

SPREADING THE RISK OF EXTINCTION BY GENETIC
DIVERSITY IN POPULATIONS OF THE CARABID BEETLE
PTEROSTICHUS OBLONGOPUNCTATUS F. (COLEOPTERA,
CARABIDAE)

by

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ABSTRACT

Identification of insect species often is only possible with the help of characters that do not have a direct selective value. Such characters may reflect pleiotropic action of genes. This hypothesis was tested in the carabid *Pterostichus oblongopunctatus*. The closely related species *P. quadrioveolatus* has 3 large pits on each elytron, and prefers sites where wood has been burned. *P. oblongopunctatus* is a common forest species and two groups of morphs can be recognized: *low-pitters* with 4-5 pits on each elytron in a somewhat winding row, and *high-pitters* with 6-8 (or more) pits in a straight row. In dry forests the proportion of high-pitters is lower than in moist forests. Assuming pit numbers are genetically determined this suggests that low-pitters are favoured by relatively dry conditions, and high-pitters by moist conditions. Moreover, the shift of the proportion of high-pitters from year to year is correlated with the amount of precipitation in May-August, the period of larval development, especially with the accumulated deviations from the normal amount of rain. The latter suggests a genetical base for the two groups of morphs, which was supported by comparing the progeny of low-pitters with that of high-pitters. Selection experiments suggest that low-pitters are favoured by dry conditions and high-pitters by moist conditions during larval development. Samplings from different parts of Europe were in accordance with the hypothesis: In Poland, with a lower precipitation than Drenthe (The Netherlands), the proportion of low-pitters was higher, and in the Bavarian Alps, with about the same mean amount of precipitation as Drenthe, but on heavy loam, the proportion of high-pitters was higher than in Drenthe. The occurrence of some genotypes with a different moisture tolerance in the same population allows the species to occupy a wide range of forests, and to live with relatively small fluctuations in numbers in areas with highly unpredictable rainfall. The chance of the population to go extinct is decreased by *spread of the risk* over some genotypes with a differing tolerance of moisture conditions. *P. quadrioveolatus* (with only 3 pits and considered to be a good species) represents the morph with a high tolerance of dry conditions, *viz.* after a forest fire.

KEY WORDS: risk spreading, carabid beetles, genetic diversity, natural selection, extinction.

INTRODUCTION

Many characters by which insect species are separated taxonomically seem to be biologically irrelevant at first sight. Nevertheless, it could be

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an interesting question whether or not small but distinct differences in form and surface-structure of the clypeus, in the surface-structure of the elytra of beetles and of the scutellum of aculeates, in the exact number and position of bristles, *etc.*, have any direct selective value. It can be supposed that natural selection has worked indirectly upon such properties. They could be the result of pleiotropic actions of genes with a paramount importance, by which they might be used as a kind of indicators. The indirect selective value of such 'indicators' might even be more vital than the direct value of many evidently useful morphological properties, because the former are more rigidly separated (by definition) in closely related species than the latter kind of properties.

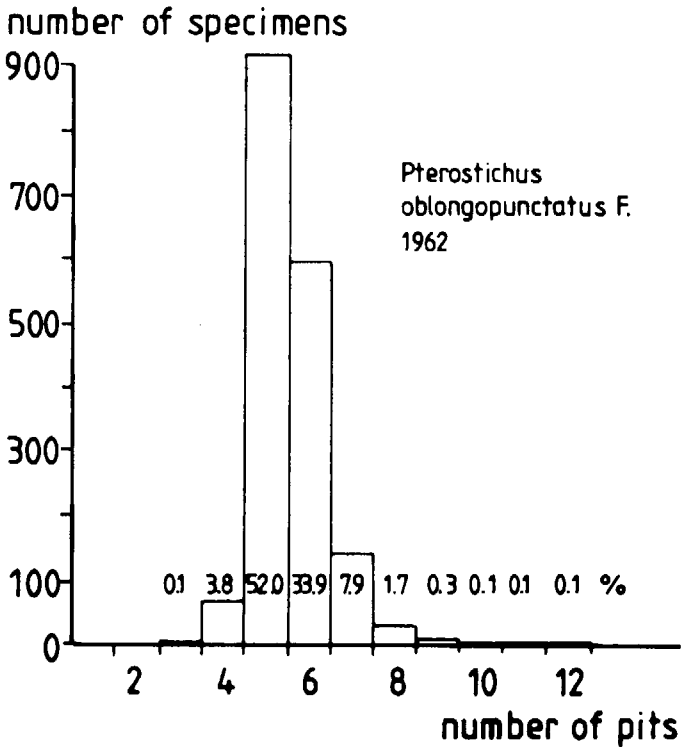
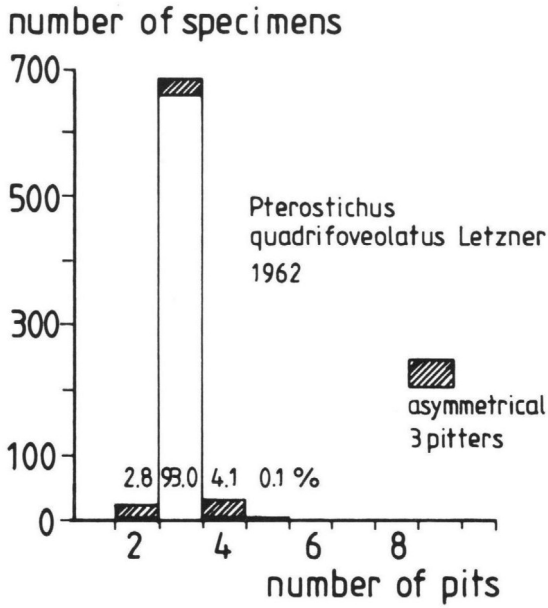
To be able to test the possible indirect selective value of such a character, an 'indicator' had to be found that, in spite of its high distinguishing power, also showed a measurable amount of variation, at least in one of the related species. For, in that case it might be possible to demonstrate the connection with the supposedly vital property. In the present paper we use as such a character the number of pits on the elytra of the ground beetle *Pterostichus oblongopunctatus* F.

