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Reproductive Types and Mobility of Carabid Assemblages: Effects of Landuse Intensity of Extensively Managed Orchards

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Abstract. From April 1995 to November 1997 investigations were carried out in orchards (48.36N/9.23E): data were collected on the type and frequency of grassland use and on the carabid fauna. Seventeen sample plots were selected. Part of the plots had 25 years of unchanged management regimes: three-cutting meadows (3), two-cutting meadows (3), mulched meadows (4), abandoned meadows (3), a horse pasture, a sheep pasture with rotational grazing, a continuously grazed sheep pasture, and a sheep pasture abandoned in 1994.

A total of 68 carabid species was registered. Two-cutting meadows (20-24 species), three-cutting meadows (17-30 species), and pastures (16-27 species) showed a significantly higher diversity than mulched meadows (13-19 species), and abandoned plots (7-18 species). The diversity and activity densities on the studied plots decrease with lower land use intensity.

Reproduction: Spring breeders were more frequently found on sample plots than autumn breeders (63-87% to 12-38%) or species reproducing all year (0-11%). Increased shading by fruit trees lead to a decrease of the percentage of spring breeders.

Type of alae: The percentage of macropterous species was between 29 and 69%. Alae dimorphous species showed a percentage between 0 and 40%, and for brachypterous species the percentage was between 10 and 71%. The percentage of brachypterous species diminished along the land use gradient, while the percentage of alae dimorphous species increased.

Key words. Ground beetle, land use systems, mobility, reproductive types, species community.

1. INTRODUCTION

Vegetation and fauna of extensively managed orchards are mainly determined by the site and its maintenance, the type of grassland management and its land use intensity (DEUSCHLE et al. 2002). Until now animal assemblages of extensively managed orchards have not been analysed based on the direct comparison of different forms of grassland management. Forms like continuous and rotational grazing (sheep, horses) have not been taken into account. There are few investigations dealing with the influence of management systems on arthropod assemblages in extensively managed grassland, whereas the effects of grazing have been documented more frequently (HANSSEN & HINGST 1995; MAELFAIT et al. 1988; RUSHTON et al. 1989; SCHNITTER 1994).

Normally, orchards are regarded as ecologically high valid systems, but it is yet not known if and to what extent the management influences carabid assemblages. Is there an influence on the number of species or densities or on the capability for large or small species? Furthermore, it is asked whether resources are equal or randomly distributed in the orchard area or overwhelmed by the management regimes of the individual plots, thus the captured individuals show differences in their occurrence due to different management forms on the basis of their ecological characteristics.

Larval and adult hibernation are the two basic forms of reproductive strategies of carabids (autumn breeders, spring breeders). Differences in the reproductive strategies allow the carabids to live in spatial coexistence by exploiting the same resources at different times (MÜLLER 1987). Eurytopic woodland species are less dependent on specific reproductive forms (RODE 1993; OTTESEN 1996).

The capability of carabids to disperse is regarded as an important prerequisite for the survival of the species under frequently changing external conditions (DE VRIES et al. 1996). This holds especially true for the cultural landscape (DEN BOER & VAN DIJK 1994; RODE & DÜLGE 1994). It is known that macropterous individuals inhabit dynamic, continuously changing habitats in open cultural landscape. The species are often very small and have a high potential of dispersion for the colonisation of new habitats. But their populations are therefore exposed to a significantly higher risk of extinction (DEN BOER 1987; DINGLE 1996).

Brachypterous species are thought to have a smaller potential of dispersion. Especially eurotopic woodland species are brachypterous and in comparison they are quite mobile. From their original habitat they can migrate to explore and colonise suitable new habitats (GLÜCK & KREISEL 1986). Woodland species are regarded to be typical inhabitants of habitats with nearly constant living conditions. During the advancement of succession they are found more frequently in the spectrum of species (BUREL & BAUDRY 1994; POLLARD 1968).

So far the ecological characteristics of the species belonging to the carabid assemblage should be different if the beetles react to resources (GLÜCK & DEUSCHLE 2003). The capability of using the resources should then be reflected in their occurrence on different plots.

The aim of this investigation is to demonstrate how different management systems (meadows: two or three cuttings a year, pastures: continuous and rotational grazing with horses and sheep, mulched meadows, abandoned meadows) have influence on the mobility of the carabid assemblage. Mobile species should be more common under rapidly changing conditions like intensive mowing. It will be examined, if the reproductive strategies (spring breeders/autumn breeders) of carabid assemblages are influenced by the management system in specific areas. It will also be shown, which type of management favours brachypterous or macropterous individuals of certain species. The advantages and disadvantages of reproductive strategies and increased mobility will be discussed considering the small-patterned mosaic structure of extensively managed orchards with its inherit changing living conditions.

