

ON THE TURNOVER OF CARABID POPULATIONS IN CHANGING ENVIRONMENTS

P. J. den Boer

Biological Station of the Agricultural University, Wageningen, (Nature conservation Department) Kampsveg 27, 9418 PD Wijster (Drenthe), The Netherlands

Concerning the "turnover" (frequency of extinction/(re)-founding) of population units, two kinds of carabid beetles can be distinguished: species with a high turnover (around 10% per year): T-species, and species with a much lower turnover (1-2% per year): L-species. T-species show high powers of dispersal (flight activity), and from year to year population densities fluctuate more than at random; they are adapted to living in unstable and/or temporary habitats. L-species have low powers of dispersal (often wingless), and population densities fluctuate randomly; they are adapted to living in stable and/or permanent habitats.

If the environment changes from stable to unstable the primeval L-species will disappear, but the T-species will hardly be affected. If the environment changes from unstable to stable some (or even many) T-species may eventually evolve into L-species, but colonization by other L-species will often be severely hampered by the great distances to older, stable habitats in cultivated areas (isolation effects). Successional trends in environmental conditions can easily be withstood by T-species, and by some L-species, if the succession is a gradually occurring one at a not very large surface. In other cases of environmental change (e.g. in forestry) L-species are expected generally to persist, if source populations are available within dispersal (in most cases walking) distances, and the frequency of change is not higher than the mean turnover rate of population units (40-50 years).

Baars (1979a) and den Boer (1979a) showed that the catches of some carabid species in a standard set of pitfalls, summed over the whole year, is a reliable relative estimate of mean density of the population unit around the pitfalls during that year (year-catch). During more than twenty years we thus sampled many different sites in Drenthe (The Netherlands), and at the end of 1981 we had 290 year-samples, each consisting of year-

catches of a number of carabid species. This enabled me to study the frequency distribution of population densities (year-catches) of the sufficiently abundant species over logarithmic density-classes (in this case $\times 3$ -classes, i.e. $< 1/2$ (0-class), $1/2-1 1/2$ (class I), $1 1/2-4 1/2$ (class II), etc., see figures).

Distributions of densities

The most eurytopic species of our area, Pterostichus niger, which was caught nearly everywhere, showed an almost perfect log-normal distribution of densities (the 32 zero year-catches included): Fig. 1. This is in-

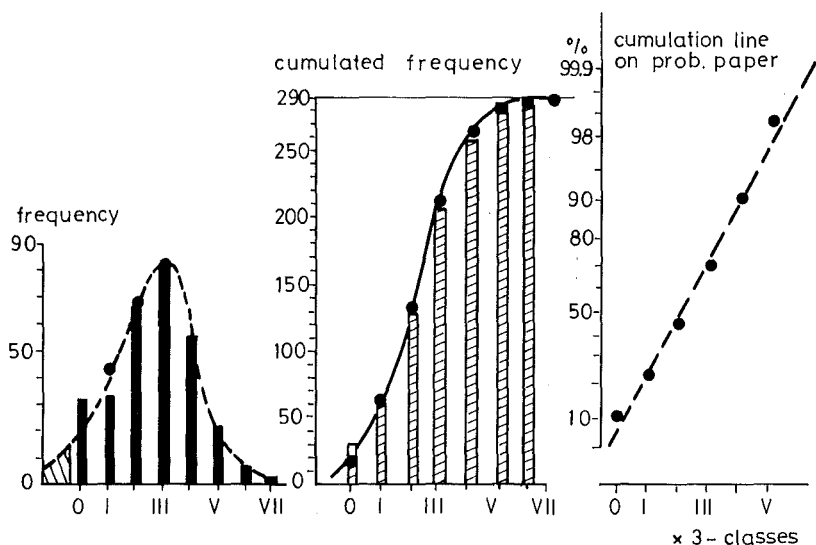


Fig. 1. Distribution of population samples (year-catches present in 290 year-samples) of Pterostichus niger Schall. over 3-classes of catch-levels (32 zero year-catches-in class 0-included), i.e. in class I: year-catches between $1/2$ and $1 1/2$ (one ind.); in class II those between $1 1/2$ and $4 1/2$ (2-4 ind.); in class III those between $4 1/2$ and $13 1/2$ (5-13), etc. At left: actual frequencies (solid bars) with fitted log-normal distribution (dots and broken line); centre: cumulative frequencies (hatched bars) with fitted cumulated log-normal (dots and line); at right: cumulated frequencies (as % of 290 year-samples) plotted on probability paper (see e.g. Southwood 1966) with fitted cumulation line

deed the most probable distribution of population densities, if all degrees of favourableness of sites and years for that species are sufficiently rep-

