again. The results of enclosure experiments in spring 1993 are given for the females (enclosure A, B, C, Ø 20 m, scale-true mapped). In the enclosures the length and the direction of individual mean vectors, around which recatches are significantly clustered, are figured (see chapter 3.7 for further details). The maximum length of the mean vector (a = 1)corresponds to the radius of the enclosures. The following

parameters are given next to the enclosures: the total number of beetles in the enclosure; the number of beetles with at least one orientation sequence (some animals changed the preferred direction); the total percentage of recatches belonging to orientation sequences; the parameters of the overall mean vector (if significant) calculated from the individual mean vectors.

sequences in Fig. 5 and 6). Several potential bee-line distances were in the range of some 100 m (maximum values: 600 m covered during 58 days by a female and 528 m covered during 55 days by a male).

### 3.7. Survival and reproduction on fallow land

The enclosure experiments revealed that *C. auronitens* is able to feed and to overwinter on fallow land (Table 5). However, the survival rates from spring to spring and from autumn to spring, respectively, were smaller than in the forest. This was not due to high winter mortality, but probably to predation during the activity seasons. In 1993, *C. auronitens* was even able to reproduce on fallow land (Table 5).

## 4. Discussion

## 4.1. The esterase cline seems not to be controlled by selection

The Baumberge are a hilly country with well-drained soils on lime stone. The Davert is characterized by high levels of groundwater and water-damming soils. Therefore, adaptation to different environmental conditions could be the cause for genetic differences between local populations in the region of Münster. However, populations of *C. auronitens* in the western part of the Westphalian Bay living on soils as

Table 5. Development of the experimental populations in circular enclosures on fallow land (A, B, C; cf. Fig. 5, 6). First number: females, second number: males.

circular enclosure	А	В	С
(1) released on Sep. 11, 1992	29/21	29/21	29/21
(2) surviving beetles from (1)			
in spring 1993	21/18	26/18	21/21
(3) released on April 7, 1993	15/15	15/15	15/15
(4) active from (2) and (3)			
on May 24, 1993	10/10	2/9	3/10
(5) released on May 24, 1993	5/4	7/7	8/7
(6) number of beetles hatched			
until Sept. 21, 1993	21/24	9/13	6/4
(7) unmarked beetles in			
spring 1994 (hatched			
during autumn 1993)	16/11	4/6	2/3
(8) surviving beetles from (4.5)			20
in spring 1994	3/4	5/8	2/1
(9) sunviving beetles from (6)	0/4	5/0	2/1
in spring 1994	1/17	1/0	1/2
1115pm/g 1994	144/17	4/9	4/2

wet (or even wetter) as in the Davert have small frequencies of the f-allele (unpubl. results). Therefore, it seems that the esterase cline did not originate under the influence of selection, but by secondary contact between two (or a few) previously isolated populations, which had experienced genetic drift (Endler 1977).

### 4.2. Isolation and drift, expansion and gene flow

In Westphalia, woodland destruction culminated in the 18th century (Hesmer & Schröder 1963, Rothert 1981b pp. 264–268), nearly all woodlands had degenerated to heathes and brushwoods. We assume that *C. auronitens* survived in a few isolated populations, which were temporarily so small that allele frequencies shifted by genetic drift (Wright 1931, Leberg 1992). From the detected cline of the Est-1 alleles we conclude that in the region west and south of Münster at least two isolates survived: one in the Baumberge and another in the Davert (perhaps a third west of Senden). In the Baumberge and in the Davert isolates, the allele frequencies changed accidentally inversely: in the Baumberge isolate the f-allele was lost, whereas in the Davert isolate the f-allele became frequent.

The question arises how such bottleneck populations could recover and survive. Gilpin (1991) has shown by simulations that the effective size of a metapopulation (i. e. the ability to retain genetic variation in the face of drift) can be one or two orders of magnitude lower than the maximum total number of indiviudals. Thus, a metapopulation consisting of only a few local populations has the chance to survive (if the recolonization probability is higher than the extinction probability of local populations), although the probability to lose genetic variability is high. Moreover, in the case of X-linked loci the effective number of individuals is 3/4 of the effective number in the case of autosomal loci. Thus, the chance of C. auronitens persisting at the metapopulation level could have been much larger than the probability to be preserved from genetic drift.

During the 19th century brushwoods renaturated to semi-natural woods, and heathes were afforested. Probably, at the end of the last century, woods and forests had reached conditions suitable for *C. auronitens*. The refugial populations expanded and fused to a large metapopulation, the cline evolved by migration and gene flow (Slatkin 1985).



Fig. 6. Orientation of females investigated in enclosures on fallow land in autumn 1992 (cf. Fig. 5).

### 4.3. Evidences for a recent evolution of the cline

Four lines of evidence point to recent evolution of the cline.

(1) In 1881/82 the Münsterean entomologist Fritz Westhoff published a catalogue on the occurrence and distribution of beetles in Westphalia. Remarkably, he mentioned *C. auronitens* from a site in the Baumberge, but not from the region southwest and south of Münster where abundant local populations are now present. For the first time in 1922/24 *C. auronitens* was reported from sites in the middle of the present cline (Peus 1922/1924).

(2) The canal, which crosses the region of investigation, was flooded in 1895 (Budde & Runge 1940). Presently, several local populations showing different allele frequencies are separated from each other by the canal. This observation points to migrations, which happened later than 1895. However, because of the occurrence of the f-allele northwest of the canal it seems that the canal is not an effective barrier to migration. *C. auronitens* is rather resistant to drowning, and thus the beetles may easily drift across. The decisive difference to streams, which can be effective barriers, may be that the canal is not lined by meadows with dense vegetation, but crosses woods and forests.