2. METHODS

2.1. Census and registration of land use in the orchards

From the beginning of April until mid October 1997 in the study area in the nature reserve "Limburg" (48.38N/9.23E, Fig. 1, Table 1), southwest Germany, the following parameters were recorded weekly or every two weeks: type of use, time of mowing, "mowing device", "whereabouts" of mowed grass, and number of grazing animals. The amount of ground shaded by trees under perpendicular solar radiation was estimated and assigned to the following categories (0, 1-20, 21-40, 41-60, 61-80, 81-100%). All areas, which are mowed completely on a regular basis every year and where the cut grass is removed, will be called "typical meadows". On "mulched meadows" the cut grass remains on the areas. "Continuous grazing" defines the management type of pastures, where the grazing animals can be found per-

Table 1. Morphology and land use of sampled plots

Plot	Land use	Type of land use	Area (Ar)	Circumference (m)	Altitude (mNN)	Shading (%)	Sampling period
3CM2	3-cutting meadow	meadow	26	209	405	20	`97
3CM3	3-cutting meadow	meadow	51	287	425	20	`97
3CM1	3-cutting meadow	meadow	16	204	392	20	′95,′96,`97
2CM3	2-cutting meadow	meadow	40	446	415	80	`97
2CM1	2-cutting meadow	meadow	10	218	445	60	′95,′96,`97
2CM2	2-cutting meadow	meadow	15	250	410	60	`97
SPA	abandoned sheep pasture (cont. grazing), see text	pasture	34	234	405	60	′95,′96,`97
SPC	sheep pasture (continuous grazing)	pasture	15	213	415	80	`97
HP	horse pasture	pasture	124	580	400	20	′95,′96,`97
SPR	sheep pasture (rotational grazing)	pasture	11	259	445	20	′95,′96,`97
MMI	mulched meadow (4 - 6 cuttings)	mulched meadow	12	162	455	20	′95,′96,`97
MME1	mulched meadow (3 cuttings)	mulched meadow	47	380	440	100	`97
MME2	mulched meadow (2 – 3 cuttings)	mulched meadow	29	217	420	60	′95,′96,`97
MME3	mulched meadow with 1 cutting	mulched meadow	25	206	517	80	`97
AMR	recently abandoned meadow (4 years)	succession	13	153	445	0	′95,′96,`97
AMO	old abandoned meadow (10 years)	succession	13	202	420	100	′95,′96,`97
WDL	woodland	succession	13	222	520	100	`97

manently on the same area, while "rotational grazing" is the type, where a particular area is grazed for a period of only a few days, but several times a year. Combinations of the three types of management forms can also be found in the extensively managed orchards of the nature reserve area. Management oriented ranking of plots on the basis of land use intensity was calculated (Table 2).