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represented in the year-samples, and the dispersal capacities of the individuals are such that nearly every site that becomes suitable can be colonized within a few years. As in P. niger both conditions are fulfilled its frequency distribution of year-catches (Fig. 1) illustrates the representativeness of our collection of 290 year-samples. The frequency distribution of a well dispersing (by flight), but somewhat less eurytopic, species – such as Loricera pilicornis, which lives in all kinds of moist to wet places – is a left-truncated log-normal distribution, which in this case does not significantly differ from expectation ($\chi^2 = 7.41$; d.f. = 4; $p \sim 0.10$): Fig. 2 (at left). The left part of the distribution, which contains samples from un-

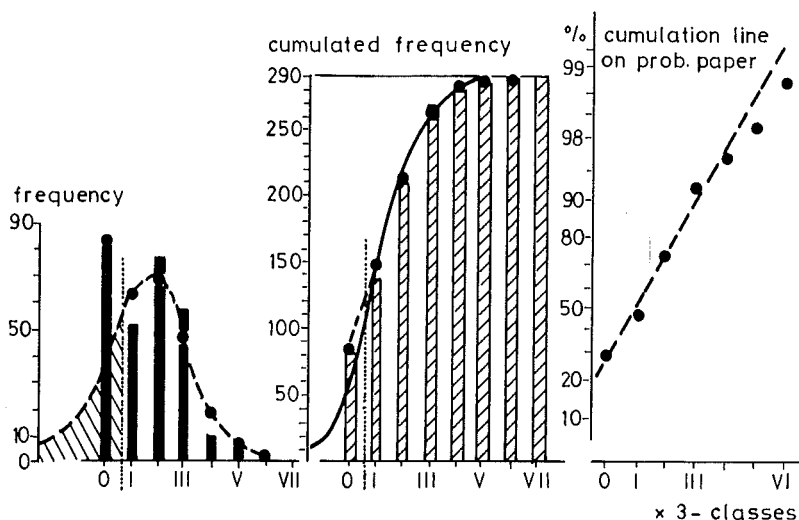


Fig. 2. Distribution of population samples (year-catches) of Loricera pilicornis Fabr. over x3-classes (86 zero year-catches included). See further Fig. 1

suitable habitats, is compressed in the zero class. Apparently, the powers of dispersal of L. pilicornis suffice to adequately colonize suitable sites when these arise, for the high frequency in the zero class well matches the cumulation line on probability paper (Fig. 2, at right). About the same can be said of Amara plebeja (Fig. 3), which mainly reproduces in grassy agricultural fields and overwinters in the forest (Van Huizen 1977). In spite of its still more restricted choice of habitat, the yearly migration flights

from the forest apparently enables it to reach the majority of suitable reproduction sites. The shortage in class I (Fig. 3, at left), which is more pronounced than in Figs 1 and 2, is not that important as to disturb the cumulative curve (Fig. 3, at right). Many more species that disperse well show comparable distributions and cumulation lines.