(3) From the simulation experiments we may conclude that the abiotic conditions for population growth were unfavourable before 1905, but rather favourable since 1905. Thus, it seems that the populations of *C. auronitens* did not expand before 1905. A weak point concerns the possible effects of selection (Den Boer 1979). We simulated the fluctuations of abundance by projecting the present dependence of net reproduction on temperature into a former time. However, climatic changes, if they are not too drastic, may select traits that affect the temperature dependence of net reproduction.

(4) Within the cline conspicuous discontinuities of the allele frequencies over rather short distances have been observed, which are not due to barriers to migration. Such discontinuities point to recent population dynamic processes, e.g. to recent colonization events. Within an evolving cline colonization can cause discontinuities over short distance, if animals immigrate from only one direction into a new site, or from opposite directions, but with different rates. The neighbouring sites nos. 112 and 118 (with deviating allele frequencies, although connected by a mound) are good examples for this case: site no. 112 seems to have been colonized from the south, and site no. 118 from the east/southeast (cf. arrow in Fig. 1). Of course, discontinuities within a cline can also be due to drift by bottlenecks (Wright 1931) or founder effects (Mayr 1942). However, drift is probably not the cause of the discontinuity between the sites nos. 112 and 118, as the frequency in site no. 112 corresponds to the frequencies in the sites nos. 44 and 145 in the south, whereas the frequency in site no. 118 corresponds to the frequencies in the sites nos. 8 and no. 9 in the east / southeast. Drift is a more likely explanation, if a discontinuity does not follow the overall trend of the allele frequency change within the cline. For example, the deviating allele frequencies northeast of the village of Ascheberg, northwest of the city of Münster, and at the sites nos. 144 a and b in the middle of the cline (cf. Fig. 1) could be due to drift (probably founder effects) during the process of population expansion.

#### 4.4. Power of dispersal in Carabus auronitens

Generally, a successful colonizer should have the following attributes: (1) an effective power of dispersal (Lindroth 1949, Den Boer 1970), (2) a rapid population growth (high rates of net reproduction, advantageously combined with adult longevity; Paarmann 1966, Ebenhard 1991), and (3) if colonization is borne by single individuals or small groups, aggregating behaviour (Brandmayr 1992) is a further important attribute, as long as the newly founded group is small (cf. Andrewartha & Birch 1954 pp. 337–343). In the following paragraphs the colonization ability of *Carabus auronitens* will be discussed.

Above we have concluded that the expansion started not earlier than 1905. Approximately 15 years later, sites in the middle of the present cline were already occupied. That means, we have to assume a rate of dispersal of at least 10 km in 15 years (= 650 m per year = 7.2 m per 24 h during 3 months of running activity per year). In the forest and on the fallow land maximum distances covered per 24 h by females and males were much larger (cf. results of radar tracing in Table 2).

Moreover, radar tracing and enclosure experiments revealed the beetles' ability to cover large distances during a season of activity. The colonization of the area was obviously not a random walk process comparable with simple diffusion (Lima & Zollner 1996), but characterized by oriented and directed movement, respectively. It seems that the beetles orient preferentially along the edges of forests and along corridors. Especially, mounds, medieval country fortifications formerly characteristic for the Westphalian landscape, could have been important as corridors for the colonization of the regions. For example, we found C. auronitens in a preserved mound connecting the forests nos. 112 and 118 (Fig. 1). Moreover, the numerous hedges, which formerly lined arable fields in the Westphalian landscape, may have functioned as corridors for a directed dispersion (Niehues 1995).

On fallow land, the beetles are able to cover long linear distances by directed movement. This running behaviour is an efficient strategy for escaping from unfavourable sites (Baars 1979). When the beetles come across the front of a forest, a mound or a hedge, they orient towards the dark silhouette. The ability of *C. auronitens* to feed, to reproduce and to overwinter on fallow land could considerably improve the possibility to reach forests and woods, respectively, which are not connected with occupied sites by corridors. Thus, it seems that in *C. auronitens* running performance as well as orientation ability are high enough to disperse in a mosaic landscape over several km during a few years.

# 4.5. Rates of population growth and crucial minimum abundances in *Carabus auronitens*

The question arises whether also the rates of population growth were high enough to expand the area up to the middle of the present cline between 1905 and 1922/24. With individual surviving rates of 0.75 from autumn to spring and of 0.55 from spring to spring the simulated population grows during this period by the factor of 4.7. The number of individuals increases even by the factor of 14.7, when the rates of survival are a little higher (0.8 and 0.6). Thus, also the rates of population growth could have been high enough to produce large numbers of migrants, and to fill up the newly occupied sites quickly.

On the other hand, we do not know how C. auronitens is able to overcome crucial minimum abundances, after a new site has been occupied. When - as an extreme case - a single fertilized female has reached an uninhabited suitable wood, it may lay several eggs, and with good luck in late summer / autumn some young beetles will emerge. Now, the success of the colonization event will depend on their behaviour. If during autumn season they disperse over the forest, their chance to mate in the following spring will be low and the small group may become extinct (in C. auronitens mating has never been observed during autumn season). If, however, they stay together, the chance to find a mate during spring increases considerably. Sometimes aggregated individuals are found in winter resting places. However, gregarious behaviour in C. auronitens has not yet been studied experimentally. Adult longevity may also be important to overcome crucial minimum abundances in a newly occupied habitat (Ebenhard 1991). In the Westphalian Lowlands the age pyramid of C. auronitens populations is composed of several generations.

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