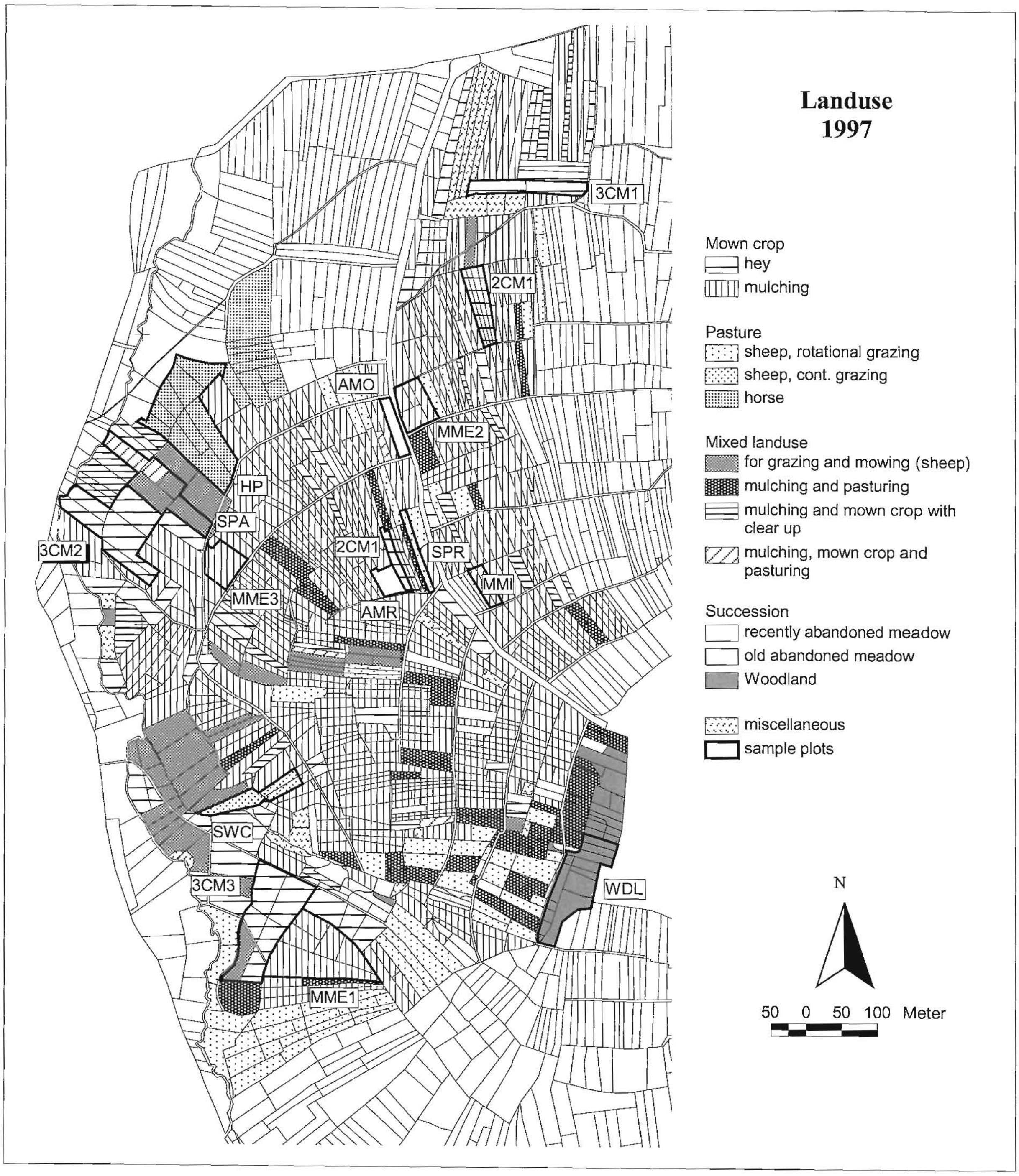

Fig. 1: Land use intensity of grassland in the study area during the vegetation period of 1997.

Table 2. Management oriented ranking of plots. The column rank I scales exclusively the nine in 1995 to 1996 studied plots, rank II scales all studied plots in 1997 (see Figs. 2, 3)

Area plot	Rank I ('95/'96)	Rank II ('97)	Explanation
3CM2	-	2	
3CM1	1	2	From all plots here the strongest interference in the ecosystem appeared. Essential characteristic is a high biomass withdrawal in combination with comparatively frequent mowing.
3CM3	-	2	
2CM3	-	5	
2CM1	2	5	Same, however on a lower intensity.
2CM2	-	5	
SPA	-	7	The change in management from intensively pasturing in 1995/96 allows no clear allocation in the ranking. The up to now management as mowing pasture allows the position between the categories pastures and mowing meadows.
SPC	-	8	A nearly throughout the year intensively pasturing entails a high withdrawal of material during the vegetation period.
HP	3	9	In dry years the intensive pasturing leads to a high withdrawal of material during the entire vegetation period, whenever not only on etiolation spot a considerable part of the plant material is trampled down and therefore a further mulching is necessary.
SPR	4	10	During the yearly grazing, only a small part of biomass is removed, the larger part is trampled down by the animals and remains at the plot. The grazing corresponds to one mowing event on a mulching meadow.
MMI	5	11	On the whole area there is no withdrawal of biomass, but frequently mowing happens. The entire material is reduced to small pieces and remains until it is decayed as mulching layer on the soil surface.
MME1	-	12	Same, but with a lower cutting frequency (3x) and partly with a beam mower.
MME2	6	13	Same, but with a lower cutting frequency (2-3x) and partly with a beam mower.
MME3	-	14	Same, but with a lower cutting frequency (1x) and partly with a beam mower.
AMR	7	15	Since 5 years there is no withdrawal of material and no mowing.
AMO	8	16	Since 11 years there is no withdrawal of material and no mowing.
WDL	-	17	The area is at least 50 years out of management.

2.2. Selection of sample plots and population census of carabidae

In 1995 the selection of sample plots took into consideration areas which had been under the same management system for more than 25 years (Fig. 1, Tables 1, 2).

Six pitfall traps were placed in a single line 10 m apart on a transect through the centre of each sampling plot. Ethylene glycol (50%) was used as preservative solution, with detergent added to reduce surface tension. A cover made of Perspex (120 by 120 mm) was installed 30 to 50 mm above ground level. In 1995 (5 April to 1 November) traps were controlled and emptied regularly every week. In 1996 (5 May to 4 November) and 1997 (8 April to 4 November) the control interval was two weeks (DEUSCHLE & GLÜCK 2001).

2.3. Analysis of data and statistical methods

All registered data concerning management practices, vegetation, soil condition, and carabid population were integrated into a database. After examining the necessary conditions the following statistical tests were applied: U-test by Mann & Whitney (MWU-test), and chi^2-test. The rank correlation was calculated according to Spearman and the coefficients were tested on their significance.

3. RESULTS

3.1. Number of species and activity density of carabids

A total of 5229 beetles representing 68 carabid species were caught in pitfall traps during the three years of investigation. Eighteen species were caught only once. Regarding their mean number of species, meadows cut once or twice a year do not differ essentially from pastures. But all three management forms show a significantly higher number of species compared to mulched meadows or abandoned plots (Fig. 2). The number of species on the sample plots decreases with lower land use intensity. This trend is significant over all three years of investigation as well as for the cumulative number of species for the years 1995 to 1997. A decreasing density in the number of individuals along a gradient of land use intensity does not show a consistent annual tendency.