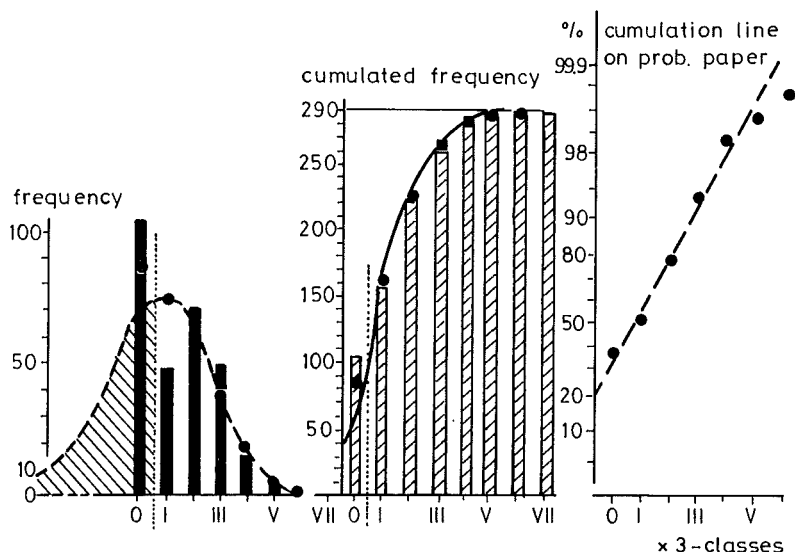


Fig. 3. Distribution of population samples (year-catches) of Amara plebeja Gyll. over x3-classes (104 zero year-catches included). See further Fig. 1.

The situation is different, however, in species that have both a restricted choice of habitat and relatively low powers of dispersal. Pterostichus oblongopunctatus, for instance, which in our area is restricted to wooded sites, has small wings that only exceptionally are used for flight (Lindroth 1945, den Boer 1977: Table 3, Van Huizen 1979: 209, den Boer et al. 1980: Table 3). Figure 4 (at left) suggests that there are two groups of populations, those with very low densities (year-catches in classes I, II and III), and populations with high densities (year-catches in classes V, VI and VII). Although there were a few places far from forest where single specimens of P. oblongopunctatus were caught, most low year-catches originated from sites close to forest (den Boer 1977: 168, and Appendix A, Part II), where marginal populations were kept going by migrants walking in from the forest (see also den Boer 1986a). Thriving populations, i.e. with

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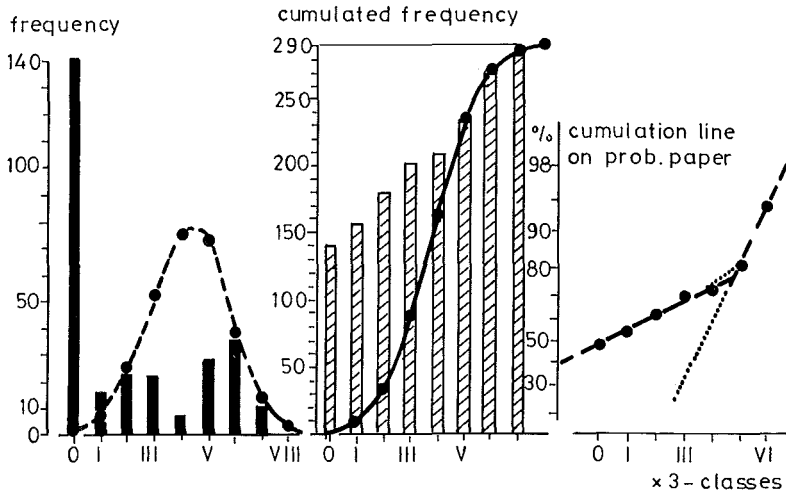


Fig. 4. Distribution of population samples (year-catches) of Pterostichus oblongopunctatus F. over x3-classes (141 zero year-catches included). See further Fig. 1

densities at the catch-levels V, VI and VII (41–1093), give the normal (steep) part of the cumulation line (Fig. 4, at right). However, populations with somewhat lower densities are severely under-represented because most shaded sites outside the forest, where marginal populations could survive for some time, have become unreachable by the excessive state of reduction and fragmentation of forest in our area (den Boer 1977: Fig. 5).

A similar picture is shown by the brachypterous Pterostichus lepidus (Fig. 5), a species of dry sandy soils with sparse vegetation. At the beginning of the 20th century most of these areas were planted with conifers to stop blown sand. Consequently, only a few, widely separated, suitable sites were left, and more marginal habitats usually have become unreachable. The decrease in this species is not restricted to our area (Turin and Peters 1986: Figs 3 and 4). Most other species, which show the same kind of deviation from a log-normal distribution of year-catches, i.e. a characteristically broken cumulation line on probability paper (Fig. 6) — a high to very high frequency in the zero class followed by much too low frequencies in the classes of lower catch-levels — have relatively low powers of dispersal, and live in habitats that were once extensive areas, and which now have