The character

The number of pits on each elytron is an important character to separate the ground beetle species (Carabidae) *Pterostichus oblongopunctatus* F. from *P. quadrioveolatus* Letzner (= *angustatus* Dfts.). At least in The Netherlands, in spite of its name, *P. quadrioveolatus* has 3 large pits on each elytron (only rarely 2 or 4: fig. 1). Throughout Europe, *P. oblongopunctatus* has 4-7 or more (up to 12) of such large pits on each elytron (only very rarely 3: fig. 1). *P. oblongopunctatus* is usually the most abundant carabid species in nearly every kind of forest of the Palearctic region. *P. quadrioveolatus*, on the other hand, shows a highly fragmented distribution, because it has a preference for sites where wood has been burned.

A simple experiment showed this preference at the fields of the Biological Station (Drenthe, The Netherlands), where only incidentally single specimens of this species were found. After clearing of an area of wildshoots of pine in 1965, all branches were burned at a site of a few m² in 1966. In 1967 more than a hundred specimens of *P. quadrioveolatus* were caught in a few pitfalls at or close to this burned site (DEN BOER, 1977: 164, BR*). A site where wood has been burned seems to be highly attractive for this species, and apparently it reproduces

* Here, and in the following, such capitals refer to sample sites that are described, and sometimes pictured, in DEN BOER (1977).



successfully there. This is also demonstrated by a sample of 984 individuals caught in 1962 at a site where in 1959 waste matter from peat cutting, mainly fossil wood, had been burned (fig. 1).

The hypothesis

Led by these and related observations I hypothesized that the number of pits on the elytra of these two species might be related to moisture tolerances of the larvae. In the past, forest burnings may have had a strong selective effect, and only larvae of the ancestor of these two species with low moisture needs, the ones with few pits, could develop at the burning sites. On the other hand, such larvae could develop more rapidly because of the higher temperatures at burned sites, which may have contributed to speciation. According to this assumption it can be expected that adults of *P. oblongopunctatus* with a low number of pits on the elytra have developed from larvae with lower moisture needs than specimens with a high number of pits on the elytra. The above assumption implies that the distribution of individuals with different numbers of pits on the elytra shifts from year to year under the influence of the moisture conditions during the period of larval development (May-August). In table I this distribution is presented for

TABLE I

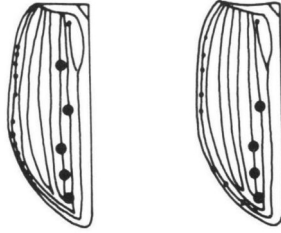
Distribution of pit numbers on the left elytron of individuals of *Pterostichus oblongopunctatus* in year-catches from the same forest population in Drenthe (The Netherlands) in four successive years to show the pattern of clustering of pit numbers.

year	% of individuals with .. pits						number of beetles in the sample	χ^2 -values (d.f.)
	3	4	5	6	7	> 7		
1959	—	7.8	45.5	38.9	6.7	1.1	90	
1960	—	8.3	67.7	21.7	1.7	1.1	288	19.94(4)**
1961	—	6.8	63.2	23.3	6.1	0.6	296	8.48(4)*
1962	0.2	3.6	54.6	30.5	8.8	2.3	531	14.55(5)**

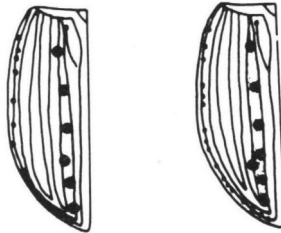
* $0.10 > P > 0.05$ ** $P < 0.01$

samples from the same population in four successive years. When the proportion of 5-pitters increased (from 1959 to 1960) also that of 4-pitters did, and when the proportion of 5-pitters decreased (e.g. from 1961 to 1962) also that of 4-pitters decreased. Similarly, when the

Fig. 1. Distribution of the numbers of pits on the left elytron in the closely related ground beetles *Pterostichus quadrioveolatus* Letzner (= *angustatus* Dfts.), above, and *Pterostichus oblongopunctatus* F., below, in samples from populations in Drenthe, The Netherlands, in 1962.