The activity densities of the sample plots for the years 1995 to 1997 show significant differences (Chi^2-Test, $p < 0.001$, $n = 9$). The mean densities of the number of individuals according to the management type do not differ substantially. Only three-cutting meadows show a tendency towards higher activity densities (Fig. 3, Table 3).

Table 3. Differences in mean number of carabid species and individuals on sampled typical meadows, mulched meadows, pastures, and abandoned meadows: Level of significance of paired MWU-tests (n.s. = not significant, * = p < 0.05, ** = p < 0.001, *** = p < 0.001)

	3-cutt. meadows (n = 5)	2-cutt. meadows (n = 5)	Pastures (n = 10)	Mulched meadows (n = 8)	Areas under Succesion (n = 7)	
3-cutt. meadows	-	n.s.	n.s.	p < 0,05	n.s.	
2-cutt.meadows	n.s.	-	n.s.	n.s.	n.s.	Number of Individuals
Pastures	n.s.	n.s.	-	n.s.	n.s.	
Mulch.meadows	p < 0,05	p < 0,01	p < 0,05	-	n.s.	
Areas and Suc.	p < 0,05	p < 0,01	p < 0,01	n.s.	-	
	Number of species					

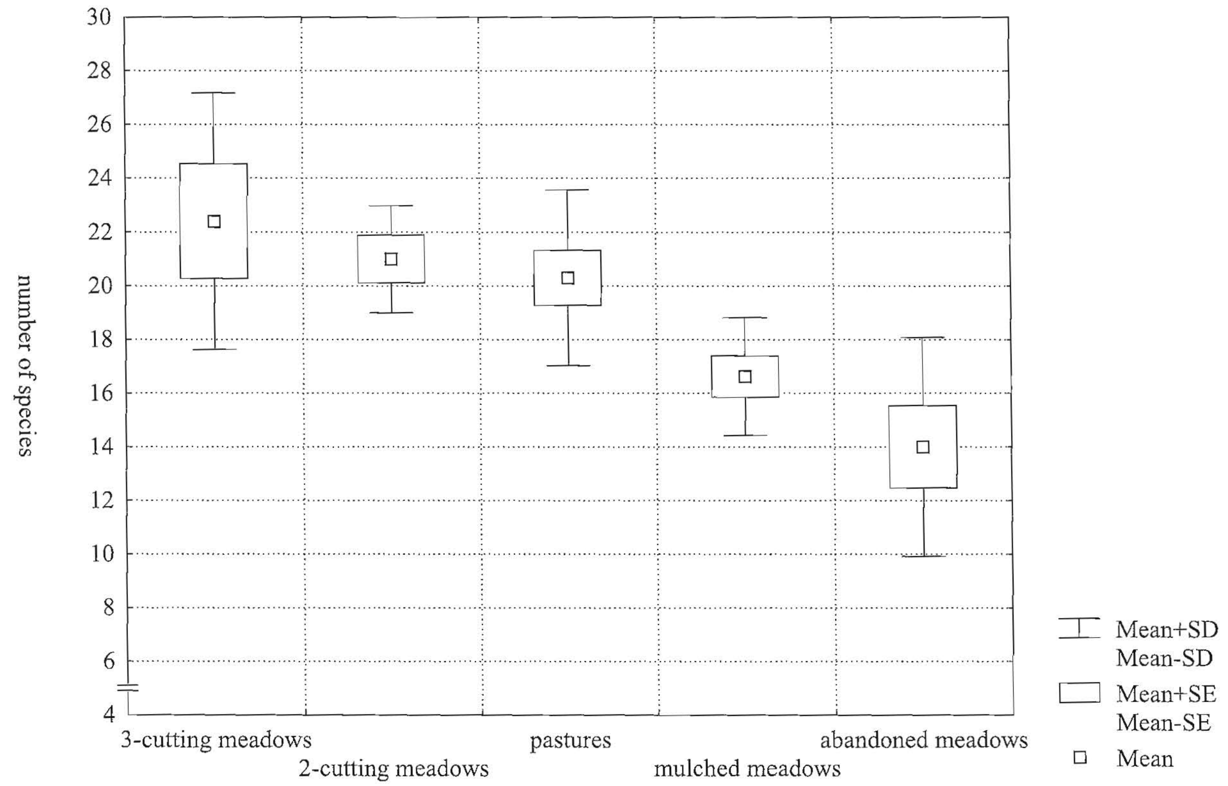

Fig. 2: Mean number of carabid species on sampled two-cutting and three-cutting meadows (each n = 5), pastures (n = 10), mulched meadows (n = 8) and abandoned meadows (n = 7), SE = standard error, SD = standard deviation.

3.2. Reproductive types

The highest percentages of adult hibernators were found on meadow 3CM1 (1995: 87%, 1996: 86%) and on the mulched meadow MMI (1995: 84%). The lowest percentages in 1997 responded to woodland (61%), as well as to the areas MME1 (62%) and 2CM3 (64%), and in 1996 to the mulched meadow MMI (64%). The areas which were sampled for three years showed differences in the yearly percentages between 2% and 14%. The smallest difference were registered on the horse pasture HP and on the mulched meadow MME2, the highest on the mulched meadow MMI (15%), the pasture SPR (14%), and on meadow 2CM1 (13%, Table 4).