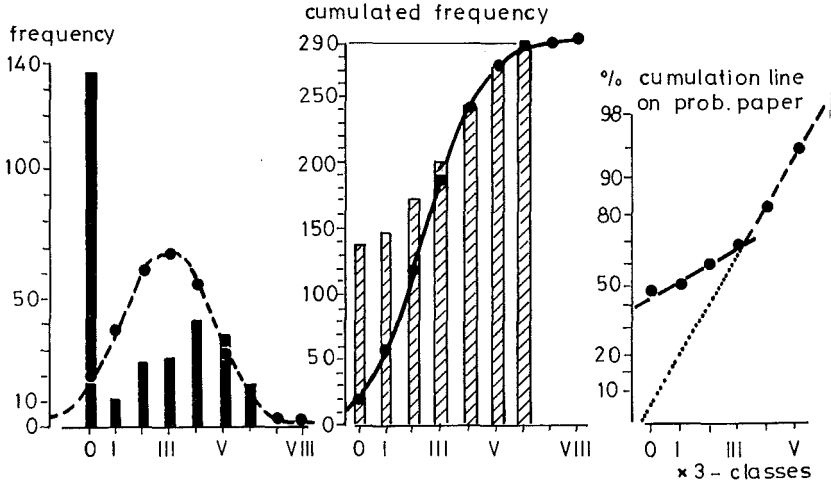


Fig. 5. Distribution of population samples (year-catches) of Pterostichus lepidus Leske over x3-classes (136 zero year-catches included). See further Fig. 1

been severely reduced and fragmented. Even some carabids that regularly show flight activity present these features, e.g. the species of deciduous forest Trichocellus placidus (Fig. 6: 150; compare den Boer 1977: Table 3). In such cases the still reasonable powers of dispersal are no longer sufficient for colonization of more than a few widely separated, suitable remaining habitats. Marginal habitats apparently are hardly colonized any longer.

The above differences in the frequency distribution of year-catches between carabid species can be adequately quantified by the distribution-free number, called DPS (Distribution of Population Samples):

$$\frac{\sum \ln(n_i+1)}{j \times \ln(N+j)},$$

in which n_i = year-catch of year i ; j = number of positive year-catches, and $N = \sum_{i=1}^j n_i$ (Reddingius in Appendix B, Part II of den Boer 1977).

T- and L-species

If we arrange the cumulation lines for the 64 sufficiently abundant carabid species according to their values of DPS, we can differentiate be-

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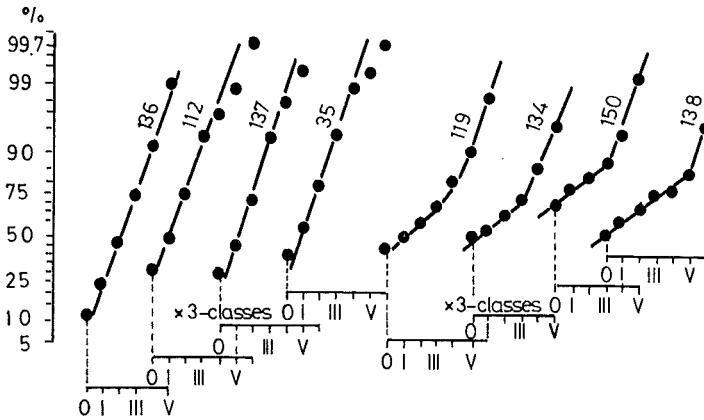


Fig. 6. Two kinds of cumulation lines on probability paper: (1) straight lines of well-dispersing species, i.e. 136 = *Pterostichus niger*, 112 = *Loricera pilicornis*, 137 = *Pterostichus rhaeticus* Heer (+ some *nigrita* Payk.), 35 = *Amara plebeja*; (2) broken lines of species with low powers of dispersal, i.e. 119 = *Notiophilus aquaticus* L., 134 = *Pterostichus lepidus*, 150 = *Trichocellus placidus* Gyll., 138 = *Pterostichus oblongopunctatus*

tween two kinds of species: species with high values of DPS and straight cumulation lines, and species with low values of DPS and broken cumulation lines: Fig. 7. I called the first kind, especially the 23 species with $DPS > 0.753$, T-species, and the second kind, especially the 21 species with $DPS < 0.715$, L-species (den Boer 1985, 1986a).