Pterostichus oblongopunctatus F.

pattern of low-pitters



pattern of high-pitters

Fig. 2. Patterns of pits on the left elytron of the ground beetle *Pterostichus oblongopunctatus* in Drenthe, The Netherlands. Above: wined pattern of 'low-pitters'; below: straight pattern of 'high-pitters'.

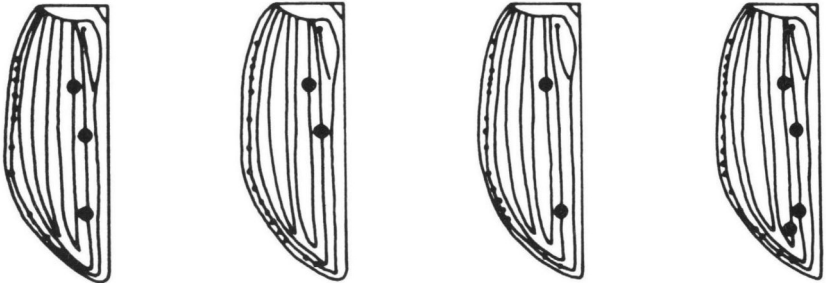
Pterostichus quadrifoveolatus Letzner

Fig. 3. Pattern of pits on the left elytron of the ground beetle *Pterostichus quadrifoveolatus* in Drenthe, The Netherlands. For the chance to meet patterns deviating from 3 compare fig. 1.

TABLE II

Distribution of numbers of pits on left and right elytron respectively in year-catches of *Pterostichus oblongopunctatus* collected in 1964 in the neighbourhood of Wijster, Drenthe, The Netherlands.

A. Exact distribution				B. Distribution according to number of pits								
				# pits	4	5	6	7	8	9	total	
		4-4										
			3		left	42	625	415	78	23	3	1186
	4-5			5-4	right	46	595	434	95	14	2	1186
	31		30		$\chi^2 = 5.396$ (d.f. = 4) 0.30 >P >0.20							
4-6		5-5		6-4								
8		377		13								
	5-6		6-5									
	202		168		C. Distribution of low- and high-pitters							
5-7		6-6		7-5	low			high		total		
16		183		19	left	667		519		1186		
	6-7		7-6		right	641		545		1186		
	47		29		$\chi^2 = 1.152$ (d.f. = 1) 0.30 >P >0.20							
6-8		7-7		8-6								
4		23		12								
	7-8		8-7									
	6		7									
7-9		8-8		9-7								
1		3		2								
	8-9		9-8		in A:							
	1		1		left right							
	9-9											

proportion of 6-pitters decreased (from 1959 to 1960) also that of 7-pitters did, and when the proportion of 6-pitters increased (*e.g.* from 1961 to 1962) also that of 7- and more-pitters increased. Apparently 4- and 5-pitters have a tendency to react similarly, as do 6-, 7- and more-pitters, but in the opposite direction. This suggests that there might be two groups of morphs: 'low-pitters', 4- and 5-pitters, and possibly also the few 3-pitters, and 'high-pitters', 6-, 7- and more-pitters.

These two groups of morphs also show a small difference in the form of the pit rows: the pits of low-pitters form a somewhat winding row, whereas those of high-pitters are in a nearly straight row within the third elytral interval (fig. 2). As expected, all specimens of *P. quadri-foveolatus* we examined showed the pattern of low-pitters (fig. 3). In about half of the individuals the number of pits on the left elytron differed from that on the right one (table IIA). However, this asymmetrical distribution of pits does not conflict with the assumption that deviations from a symmetrical distribution are random deviations

(table IIB). Fortunately, low-pitters with more than 5 pits at one elytron, and high-pitters with less than 6 pits at one elytron, usually can be recognized. But, as only in low-pitters with exactly 5 pits and in high-pitters with exactly 6 pits the position of the pits is fixed (fig. 2) this variation is a possible source of errors, especially when different students collect the data on pit numbers.

Nevertheless, it seemed worthwhile to test the hypothesis that larvae with relatively low moisture needs become low-pitters, whereas larvae with higher moisture needs become high-pitters. Or formulated the other way round: when the substratum for larval development becomes dryer larvae of low-pitters survive better than larvae of high-pitters, so that the proportion of high-pitters among the young beetles decreases, or, increasing moisture of the substratum results in a better survival of larvae of high-pitters as compared with those of low-pitters, so that the proportion of high-pitters increases.