Species reproducing the whole year – for example *Abax parallelepipedus* – were not found on pastures SPA, HP, and SPR during the whole investigation period, while on meadows 2CM1 and 3CM1, they were only detected in 1996. They were present on the mulched meadow MME2 and on the abandoned plots AMR and AMO in all three years. The only areas, which were sampled for the first time in 1997 and included reproducing species all year, were the plots 3CM3, 2CM3, SPC, MME3 and the woodland. This group had a low percentage of the total carabid assemblage, the highest appearing in 1996 on the abandoned plots AMR and AMO (14% and 15%, Table 4).

The reproductive strategies hardly seem to correlate with parameters like area, perimeter, and altitude of the sample plots. But the percentage of all-year reproduction types increased with decreasing land use intensity during the whole investigation. For the years 1995 and 1997 the correlation was significant (Table 5). The main reason was the high activity density of *Abax parallelepipedus*, as well as the lower number of typical carabids of extensively used open lands on mulched meadows and abandoned land.

In 1997 the percentage of spring breeders diminished significantly with decreasing land use intensity. A similar trend could not be detected for 1995 and 1996. It is also quite possible that the shading by fruit trees has an effect on the presence of spring breeders. During the three years of investigation the percentage of spring breeders decreased with increasing shading. The correlation is significant for 1997 (Table 5).

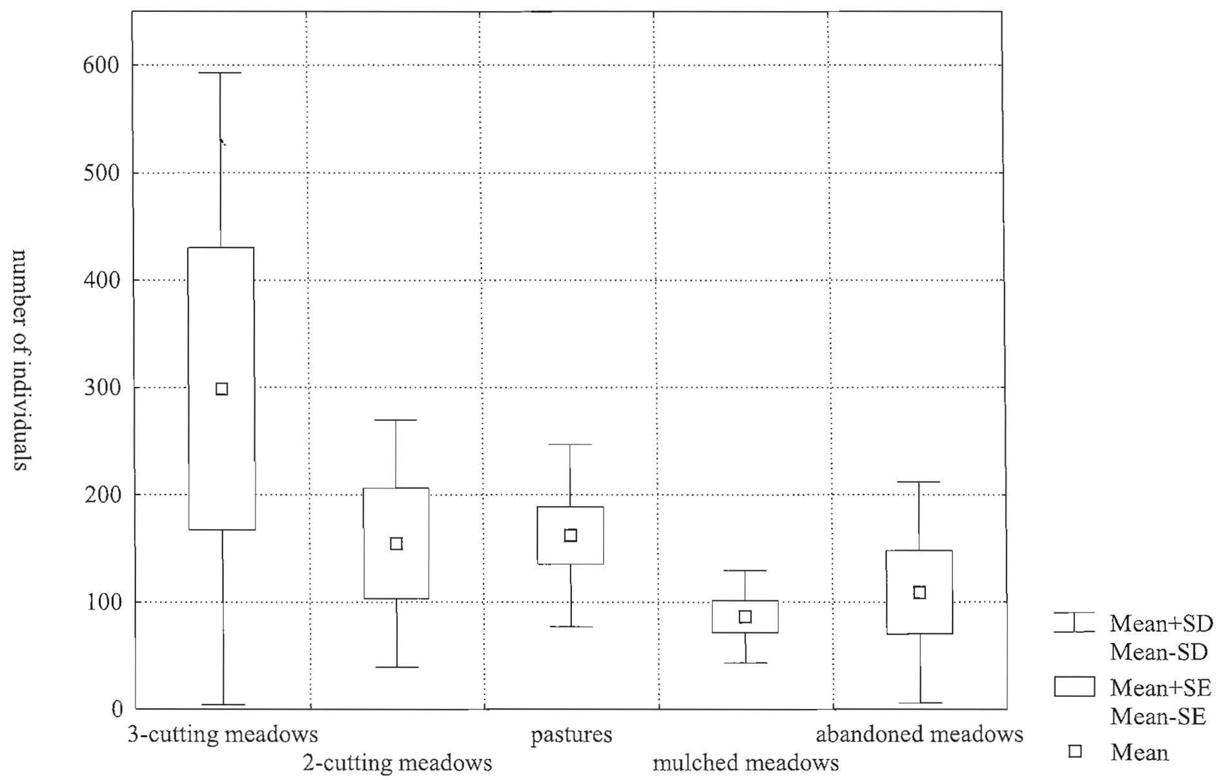

Fig. 3: Mean density of carabid individuals on sampled two-cutting and three-cutting meadows (each n = 5), pastures (n = 10), mulched meadows (n = 8) and abandoned meadows (n = 7), SE = standard error, SD = standard deviation.

