# Survival and reproduction in relation to habitat quality and food availability for *Pterostichus oblongopunctatus* F. (*Carabidae*, Col.)

*J. Szyszko*[1], *H.J.W. Vermeulen*[2] & *P.J. den Boer*[2]

[1]Department of Zoology Warsaw Agricultural University, 02-528, Rakowiecka 26, 30, Poland
[2]Biological Station Wijster, Kampsweg 27, 9418 PD Wijster, Drenthe, The Netherlands

**Abstract**
Observations were made of the Carabid fauna in more than a dozen stands in Holland, Poland and Germany. Special attention was paid to *P. oblongopunctatus.* Everywhere possible for this species was estimated: the male-to-female ratio; individual biomass at the moment of capture, after 24 hrs of starvation and after 24 hrs of feeding; respiration; consumption; number of eggs in ovaries; number of eggs laid; age structure of adults and the period of activity. Differences in the characteristics studied were found between the groups of individuals from different stands. Frequently there were differences between neighbouring stands, and these were more pronounced than those between stands some hundred kilometres apart. It is suggested that, with successional changes of habitat *P. oblongopunctatus* changes its life history pattern in a way that becomes apparent by larger body dimensions, lower respiration and consumption, a shorter lifespan of the adults, a larger number of eggs in the ovaries and different activity of males and females giving rise to differences in the sex ratio in the pitfall trap. The supposition is advanced that the main factor governing the way of life is food. An estimate of food conditions for larvae and adults respectively may be derived from the dimensions of the adult and the ratio of males to females in pitfall traps.

**Key words**: Biomass, habitat changes, consumption, egg production, food, respiration, *Pterostichus oblongopunctatus*, sex ratio, size

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# Introduction

Survival and reproduction are two basic, interlinked phenomena which guarantee the existence of the species and influence the population dynamics. Much attention has been paid to these phenomena in scientific works and it has been demonstrated that survival and reproduction are modified by both abiotic, mainly temperature and moisture, and by biotic ones, mainly food, its accessibility and quality. With *Carabidae* this has been demonstrated both under laboratory and field conditions, and a review of this knowledge may be found in the works of Van Dijk & Den Boer (1992) and Van Dijk (1994).

In spite of the extensive information accumulated, it is difficult to establish which of these factors is decisive under natural conditions, and the main cause of this lack of simple but exact indicators allowing the phenomena in the field to be recorded.

The direct reason to the present study was the repeated demonstration that individuals of the same species of *Carabidae* from various forest habitats, differing in stand age and past use of the soil, are characterized by different dimensions (Szyszko 1978), varying biomass (Szyszko et al. 1978), different proportions of males and females in surface traps (Szyszko 1976, 1977) and different numbers of eggs in the ovaries (Borkowski & Szyszko 1984). On the assumption that the above mentioned characteristics might be indices of differences in survival and reproduction, it was decided to compare one of the most common of the forest *Carabidae* – *Pterostichus oblongopunctatus* in various forest stands in several European localities.

# Materials and Methods

## Collection of material

Material was collected in 16 forest stands (Szyszko et al. 1992), two of which were situated in Holland (near Wijster in 1986), five in north-west Poland (near Tuczno in 1987), and nine in southern Germany, with six near Bayreuth in 1988 and three in the Bavarian National Park in 1990. In each country the stands were visually examined and the only criterion for selection was the presence of *P. oblongopunctatus*. A brief description of the stands is given in Table 1. In all stands observations were made in the period of activity of the adults of *P. oblongopunctatus* by catching individuals (of the interaction group in the sense of Den Boer 1968, 1977) in live traps. The traps differed between countries on account of the different soils and different numbers of beetles. In Poland, a representative sample could be obtained from four 1-m catching grooves in the soil bordering a square with 10 m sides. In contrast the stony soils and small numbers of insects in Germany made it necessary to use 9-m plastic fences buried vertically into the soil with ten cylinder traps distributed along the sides. In all countries traps were inspected every three days. In the laboratory all the *Carabidae* individuals were counted according to species and their live biomass was determined. Further work was restricted to *P. oblongo-punctatus* and, depending on the availability of a laboratory or the possibility of killing beetles, concerned following features:

– the numbers of males and females
– the individual (mg) biomass of males and females at the moment of capture, after 24 hrs of starvation in the laboratory and then after 24 hrs of feeding in the laboratory with larvae of insects as food
– respiration of males and females in 24 hrs, estimated as the mg difference between biomass at the moment of capture and at the end of the period of starvation
– the consumption of males and females in 24 hrs, estimated as the difference between biomass after feeding and at the end of starvation
– the number of eggs deposited in the laboratory (in the starvation + feeding periods)
– the surface of the left elytron in $mm^2$ (determined by measuring length and breadth)
– the age of individuals, divided into young and old (from preceding years) specimens
– the number of eggs in ovaries
– the period of activity in days for males and females (the end of the period was considered to be the first day of the absence of individuals from traps after the period of culmination of numbers, with the restriction that this absence continued for three successive collection periods.

Determination of the age of individuals and of the numbers of eggs made it necessary to kill the beetles, so that attention could be paid to the degree of development of the flight muscles of the wings and to the presence of parasitic *Nematoda*.

A list of observations in the different stands (of the interaction groups) is given in Table 1. All field work and work on biomass estimation was done in Holland and Poland by H.J.W. Vermeulen, in Bayreuth (Germany) by J. Szyszko and in the Bavarian National Park by N. Schaffer from Bayreuth University. Elytra measurements, age determinations, establishment of the

**Table 1.** Number of males (M) and females (F) of *Pterostichus oblongopunctatus* caught and studied in the different stands for sex ratio, mean surface of elytra, biomass, consumption, respiration, number of eggs in the ovaries, number of eggs laid and age classes. N = Netherlands, PL = Poland, G = Germany.

| | | | | Sex-ratio | | Mean surface of left elytra | | Mean biomass | | Mean consumption & respiration | | Number of eggs in the ovaries | Number of eggs laid | Age class | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nr. of stand | Country | Description of stand | Individuals caught M+F | M | F | M | F | M | F | M | F | F | F | M | F |
| 1 | NL | Oak-birch 30 years old | 615 | | | 93 | 230 | | | | | 229 | | 49 | 229 |
| 2 | NL | Oak-pine 70 years old | 250 | | | 88 | 198 | | 198 | | | 75 | | 87 | 75 |
| 3 | PL | Pine 43 years old | 752 | 294 | 458 | 35 | 35 | 71 | 70 | 71 | 70 | 101 | | 99 | 101 |
| 4 | PL | Pine 52 years old | 599 | 249 | 350 | 32 | 46 | 52 | 105 | 52 | 105 | 110 | | 68 | 110 |
| 5 | PL | Pine 27 years old | 434 | 177 | 257 | 55 | 70 | 63 | 90 | 63 | 90 | 100 | | 77 | 100 |
| 6 | PL | Pine 43 years old | 326 | 114 | 212 | 46 | 64 | 58 | 81 | 58 | 81 | 88 | | 70 | 88 |
| 7 | PL | Pine 95 years old | 89 | 37 | 52 | 12 | 25 | 17 | 28 | 17 | 28 | 18 | | 21 | 18 |
| 8 | G | Multispecies 4 years old | 6 | 3 | 3 | | | | | | not analysed | | | | |
| 9 | G | Spruce 90 years old | 89 | 36 | 53 | 32 | 45 | 33 | 48 | 33 | 48 | 45 | 48 | 32 | 45 |
| 10 | G | Beach-oak 140 years old | 124 | 30 | 94 | 24 | 76 | 17 | 52 | 17 | 52 | 76 | 52 | 24 | 76 |
| 11 | G | Oak 4 years old as undergrowth in Pine | 52 | 19 | 33 | 18 | 17 | 17 | 23 | 17 | 23 | 20 | 23 | 19 | 20 |
| 12 | G | Pine 35 years old | 27 | 3 | 24 | 3 | 22 | 3 | 20 | 3 | 20 | 23 | 20 | 3 | 23 |
| 13 | G | Pine 100 years old | 51 | 16 | 35 | 15 | 29 | 15 | 32 | 15 | 32 | 29 | 32 | 15 | 29 |
| 14 | G | Multispecies 2 years old | 4 | 2 | 2 | | | | | | not analysed | | | | |
| 15 | G | Natural mixed forest | 29 | 15 | 14 | | | 15 | 14 | 15 | 14 | | | | |
| 16 | G | Windfall in natural forest | 32 | 16 | 16 | | | 16 | 16 | 16 | 16 | | | | |

numbers of eggs in ovaries and observations concerning the development of flight muscles and parasitism were made by H.J.W. Vermeulen.