MATERIAL AND METHODS

Experiment 1. Comparable year-catches were obtained by sampling continuously through the whole year in different kinds of forest in the same area with standard sets of pitfalls (DEN BOER, 1977: Ic). In 1959 two extreme situations were sampled: two coniferous forests on blown sand, an open pine forest (E*) and a plantation of *Larix* (F*), on the one hand, and two deciduous forests on loamy sand (B* and C*) on the other (DEN BOER, 1977: 117, 123, 124, 168). Even apart from the amount of precipitation, the layer in which the larvae grow up was much dryer in the coniferous forests than in the deciduous ones. This not only results from the difference between needle litter and leaf litter to retain water, but probably even more from the structure of the soil, because blown sand above the water table is much more permeable for water than loamy sand at groundwater level.

Exp. 2. The latter difference was tested with the water-retaining ability of the litter reversed in relation to that of the soil. In samples taken in 1986 we compared the fraction of high-pitters in a population of an old pine stand at groundwater level with that in a dry oak forest at blown sand far above the water table. In 1962 and 1963 three populations of *P. oblongopunctatus* were compared: (1) in a wet forest of birches, willows and oaks on loamy sand at groundwater level (AL*), (2) in a dry oak forest with a heavy layer of litter on blown sand above the water table (X*), and (3) in a small birch forest with hardly any litter on blown sand far above the water table (AE*); see DEN BOER (1977: 117, 119, 127, 128, 168).

Exp. 3. It should also be possible to predict changes in the proportion of high-pitters when moisture conditions change in time. *P. oblongopunctatus* is a univoltine spring-breeder with overwintering of adults (DEN BOER & DEN BOER-DAANJE, 1990), so that the effect of moisture conditions on the adults can only be observed in the spring and summer after growing up of the larvae. Although young adults do already emerge in the preceding autumn they are not very active then and can only be sampled quantitatively within enclosures. Changes in the proportions of high-pitters in samples from populations of *P. oblongopunctatus* were followed in three deciduous forests (B*, C* and G* or X*, DEN BOER, 1977: 117, 168) from 1959 (856 beetles) to 1960 (1569 beetles), from 1960 to 1961 (1432 beetles), from 1961 to 1962 (1764 beetles), and from 1962 to 1963 (1833 beetles). These changes were compared with the amounts of rain during the period of larval development (May-August) in the previous year, *i.e.* in 1958 (372 mm), in 1959 (145 mm), in 1960 (350 mm), in 1961 (368 mm), and in 1962 (243 mm) respectively. Because part of the adults hibernate a second—and sometimes even a third—time and reproduce again in the next year (DEN BOER, 1979: Table 1), the effect of the moisture conditions during larval development should not only affect the proportion of high-pitters in the next spring, but also that in the spring(s) after it. Therefore, we also compared the changes of the proportion of high-pitters from year to year with the changes of the accumulated deviations from the normal amount of precipitation during the periods of larval development (283 mm for the period 1928-1949; 314 mm for 1958-1978).

Exp. 4. Although observations of the changes in the proportion of high-pitters from year to year in relation to changes in the precipitation in the year before may give useful indications about the underlying process, they do not inform us whether or not this process is selective survival. To meet this drawback a field experiment was done in 1964 in a deciduous forest: in each of two enclosures (2×4 m) 146 marked individuals of *P. oblongopunctatus* (68 males and 78 females) were released. Each enclosure contained an identical collection of beetles: 5-5-pitters (28 males, 31 females), 5-6-pitters (14 males, 18 females), 6-5-pitters (17 males, 12 females) and 6-6-pitters (9 males, 17 females). In one enclosure rain was kept out by a plastic roof during about half of the days regularly divided over May, June, July and August, so that only 33% of the 269 mm of rain of that period, *viz.* 89 mm, could reach the litter inside the enclosure. In the other enclosure each day 1-2 mm of rainwater was spread over the litter inside the enclosure with a watering-can so that 52% of precipitation was added to the natural amount, *viz.* 410 mm in total. The composition of the progeny of these

beetles, which could be collected in autumn, should tell us whether or not moisture is a selective force in the larval stage.

Exp. 5. In 1970 the late HANS-ULRICH THIELE did a rearing experiment with *P. oblongopunctatus* under dry and moist conditions. The eggs laid by 6 females (+ 3 males) were mixed and divided equally over the two rearing conditions. As THIELE kindly handed over both the parents and the progeny to us the effect of different moisture conditions on the composition of the progeny could directly be established. Among the parents were 3 high-pitter females and a single high-pitter male.