3.3. Mobility and Dispersion

Forty of the total of 68 species caught in pitfall traps were macropterous and 16 were brachypterous species. Twelve additional species do not show a constant development of the alae and are therefore considered to be (alae) dimorphous. Brachypterous species are especially relevant, because their distribution is exclusively related to ground movement. The percentage of species in this group varied between 10% on sheep pasture SPA (1995 – 1997), and 71% on the abandoned plot AMO (1996). All meadows showed a smaller percentage. On pastures and mulched meadows it was generally higher. Especially on plot AMO, which was in a stage of succession, and in woodland, species of flightless carabids were quite frequent, while on the recently abandoned plot AMR few brachypterous species were found (Table 6).

In all three years the percentage of brachypterous species increased significantly with decreasing land use intensity. The smaller the perimeter of a sample plot, the less individuals of these species were found. On the other hand the percentage of alae dimorphous and completely macropterous species had the tendency to decrease with lesser land use intensity. In 1995 and 1996 the corresponding correlations for all flying species and in 1997 also for alae dimorphous species were high and significant (Table 7).

The alae morphology of all beetles caught was examined. Only *Bembidion properans* presented the macropterous and brachypterous forms (Table 8). Females were significantly more frequent than males (sex ratio 1:2.1 (m : f) MWU – Test $p < 0.05$). The sex ratio of macropterous beetles was 1: 3.2 (m : f). In the population of

Table 4. Dispersion strategies of carabids on sampled plots with different management regimes 3CM1, 2CM1, SPA, HP, SPR, MMI, MME2, AMR and AMO during the years 1995 to 1997 and 1997 only (species percentages)

		Macropterous	Dimorphous	Brachypterous
3CM1	1995	60.9	26.1	13.0
	1996	58.8	23.5	17.6
	1997	47.6	33.3	19.0
2CM1	1995	66.7	16.7	16.7
	1996	66.0	25.0	15.0
	1997	60.0	20.0	20.0
SPA	1995	55.6	33.3	11.1
	1996	60.0	30.0	10.0
	1997	40.0	35.0	25.0
HP	1995	50.0	31.8	18.2
	1996	45.0	40.0	15.0
	1997	58.3	25.0	16.7
SPR	1995	55.0	22.2	27.8
	1996	55.6	22.2	22.2
	1997	50.0	31.3	18.8
MMI	1995	52.6	21.1	26.3
	1996	43.8	25.0	31.3
	1997	56.3	25.0	18.8
MME2	1995	47.4	15.8	36.8
	1996	53.3	6.7	40.0
	1997	37.5	18.8	43.8
AMR	1995	52.9	17.6	29.4
	1996	58.8	11.8	29.4
	1997	50.0	25.0	25.0
AMO	1995	41.7	8.3	50.0
	1996	28.6	0	71.4
	1997	45.5	18.2	36.4
3CM2	1997	47.6	38.1	14.3
3CM3	1997	50.0	36.7	13.3
2CM3	1997	50.0	31.8	18.2
2CM2	1997	52.6	26.3	21.1
SPC	1997	55.6	25.9	18.5
MME1	1997	69.2	7.7	23.1
MME3	1997	52.6	21.1	26.3
WDL	1997	61.1	0.0	38.9

Table 5. Rank correlation coefficients regarding percentage of carabid species of different reproductive strategies with area parameter (1995/96: n = 9; 1997 n = 17; level of significance: * = p < 0.05, ** = p <= 0.01, *** = p < 0.001)

	Portion of species	Land use	Area	Perimeter	Altitude	Shading
1995	Spring breeders	-0,38	-0,58	-0,25	0,26	-0,54
	Autumn breeders	-0,15	0,56	0,76*	-0,38	0,56
	All-year reproductive	0,84**	0,05	-0,57	0,09	0,23
1996	Spring breeders	-0,09	0,04	0,10	-0,25	-0,56
	Autumn breeders	-0,20	0,10	0,27	0,19	0,20
	All-year reproductive	0,45	0,02	-0,53	-0,16	0,37
1997	Spring breeders	-0,65**	0,12	-0,19	-0,48	-0,70**
	Autumn breeders	0,31	-0,07	0,40	0,33	0,47
	All-year reproductive	0,64**	-0,10	-0,29	0,33	0,42

surveyed *B. properans,* females seem to be more alate than males. A total of 25% of all males and 38% of all females were macropterous. *Bembidion properans* was only detected on three-cutting meadows and pastures. But it was present on all plots of this type. Only a few macropterous males were caught on sheep pastures. The presence of *B. properans* on typical meadows and on the horse pasture was much higher. Females were found more frequently than males (Table 8).

4. DISCUSSION

Sixty-eight species of carabids were found on the sample plots under different conditions of land use intensity. The analysis of the reproductive types (adult hibernators, larval hibernators, and all year reproductive species) show that the percentage of spring breeders per plot decreases only slightly with diminishing land use intensity and shading (land use 1995: r_s= -0.38, 1996: r_s= -0.09, 1997: r_s=-0.65; shading 1995: r_s= -0.54, 1996: r_s= -0.65, 1997: r_s= -0.70). The corresponding correlation coefficients were significant in 1997 (Table 5).