**Data collected**

Because of the complicated processes occurring within each interaction group studied, the high degree of variability between individuals and the fact that the aim was to detect trends and regularities, it was decided to concentrate upon the data for *P. oblongopunctatus* obtained from each forest stand (one interaction group) for the whole period of activity of adults. Therefore we will restrict ourselves to indices such as sex ratio, the percentage of young individuals, and arithmetic means for the surface area of elytra, biomass, respiration, consumption, the number of eggs in ovaries etc., estimated for samples of individuals from different stands. Coefficients of correlations between the characteristics mentioned were established. Data from two stands in Germany were excluded from the study since as few as four and six individuals of *P. oblongopunctatus* were found there (Table 2). The authors thus had 12 samples for sex ratio, 13 samples for biomass at the moment of capture for females and 12 for males, 12 samples for biomass of males and females, 12 for separating young from old males and females, 12 for number of eggs in ovaries, 5 for eggs laid in the laboratory and 14 for determining the period of activity in days for males and females. These data are listed in Tables 1 and 2, together with the numbers of individuals from which they were obtained. A description of the carabid fauna in the stands (Table 2) was made on the basis of mean individual biomass (MIB), i.e. the quotient of the total biomass of all carabid individuals caught during the observation period and their numbers. According to Szyszko (1987, 1990), the higher the MIB value in milligrams, the higher the contribution of individuals of forest species and of species with large body dimensions that are characteristic for advanced stages of succession. Szyszko applies this characteristic as an indicator of the state of development of the fauna, with higher MIB indicating more advanced development of the fauna of *Carabidae* and a more advanced state of succession.

## Results

Compilation of all data for the particular interaction groups of *P. oblongopunctatus* from each of the different stands shows a high degree of

**Table 2.** Short description of results obtained in the different stands from different countries. Full explanation in the text. * Data from the paper of Szyszko et all. 1992