Exp. 6. A possible shift of the proportion low-/high-pitters under the influence of changing moisture conditions does not necessarily result from selective mortality of low-pitter and high-pitter genotypes. The change in the number and pattern of pits on the elytra could well be a phenotypical effect. To test the hypothesis of a genetical base, both in 1963 and in 1966 breeding experiments were done in two enclosures (2×4 m) in a deciduous forest. In 1963, 151 males and 217 females with 5 pits on the left elytron were released into one enclosure, the majority of which were low-pitters. In the other enclosure 66 males and 115 females were put with 6 pits on the left elytron, the majority of which were high-pitters. Note that in 1963 the difference between the patterns of low- and high-pitters, as pictured in fig. 2, was not yet known. Therefore, and because we had indications that in 1963 the densities of the beetles in the enclosures were much too high, the experiment was repeated in 1966 with 42 symmetrical 5-5(low)-pitters (27 males and 15 females) in one enclosure, and 6 symmetrical 6-6(high)-pitters (5 males and a single female) in the other. Both in 1963 and in 1966 the amount of precipitation was above normal, 361 and 320 mm respectively.

Exp. 7. The success of *P. oblongopunctatus*, *i.e.* its occurrence in high densities in nearly every kind of forest throughout Europe, could be the result of the risk of extinction of local populations being (passively) spread over two groups of morphs with a genetical background, low-pitters and high-pitters, by which the chance to survive adverse conditions would be increased (see DEN BOER, 1968; ANDREWARTHA & BIRCH, 1984). To deal with the question in other parts of Europe we studied some Polish populations of *P. oblongopunctatus* in the forest district Tuczno in 1987. Also some populations of *P. oblongopunctatus* in the Bavarian Alps near Bayreuth were studied. These investigations were especially interesting, because the studied pine plantations in Poland were not only situated in an area with a lower amount of precipitation (400-600 mm per year) than Bayreuth (700-800 mm per year), but were also situated on highly pervious, sandy soils. Some part of the deciduous and spruce forests studied near Bayreuth, on the other hand, were situated on heavy, loamy soils.

RESULTS

Exp. 1. In accordance with the hypothesis, the proportion of high-pitters seems to be higher in moist forests than in dry ones (table IIIA).

Exp. 2. Especially in 1986 the difference was distinct and highly significant: $\chi^2 = 17.9$, $P < 0.001$ (table IIIB), the samples from 1959

TABLE III

Relative frequencies of high-pitters in the carabid beetle *Pterostichus oblongopunctatus* under different conditions (between brackets: number of specimens examined).

% of high-pitters in pitfall samples from field populations in The Netherlands (province of Drenthe).

Exp. 1. A	1959 dry coniferous forests	31.6 (38)	35.4 (150)
	moist deciduous forests	46.7 (90)	41.3 (80)
Exp. 2. B	1986 moist old pine forest	54.7 (117)	
	dry birch/oak forest	32.2 (311)	
C	1962 wet deciduous forest	49.6 (127)	53.4 (120)
	dry oak forest with thick layer of litter	46.1 (295)	46.1 (256)
	dry birch forest with hardly any litter	42.9 (21)	35.6 (45)

Frequency of low-/high-pitters after rearing the larvae (from mixed parents or eggs) under dry or moist conditions respectively.

Exp. 4. D	rearing experiment in the field	low-pitters	high-pitters
	89 mm of rain from May to August	7	5
	410 mm of rain from May to August	1	4
Fisher-exact $P = 0.16$			
Exp. 5. E	rearing experiment Thiele (lab.)	low-pitters	high-pitters
	larvae under dry conditions	99	9
	larvae under moist conditions	25	6
	$\chi^2 = 3.17$ (0.10 > $P > 0.05$)		
results of D and E taken together:		$\chi^2 = 5.64$ ($P < 0.02$)	

Frequency of low-/high-pitters among progeny of low- and high-pitters respectively.

Exp. 6. F	field experiment in enclosures (1963)	low-pitters	high-pitters
	parents were low-pitters	8	4
	parents were high-pitters	7	14
$\chi^2 = 3.299$ (0.10 > $P > 0.05$)			
G	field experiment in enclosures (1966)	low-pitters	high-pitters
	parents were low-pitters	25	14
	parents were high-pitters	2	4
	$\chi^2 = 2.05$ (not sign.)		
results of F and G taken together: $\chi^2 = 6.9$ ($P < 0.01$)			