Adult hibernators show declining numbers with decreasing land use intensity. This could be the result of less shading of more intensively used plots, which holds true not only for the sampling plots but for the entire area of investigation (Table 7). Therefore, the presence of adult hibernators does not depend on the type of management regime. An altitudinal moisture gradient does not seem to influence the distribution of spring breeders very much. Only for the year 1997 a decrease in the percentage of spring breeders can be detected with increasing altitude (Table 5). A significant increase in the percentage of all year reproductive species in 1995 and 1997 can be explained by the higher presence of the two woodland species *A. parallelus* and *A. parallelepipedus*. There does not seem to exist an overall tendency for the distribution of these reproductive types to be "driven" by land use intensity (FADL et al. 1998). The reproductive forms of both species are especially successful and present on areas without high interference (mulched meadows and areas under succession).

Table 6. Species percentages of reproductive types of carabids on sampled plots 3CM1, 2CM1, SPA, HP, SPR, MMI, MME2, AMR, and AMO during the years 1995 to 1997and 1997 only (Sb = spring breeders, Ab = autumn breeders, y = all-year reproductive)

		Sb	Ab	y
3CM1	1995	87.0	13.0	0
	1996	76.5	17.6	5.9
	1997	85.7	14.3	0
2CM1	1995	83.3	16.7	0
	1996	70.0	25.0	5.0
	1997	75.0	25.0	0
SPA	1995	66.7	33.3	0
	1996	75.0	25.0	0
	1997	70.0	30.0	0
HP	1995	77.3	22.7	0
	1996	75.0	25.0	0
	1997	75.0	25.0	0
SPR	1995	83.3	16.7	0
	1996	77.8	22.2	0
	1997	68.8	31.3	0
MMI	1995	84.2	15.8	0
	1996	62.5	37.5	6.7
	1997	68.8	31.3	0
MME2	1995	73.7	21.1	5.3
	1996	66.7	26.7	5.9
	1997	68.8	25.0	6.3
AMR	1995	82.4	11.8	5.9
	1996	82.4	11.8	14.3
	1997	75.0	18.8	6.3
AMO	1995	75.0	16.7	8.3
	1996	71.4	14.3	14.3
	1997	63.6	27.3	9.1
3CM2	1997	81.0	19.0	0.0
3CM3	1997	80.0	16.7	3.3
2CM3	1997	63.6	31.8	4.5
2CM2	1997	73.7	26.3	0.0
SPC	1997	74.1	22.2	3.7
MME1	1997	61.5	38.5	0.0
MME3	1997	73.7	21.1	5.3
WDL	1997	61.1	27.8	11.1

Table 7. Rank correlation coefficients of percentage of species regarding different dispersion strategies of carabid assemblage with area parameter (1995/96: n = 9; 1997: n = 17; level of significance: * = p < 0.05, ** = p < 0.01, *** p < 0.001)

	Portion of species	Land use	Area	Perimeter	Altitude	Shading
1995	brachypterous	0,91***	-0,17	-0,40	0,37	0,12
	dimorphous	-0,63	0,43	0,52	-0,43	-0,41
	macropterous	-0,76*	-0,26	-0,03	-0,02	-0,25
1996	brachypterous	0,82**	-0,20	-0,63	0,36	0,13
	dimorphous	-0,69*	0,25	0,54	-0,20	-0,21
	macropterous	0,63	-0,13	0,20	-0,11	-0,08
1997	brachypterous	0,74***	-0,28	-0,35	0,30	0,48
	dimorphous	-0,80***	0,29	0,13	-0,55	-0,57
	macropterous	0,17	-0,17	0,29	0,41	0,25

The removal of grass alters the ecological conditions on the surface and in the upper layers of the ground resulting in pronounced changes of temperature and moisture. On mulched meadows the cut grass remaining on the ground offers hiding places. It also serves as a buffer to weather changes during the following days and weeks. Therefore, the event of cutting grass has a much stronger effect on typical meadows than on mulched meadows.

Flightless (brachypterous) species colonise mulched meadows and areas under succession more often than typical meadows or pastures. On the other hand more flying (macropterous and alae dimorphous) species can be found on typical meadows and pastures (Tables 6, 7).

Mulched meadows do not seem to be barriers to brachypterous woodland species colonizing scattered areas under succession. During the three years of investigation the percentage of wingless woodland species was higher on mulched meadows and abandoned land than on typical meadows and pastures. Mulched meadows offer better resources to woodland species in spite of equal frequencies of mowing (BUTTERFIELD et al. 1995). Large forms of brachypterous woodland carabids, which are dependent on shade vegetation, have the tendency to look for shaded areas, if the contours of these areas stand out against their surroundings. It seems that a population can comprise parts of actively exploring individuals (direct movement vs random walk, see CHARRIER et al. 1997), which are capable of overcoming not optimal areas (BURKE & GOULET 1998; GARDNER et al. 1997; GLÜCK & KREISEL 1986). If they reach suitable habitats – in this case plots like AMO or MME2 – they can found new populations. Woodland species are especially dominant or sub-dominant on the abandoned plot AMO. Newly hatched individuals of *Abax parallelepipedus* and *Molops elatus* gave proof of successful reproduction of these species in area AMO.