T-species are adapted to live in unstable and/or temporary habitats, which implies that in each generation many individuals show dispersal – usually by flight – by which the chance to colonize sites, that recently became suitable, is increased. Nevertheless, most T-species also found (more incidentally) populations in more stable habitats. It could be shown that from year to year population densities fluctuate more than expected at random, at least partly as a result of the high dispersal activities (den Boer 1985, 1986a). Because of this way of living the majority of population units of T-species show a high turnover of about 10%, which means that the chance of a population unit becoming extinct or becoming (re)founded in a given year is 10%, by which most population units show relatively low densities at the catchlevels II, III and IV (2–40: Fig. 8), and only 3% of

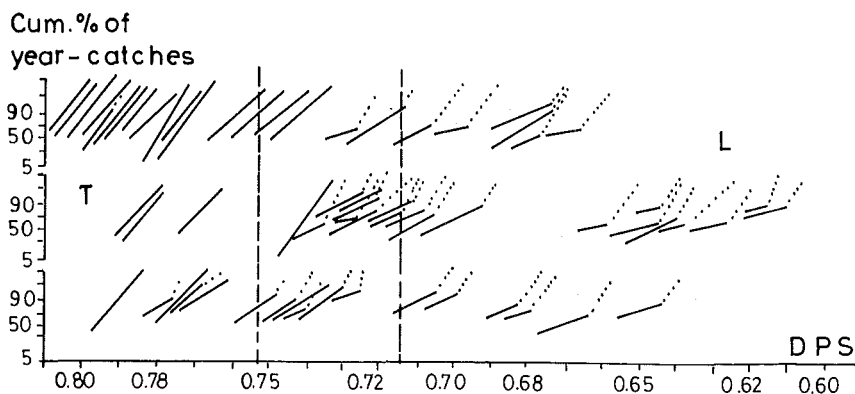


Fig. 7. Cumulation lines of the 64 sufficiently abundant carabid species of Drenthe (The Netherlands) arranged according to the matched values of DPS. The 23 T-species ($DPS > 0.753$) show high powers of dispersal, the 20 L-species ($DPS < 0.715$) only low powers of dispersal

the population units reach catch-level V, i.e. year-catches of 41-121, or higher: (high) Turnover (T)-species. It is interesting to note that this high turnover is independent of the degree of stability of the kind of habitat occupied: Fig. 9 ($\rho = +0.32$; $p = 0.43$).

L-species tend to live in stable and/or permanent habitats, which means that features favouring dispersal by flight will generally be selected against (den Boer et al. 1980). Therefore, most L-species have only low powers of dispersal (walking), and are often brachypterous. It could be shown that from year to year population numbers usually fluctuate approximately at random (apart from marginal population units at classes I and II): den Boer (1985, 1986a). As a corollary the majority of population units of L-species show a rather low turnover of about 1-2% (at the catch-levels III, IV, V and VI: 5-364): Fig. 8: Low turnover (L)-species. Contrary to T-species, in L-species the degree of stability of the habitats is distinctly correlated with the rate of turnover: Fig. 9 ($\rho = +0.93$; $p = 0.02$). In the most stable and permanent habitats, in old forests, population units of the pertinent L-species may even be expected to survive for two centuries, but in other, less stable sites they will generally become extinct within a few decades (Fig. 9).

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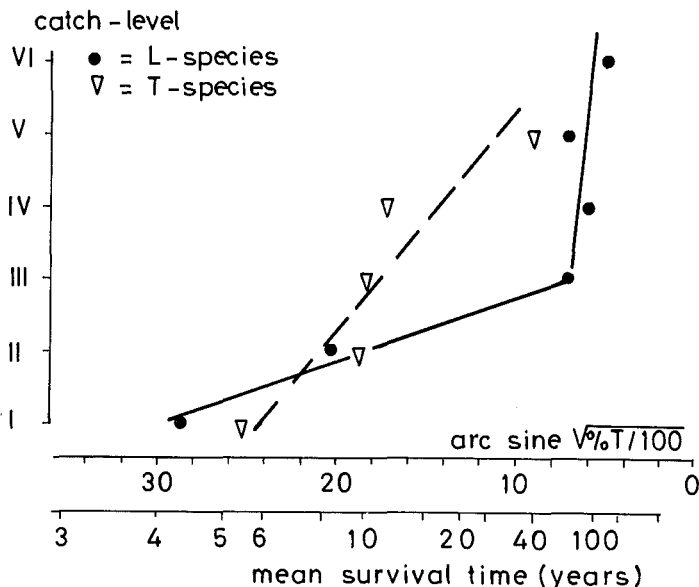