| | | | Mean surface of left elytra in mm2 | | Mean biomass at moment of catching in mg | | Mean biomass after 24h of starving in mg | | Mean biomass after 24h of feeding in mg | | Mean transpiration in mg | | Mean consumption in mg | | Mean number of eggs in the ovaries | Mean number of eggs laid | Time of activity in days | | Percentage of young beetles | | Number of beetles with flight muscles | | Number of beetles with parasites | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nr of stand | MIB * | Sex ratio M/F | M | F | M | F | M | F | M | F | M | F | M | F | F | F | M | F | M | F | M | F | M | F |
| 1 | 111 | | 14.0 | 15.5 | | | | | | | | | | | 5.81 | | 84 | 84 | 55.1 | 50.7 | | | | |
| 2 | 126 | | 14.1 | 15.6 | | 54.2 | | | | | | | | | 4.85 | | 70 | 56 | 58.6 | 38.7 | | | | |
| 3 | 156 | 0.64 | 14.5 | 16.0 | 55.1 | 65.6 | 52.4 | 61.5 | 60.8 | 73.2 | 2.7 | 4.1 | 8.4 | 11.7 | 6.06 | | 69 | 69 | 89.9 | 68.3 | | | | |
| 4 | 193 | 0.71 | 14.5 | 16.0 | 52.8 | 65.1 | 50.8 | 62.3 | 62.3 | 72.9 | 2.0 | 2.8 | 11.5 | 10.6 | 6.37 | | 69 | 69 | 79.4 | 59.1 | | | | |
| 5 | 119 | 0.69 | 13.9 | 15.5 | 52.3 | 63.6 | 50.3 | 60.8 | 60.8 | 74.0 | 2.0 | 2.8 | 10.5 | 13.2 | 7.33 | | 60 | 60 | 87.0 | 69.0 | | | | |
| 6 | 269 | 0.54 | 14.6 | 16.4 | 53.1 | 63.6 | 51.4 | 60.7 | 60.2 | 74.4 | 1.7 | 2.9 | 8.8 | 13.7 | 7.44 | | 60 | 60 | 74.3 | 58.0 | | | | |
| 7 | 243 | 0.71 | 15.2 | 16.5 | 51.5 | 64.2 | 51.0 | 62.2 | 59.8 | 72.8 | 0.5 | 2.0 | 8.8 | 10.6 | 8.50 | | 66 | 66 | 66.7 | 66.7 | | | | |
| 8 | 63 | not analysed | | | | | | | | | | | | | | | | | | | | | | |
| 9 | 215 | 0.68 | 15.5 | 17.3 | 62.4 | 73.9 | 59.2 | 69.6 | 64.9 | 78.2 | 3.2 | 4.3 | 5.7 | 8.6 | 8.82 | 0.44 | 23 | 23 | 75.0 | 64.4 | 4 | 3 | 1 | |
| 10 | 277 | 0.32 | 14.5 | 17.1 | 56.5 | 73.0 | 54.6 | 69.8 | 59.1 | 76.7 | 1.9 | 3.2 | 4.5 | 6.9 | 10.70 | 0.92 | 17 | 44 | 70.8 | 57.9 | | | 1 | 6 |
| 11 | 257 | 0.58 | 15.2 | 18.0 | 58.2 | 73.3 | 56.3 | 70.6 | 61.4 | 77.1 | 1.9 | 2.7 | 5.1 | 6.5 | 8.35 | 0.61 | 16 | 51 | 78.9 | 65.0 | | 1 | | 1 |
| 12 | 383 | 0.13 | 16.1 | 17.9 | 63.3 | 77.1 | 62.3 | 73.4 | 66.6 | 79.1 | 1.0 | 3.7 | 4.3 | 5.7 | 15.43 | 1.40 | 4 | 21 | 100 | 69.6 | | 1 | 1 | |
| 13 | 310 | 0.46 | 16.1 | 18.3 | 64.7 | 75.4 | 62.6 | 72.5 | 67.1 | 79.6 | 2.1 | 2.9 | 4.5 | 7.1 | 7.86 | 0.62 | 24 | 43 | 86.7 | 72.4 | 1 | 1 | | |
| 14 | 68 | not analysed | | | | | | | | | | | | | | | | | | | | | | |
| 15 | 193 | 1.07 | | | 66.0 | 81.2 | 62.3 | 75.1 | 75.3 | 87.9 | 3.7 | 6.1 | 13.0 | 12.8 | | | 16 | 34 | | | | | | |
| 16 | 95 | 1.00 | | | 62.7 | 77.6 | 59.0 | 69.9 | 71.3 | 88.8 | 3.7 | 7.7 | 12.3 | 18.9 | | | 46 | 48 | | | | | | |

variability, a variability which is frequently higher among stands close together than among those in different countries. For instance, the sex ratio of males to females varied between 1.07 and 0.13, with both extreme values being recorded in German stands. The other interaction groups of *P. oblongopunctatus* from both Poland and Germany gave intermediate values (Table 2).

Mean values for the elytron surface area and for biomass at the moment of capture, after starvation and after feeding also showed great differences between the different stands. Mean biomass was in general higher for stands in Germany than for those in Poland but this was not observed for the surface area of elytra. In the latter case the mean values were similar for some stands in both countries especially for males (Table 2). The means obtained for the stands in Holland were within the range of variability of the means obtained in Polish stands. High differences between groups of individuals from various stands were also found in the estimates of respiration and consumption. It is difficult to say that the groups of individuals from Poland and Germany differed in consumption. Variability was very high and the highest and lowest consumptions were observed in groups of individuals from German stands (Table 2). The contribution of young individuals in the groups from different stands also varied. The lowest figure was for the stands in Holland. The range of variability was about similar in Polish and German stands.

Variability was also high with regard to the mean number of eggs in the ovaries, and also in this case the means from various countries frequently differed less than those from stands close together. Data for the number of eggs laid in the laboratory could only be obtained from five stands in Germany, but in this case differences were observed too. Means for the number of eggs laid per female within 48 hrs of starvation + feeding varied from 0.44 to 1.40 for different stands (Table 2).