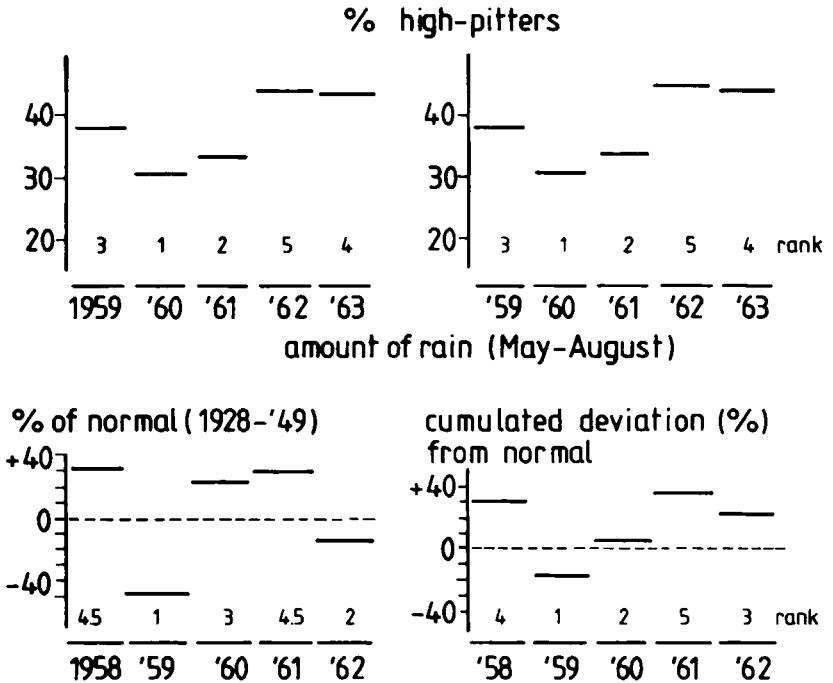


Fig. 4. Relationship between the change from year to year of the percentage of high-pitters in populations of *Pterostichus oblongopunctatus* around Wijster, Drenthe (The Netherlands), above, and the amount of rain during the period of larval development, *i.e.* during the months of May through August of the preceding year (as % deviation from the normal amounts in these months, *viz.* from the average over 20 years = 283 mm at Wijster), below. At left: the deviations from the normal amounts of rain plotted for individual years, at right: these deviations accumulated over the years starting in 1958.

(Exp. 1) differing just significantly ($P \sim 0.05$). The data of 1986 also suggests that not the kind of litter, leaves or needles, is decisive, but the overall moisture conditions are. Nevertheless, because of its water-retaining ability a thick layer of leaf litter can partly compensate for a highly pervious soil above the water table, as appeared to be the case in the oak forest sampled in 1962 and 1963 (table IIIC).

Exp. 3. The amount of rain during the period of larval development correlates with the proportion of high-pitters in the next spring in the way expected (fig. 4). However, the correlation between the percentage of high-pitters and the deviation from the normal amount of precipitation (at left) is not significant: r_s (Spearman) = +0.63 ($P = 0.09$). This

correlation becomes significant ($r_s = +0.90$, $P = 0.008$) when the accumulated deviation from the normal amount of precipitation is used (at right). Most probably this close connection also points to an accumulation of the changes in the proportion high-/low-pitters over the years. It is unlikely that this merely results from part of the reproducing adults reproducing again in the next spring(s), (about 28% on average), but it will be related with cumulating effects of the selection of genotypes that each year leads to a proportion of low-pitters among the young beetles that had to start from that already reached among their parents. We have no indications that the chance of surviving the winter differs between low- and high-pitters.

Exp. 4. Unfortunately the selection experiment executed in the field resulted in only a few young beetles (table IIID) that were collected in autumn. In spite of the small progeny this experiment suggests selection in the expected direction.

Exp. 5. In the laboratory experiments of THIELE (table IIIE) the proportion of high-pitters among the progeny was remarkably low. Possibly, apart from moisture conditions, the general rearing conditions (*e.g.* temperature) were more favourable for low-pitters than for high-pitters. Some years later (1972) we had a similar experience: low-pitters were more easily reared in the laboratory (at 15° C) than high-pitters. In the field, however, there are no indications for such a difference. Nevertheless, the trend of THIELE's experiment is in accordance with the hypothesis, though not significantly so. When combining the results of these two selection experiments (according to: SIEGEL, 1956; SOKAL & ROHLF, 1969) it becomes probable that low-pitters are relatively favoured under dry conditions, whereas moist conditions favour high-pitters. But the later part of this conclusion is less supported by these experiments than could be expected from the field observations (table IIIA, B, C).

Exp. 6. In spite of the small progeny, the results from the experiments on the genetical base of low- and high-pitters respectively (table IIIF, G) show that low-pitters produce about twice as many low-pitters than high-pitters, and high-pitters produce about twice as many high-pitters than low-pitters. This suggests a strong inheritance of pit morph. Thus, it can be concluded that low- and high-pitters indeed correspond with two groups of genotypes which are fully expressed by the two patterns (and corresponding pit-numbers: fig. 2). The two experiments gave similar results.

Exp. 7. In other parts of Europe the same relationship is found as in The Netherlands between the proportion low-/high-pitters and moisture conditions in the larval habitat (table IV). It is noteworthy that in an area where the amount of rain during the period of larval develop-

TABLE IV

Exp. 7. Relative frequencies of high-pitters in population samples of the carabid beetle *Pterostichus oblongopunctatus* from forests in different parts of Europe: different kinds of forest near Bayreuth in Germany, and different pine plantations in the forest district Tuczno in Poland.

(between brackets: number of specimens examined).