Directed migration seems to be difficult under a closed canopy. The unshaded abandoned plot AMR, however, has a small percentage of woodland species. This is not typical for areas under succession and may be partly due to the influence of the neighbouring two-cutting meadow. Larger, eurotopic woodland species like *A. parallelus* and *A. parallelepipedus* were only found as single specimens during the investigation period. A growing number of woodland species could not be detected with increasing age of the abandoned area. On the heavily shaded mulched meadows MME2 and MME3 both species were more common (Fig. 3). Area AMR is lacking trees and dark contours. Both woodland species seem to frequent this area less.

Nearly all specimens of each of the nine alae dimorphous species were either completely macropterous *(Pterostichus vernalis, Synuchus vivalis* and *Stomis pumicatus)* or brachypterous *(Carabus granulatus, Calathus fuscipes, Pterostichus melanarius, Clivina fossor, Pterostichus anthracinus, Notiophilus palustris, Dyscirius globosus, Bembidion lampros)*. They, therefore, showed a constant expression of the development of their alae. There were four wingless species found typical for three-cutting meadows *(C. granulatus, C. fuscipes, Pt. melanarius, C. fossor)*. These ubiquitous forms were able to take advantage of the intensive use of grassland (TIETZE 1985).

In a pessimal environment the allele frequency of the corresponding recessive gene can increase within the population and minimize the risk of extinction (AUKEMA 1987, DEN BOER 1987). Dimorphous species also show numerous evidence of flight. The flight activity of both forms seems to be lower under high colonisation density (optimal conditions) than under low abundance (pessimal conditions, DESENDER 1986, MEIJER 1974). Numerous marked individuals of the small, eurytopic species *Calathus fuscipes,* which is alae dimorphous but mostly brachypterous, overcame larger distances on the ground than individuals of the larger, stenoecic and macropterous species *Harpalus dimidiatus*.

Table 8. Distribution and percentage of macropterous individuals of the alae dimorphous species *Bembidion properans* on sampled plots

Area	Sex distribution (%)		Macropterous (%)	
	males	females	males	females
3CM1 (1995-1997, n = 9)	44	56	22	22
SPA (1995-1997, n = 1)	100	0	100	0
HP (1995-1997, n = 15)	13	87	0	53
SPR (1995-1997, n = 1)	100	0	100	0
3CM1 (1997, n = 19)	26	74	0	26
3CM2 (1997, n = 16)	38	62	0	6
SPC (1997, n = 1)	100	0	100	0
Σ (n = 62)	32	68	25	38

The only species which included macropterous and brachypterous individuals was *B. properans* (Table 8). But the activity densities of this species were very low. Sheep pastures were colonised discontinuously by this species. A total of 63 specimens were caught during the investigation period. Male beetles were less alate than females, though they were present on more sample plots. Females were disproportionally more alate and less present, albeit the fact that their colonisation density was higher. Considering the reproductive behaviour of the species, females are more important. The ability to fly gives them the chance to leave an area when living conditions become pessimal. They can colonise other more profitable areas in a direct way and therefore minimize risk concerning their reproductive success. In the studied case this applies to three-cutting meadows and especially to the horse pasture. The high activity on this pasture corresponds with the findings of DESENDER & POLLET (1986), who describe an increase in the colonisation density of *B. properans* during intensified grazing. The radii of action of carabids stretch beyond the area defined by management practices. This leads to edge and spillover effects. Their dimensions depend on the individual mobility of the beetles, weather conditions, and availability of food.

For reproduction both strategies need nearly one year, especially the larval overwintering species can live for longer than one year and reproduce for more times (GRÜM 1976). The high loading variables of factor 1 show the meaning of the importance of mobility and therefore the possibility leaving areas with pessimal living conditions rapidly independent from reproductive success. Resulting adaptations to extreme disturbances as they occur in orchard by pasturing or mowing, are the most important influences for the distribution of carabid beetles. Different strategies of reproduction are less important. The fact that species can migrate into new habitats is well demonstrated (VAN DIJK 1987). A high mobility reduces extinction risk of pessimal living conditions and further more buffers the inter- and intraspecific competition by the larvae as well as in adult carabids. Mobility ensures and may maximize the reproductive success independent from the overwintering strategy.

Mowing and pasturing are the ancient practises of cultivating grasslands during the past few hundred years, on which the species corresponding could adapt themselves. No negative influence could be measured so long on carabid assemblages, because immediatelly after the impact higher or lower activities on the areas of investigation could not be measured (DESENDER et al. 1994) Obviously the impact is very grave and sustained for a long period. Only highly mobile species assemblages can profit from these living conditions.

But altogether only a combination of several factors might explain the distribution and composition of the assemblage.

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