Fig. 8. General relationship between catch-level ($\times 3$ -classes, see Fig. 1) of T-resp. L-species and "turnover" (as the arcsine-value of the square root) of population units, with a scale of mean survival times added. For the procedures of turnover-estimations, see den Boer (1985, 1986a). Note that 54% of the population units of T-species are sampled at levels II, III and IV (mean survival time about 10 years), and 66% of the population units of L-species at levels III, IV, V and VI (mean survival time about 100 years).

Changing environments

Figure 9 shows what might be expected to happen, if the environment changes from stable to unstable, e.g. when forest is converted into heath, or heath into grassland or agricultural land. The T-species that already lived in the original, more stable habitats are eurytopic (mainly species of the genera Amara, Pterostichus, Agonum, and species, such as Loricera pilicornis (Fig. 2), Nebria brevicollis F., Synuchus nivalis Panz., Harpalus rufitarsis Duft., Asaphidon flavipes L., Cicindela campestris L.). Generally, such species will continue to exist under the changed conditions, i.e. they will also occupy these new environments as short-lived populations with high levels of dispersal. Therefore, T-species as a group, will be hardly affected by such environmental changes.

% Turnover

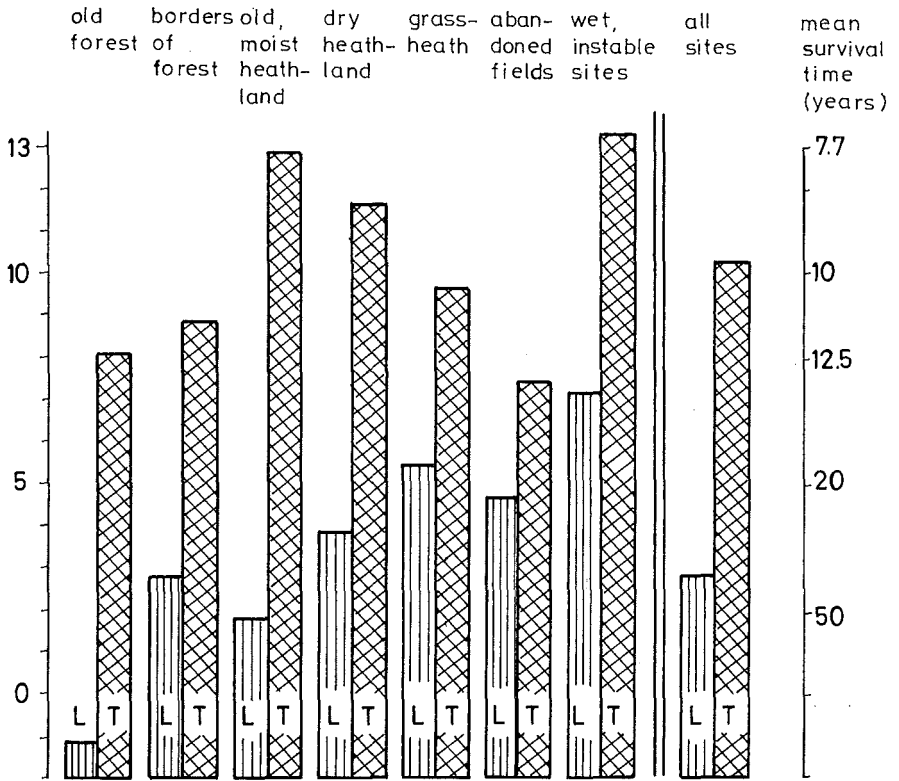


Fig. 9. Difference in mean turnover (mean survival time) between population units of L-species and those of T-species coexisting in the same habitats (sampled in the same pitfall sets). The habitats are ranked from very stable (at left) to very unstable (at right). Correlation between turnover and degree of stability of the habitat (ranks) occupied, in T-species: $\rho = +0.32$ ($p=0.43$), in L-species: $\rho = +0.93$ ($p=0.02$)