1988: Bayreuth (Germany)	
oak and spruce forest on heavy loam	53.2% (186)
pine forest on sandy soil	35.1% (111)
1987: Tuczno (Poland)	
pine forests on pervious sand in Trzcimno	29.3% (379)
pine forest in Martew, sand high above water table	9.8% (193)
pine forest in Krępa, sand above water table	26.7% (180)

ment is usually low (Poland, near Tuczno: 247 mm on average, with a range of 136-425 mm between 1970 and 1990), the proportion of high-pitters is lower than ever noted in Drenthe (with 283-314 mm rain on average). In Bayreuth, on the other hand, with a hardly lower amount of rain during larval development (1961-1980: 266 mm on average) as in Drenthe, the proportion of high-pitters in dry forests resembles that of Drenthe (compare table IIIA and table IV). In forests on a highly impervious soil (heavy loam) the proportion of high-pitters is similarly high (table IV) as in Drenthe in wet forest and in moist pine forest on sand (table IIIA: 1962, 1963, 1986). On the other hand, in pine forests on coarse sand far above the water table, as in Poland, the proportion of high-pitters was very low, especially in Martew (table IV). Hence, these observations in other parts of Europe agree with those from Drenthe. It must be noted, that the separation of the pit morphs in the samples from Drenthe in 1986, Bayreuth and Poland was done by the third author. Thus the data in table IV are best comparable with those of 1986 in table IIIB, because of possible differences in judgement between students; see Material and methods.

DISCUSSION

Although the genetic experiments did not result in abundant progeny, low- and high-pitters appeared to differ genetically. Probably, in *P. quadrioveolatus* the supposedly pleiotropic character 'number of pits' is more strongly canalized (see also THODAY, 1958; SCHARLOO, 1991), whereas in *P. oblongopunctatus* it is less canalized. In the latter species the polymorphic features of this character may be connected in some way with the high degree of asymmetry of the character (compare BEARDMORE *et al.*, 1960; SCHARLOO, 1991).

The field data showed that the spatial and temporal range, over which moisture conditions may vary, is apparently wider than the possible tolerance of individual larvae. Because of the simultaneous occurrence of genotypes with different tolerances in the larval stage in the population, the risk of extinction of the population is (passively) spread over individuals with different moisture needs: in an extremely dry summer the low-pitter larvae survive better, and in an extremely wet summer the high-pitter larvae do so. Moreover, in years with less extreme moisture conditions the joint occurrence of the various genotypes buffers density fluctuations, because they are affected to a different degree. This buffering of density fluctuations will not only result from moisture changes in time, but a heterogeneous distribution of moisture conditions in the habitat leads to spatial differences in survival of the different morphs, which again contributes to stabilization of density fluctuations. Together with the independently fluctuating survival of old adults after reproduction (DEN BOER, 1979: Table 1) this stabilization is responsible for the relatively low variance of the net rate of reproduction (R) in this species (table V; also DEN BOER, 1990). As the survival time of a population depends more on the fluctuation pattern of numbers than on the density-level at which these fluctuations occur (DEN BOER, 1981), such buffering of density fluctuations will significantly prolong the survival of many local populations of *P. oblongopunctatus*. Such a buffering of density fluctuations not only enables the species to occupy many different kinds of forests and to develop abundant populations there, but the different results of individual selection under differing environmental conditions make it also possible to inhabit regions with very different amounts of rain during the larval period.

The phenomenon considered in this paper concerns an aspect of natural selection that is not often studied, though it is probably common for most species that survive in a heterogeneous and time-varying environment. In such an environment the target of selection will shift from generation to generation (as illustrated by fig. 4), and differs at different sites within the population. As natural selection will not only affect genotypes that have different moisture tolerances, but is expected to similarly affect other properties that can be influenced by varying and/or heterogeneous environmental conditions, in such environments natural selection will continuously shift between different targets. In this way it will highly promote the variability of genotypes. Each genotype that has some advantage under a special set of environmental conditions and is not intolerably inefficient in another set of conditions will for a long time be protected by natural selection and be 'tried out', so to say, under many different circumstances. Recombina-

TABLE V

Parameters of the fluctuation pattern of numbers in local populations of the 25 carabid species most abundantly and/or frequently occurring in the surroundings of Wijster, Drenthe (The Netherlands) between 1959 and 1981. In all 25 species the R-values are log-normally distributed. See further DEN BOER (1977, 1979, 1990).