Figure 9 also shows, that the survival time of population units of L-species is expected to shorten, when the environment becomes less stable. This is not a direct effect of the decreasing stability, but of changing conditions. Most L-species are rather stenotopic, so that a change from forest into heath, for instance, will result in the disappearance of forest species with a low turnover ($< 1\%$), such as *Abax parallelepipedus* P. and M., *Trechus secalis* Payk., *Amara brunnea* Gyll., *Calathus rotundicollis* Dej.,

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Notiophilus rufipes Curtis, and in many places probably also of species, such as Notiophilus biguttatus F., Pterostichus oblongopunctatus (Fig. 4), Trichocellus placidus (Fig. 6), with a much higher turnover. Something comparable, but less markedly so, will occur if heath is converted into grassland or agricultural land.

If the environment changes from unstable to stable, e.g. if wet heath or grassland becomes drier because of lowering of the water table, or if blown sand is planted with conifers, again, T-species will hardly be affected, at least in the beginning. If they continue to found populations in these more stable habitats, however, selection against dispersal features will gradually reduce their power of dispersal, e.g. by reduction of the possibilities to develop flight-muscles (Nelemans, this volume), followed or accompanied by reduction of relative wing size (den Boer et al. 1980). In the long run, in this way some T-species may even evolve into L-species, either because wing reduction progresses so far that flight becomes impossible (as in Agonum ericeti Panz.: den Boer et al. 1980), or because the expression of the gene "macropterous" in wing-dimorphic species is greatly suppressed (Aukema, this volume).

Most L-species will only be favoured by such environmental changes, if the distances to populations in older habitats of the same kind can generally be covered by walking individuals. For small carabid beetles, such as Bembidion nigricorne Gyll. these distances should be smaller than 100 metres, but also for middle-sized carabid beetles, such as Calathus erratus Sahlb. (den Boer 1971), Cymindis macularis Dej., Pterostichus lepidus (Fig. 5) these distances should not exceed a few hundred metres (see also: Baars 1979b; Baars and Van Dijk 1984). Even for big Carabus individuals, such as those of Carabus problematicus Hbst (den Boer 1970), 1000 metres will be about the maximum distance between inhabitable sites that can still be successfully bridged. Sometimes, however, the rare, flying individuals of some L-species are able to colonize new stable habitats at much greater distances. This was observed in L-species, such as Calathus melanocephalus L., Dyschirius globosus Hbst, Notiophilus biguttatus (den Boer 1970), in the new IJsselmeer-polders in The Netherlands, possibly because the new inhabitable areas were very large. In general, however, the possibilities for L-species to colonize new sites in our present, highly cultivated landscapes are severely hampered by the distances and barriers (roads, canals, ditches) between suitable habitats (den Boer 1977, 1979b). Therefore, many L-species will gradually disappear from the smaller

remnants of old, stable habitats (den Boer, in press). Only in large nature reserves, such as the Heath of Kralo and Dwingeloo (1200 ha), multipartite populations of L-species will have a good chance to survive for thousands of years (den Boer 1981, 1986b; Andrewartha and Birch 1984).

It will be evident from the above discussions that naturally occurring successional trends in environmental conditions will easily be withstood by T-species, and also by many L-species, if the changing area is not very large (e.g. natural clearings in forest), and the surrounding areas represent stages of the same kind of succession (e.g. mature forest). A very favourable case of this kind – though not strictly natural –, the gradual change of an agricultural field into heath, is discussed by Van Dijk (this volume). Because of a general tendency in Western Europe to take out of production part of the agricultural land, the number of such cases will increase. It will be important that such fields, which are allowed to gradually develop into more natural kinds of habitat, are from – or even connected with – remnants of the kinds of habitat into which the new areas are expected to develop, in order that not only T-species, but also the L-species that can live there will be able to colonize these. Should these new habitats be changed again, e.g. for the benefit of human recreation, such changes should not occur more frequently than the mean turnover rate of population units of L-species (40–50 years), so that there would be sufficient time to compensate disappearances of population units by colonisation elsewhere. These considerations are especially important in forest areas where clear felling is practised, e.g. in Poland (Szyszko 1986): the stands cut down should not be larger than a few ha each (at best long, narrow strips that are situated between older stands), and the young trees should be allowed to grow up again during at least 40–50 years.

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