species	# R-values	mean R	Var R	mean lnR	S.d. lnR
	A	B	C	D	E
<i>Notiophilus aquaticus</i> L.	94	2.253	10.996	.211	1.111
<i>Trichocellus cognatus</i> Gyll.	56	2.100	8.518	.134	1.169
<i>Bradycellus ruficollis</i> Steph.	63	1.974	5.177	.186	1.039
<i>Loricera pilicornis</i> F.	69	2.004	10.521	.023	1.188
<i>Dyschirius globosus</i> Herbst	59	1.874	3.354	.192	0.993
<i>Amara lunicollis</i> Schiødte	112	2.045	9.408	.046	1.117
<i>Bradycellus harpalinus</i> Serv.	63	1.887	4.983	.133	1.025
<i>Metabletus foveatus</i> Fourcr.	44	1.874	3.513	.174	0.977
<i>Calathus erratus</i> Sahlberg	83	1.593	4.052	-.073	1.007
<i>Nebria brevicollis</i> F.	51	1.427	3.084	-.098	0.953
<i>Amara plebeja</i> Gyll.	66	1.172	1.268	-.188	0.859
<i>Agonum obscurum</i> Herbst	73	1.595	3.775	-.036	1.002
<i>Calathus melanocephalus</i> L.	138	1.234	1.117	-.115	0.857
<i>Amara communis</i> Panz.	63	1.326	1.881	-.106	0.856
<i>Notiophilus biguttatus</i> F.	52	1.564	1.990	.115	0.830
<i>Clivina fossor</i> L.	45	1.067	0.574	-.171	0.730
<i>Pterostichus lepidus</i> Leske	92	1.289	1.612	-.054	0.813
<i>Pterostichus nigrata</i> Payk.	78	1.344	2.061	-.042	0.804
<i>Pterostichus niger</i> Schaller	116	1.351	1.281	.008	0.838
<i>Olisthopus rotundatus</i> Payk.	44	1.396	1.960	.024	0.798
<i>Pterostichus diligens</i> Sturm	96	1.267	1.478	-.059	0.736
<i>Pterostichus versicolor</i> Sturm	136	1.341	1.328	.047	0.684
<i>Carabus problematicus</i> Herbst	58	1.352	1.424	.046	0.681
<i>Harpalus latus</i> L.	59	1.236	1.322	.004	0.607
<i>Pterostichus oblongopunctatus</i> F.	66	1.164	0.379	.025	0.517

Column A: R = coefficient of net reproduction = (year-catch of year t)/(year-catch of year t-1).

Columns B & C: mean and variance of the distribution of R-values estimated from the field data.

Columns D & E: mean and standard deviation of lnR (natural logarithms of R).

Note that *P. oblongopunctatus* has the lowest VarR and S.d.lnR of all 25 species, i.e. density fluctuations are importantly buffered.

tion will supply new genotypes, so that many gene-combinations can be 'tried out'. Hence, natural selection continuously moulds the distribution of genotypes of the population. In the course of time it will thus more and more adapt the population to the variation in space and time of the effective environment, and thus overcome exceptional combinations of environmental influences. The price of this is, of course, that

the population cannot become perfectly adapted to a fixed set of conditions, because the genetic composition of the population can never be more than an approximated compromise between the mean frequencies and the mean survival values of the various sets of conditions operating in space and time. On the other hand, the longer these selective processes operate, *i.e.* the longer the population survives, the more fluctuations of numbers will be buffered, because these processes will be accompanied by an increasing spread of mortality over genotypes (table V). In other words, a statistical effect of natural selection varying from generation to generation within an heterogeneous population is *spreading the risk of extinction over genotypes*.

The above ideas are not new. They were introduced by DEN BOER (1968), but were already precluded by other authors. SCHÜTTE (1957) found that the principal mortality factor of the Oak tortrix, *Tortrix viridana* L., is lack of coincidence between the hatching of larvae and the opening of oak buds, both of which are influenced by weather conditions. The larvae of *Tortrix* hatch within 7 days, whereas there is much more variation (19-26 days) in the time of bud opening between different genotypes of oak. In some years the hatching of *Tortrix*-larvae coincides with early opening oaks, in other years with late opening oaks. SCHÜTTE discovered that the density of *T. viridana* fluctuated least in plots where all genotypes of oaks were represented in about equal numbers. DEN BOER (1971) recognized this as a clear example of what he called *spreading of risk* (DEN BOER, 1968). MAYR (1964) emphasized the adaptive value of genetic heterogeneity in general terms, whereas BAND (1963) did so concerning *Drosophila melanogaster*. Especially FORD (1964, 1965) independently accentuated the survival value of 'genetic polymorphism' and described phenomena that resemble the pit-morphs of *P. oblongopunctatus*. Many years later ANDREWARTHA & BIRCH (1984) let inspire themselves by 'spreading of risk' (DEN BOER, 1968), and dedicated an entire chapter (Ch. 11) to spreading of risk in evolution.

Summarizing, not only will genetic heterogeneity contribute to spreading of risk, but spreading of risk will to a certain degree maintain the necessary background of natural selection, *viz.* a high genetic variability. This means that the longer a natural population persists in a certain area, the better will the frequency distribution of genotypes fit the frequency distribution of selective events, which is the same as saying, the better the population becomes adapted to the variability of local conditions. Related ideas were already formulated by WRIGHT (1931) and further elaborated by WRIGHT (1969). In our opinion this state of affairs is the base for significant evolutionary processes, because such processes can only continue over a sufficiently long

period as long as natural selection can shift from one genotype to another within a very broad frequency distribution of genotypes, *i.e.* a frequency distribution that has developed and was moulded under environmental conditions that varied in space and time and was maintained by risk spreading.

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