As Table 2 shows, the activity of males and females was also found to differ among stands. It should be noted that, in spite of important differences in the period of activity between the different stands in Germany, the activity period was generally shortest there as opposed to that in the other countries. The differences in activity in stands in Poland were similar to those observed in Holland.

It was mentioned in the method section that attention was paid to the development of flight muscles and to parasitism by Nematoda. Developed flight muscles were observed in eleven young individuals from four of the German stands (Table 2). Nematoda were found in ten old individuals, also

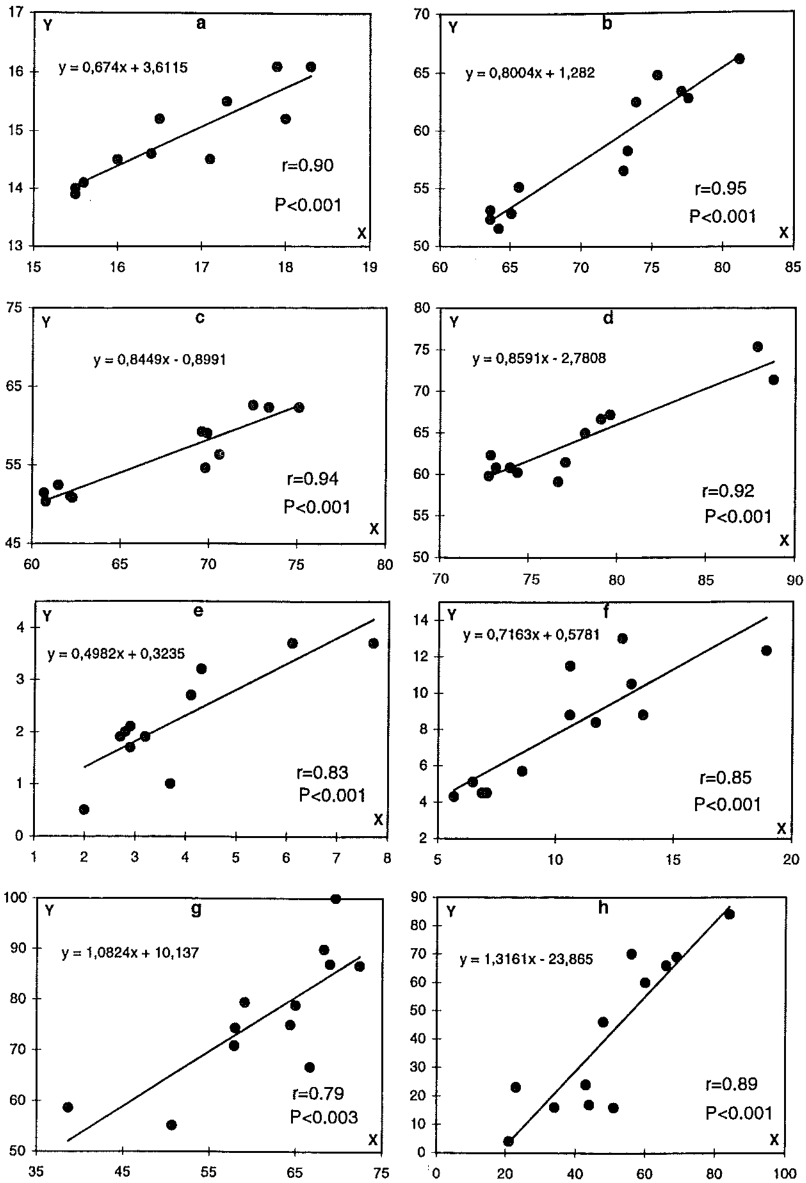


**Fig. 1.** Relationship between females (X) and males (Y) of *P. oblongopunctatus* in samples of individuals from various stands in Germany, Holland and Poland for surface area of elytra (a), biomass at the moment of capture (b), biomass after a period of starvation (c), biomass after feeding (d), respiration (e), consumption (f), the contribution of young individuals (g) and the period of activity (h).

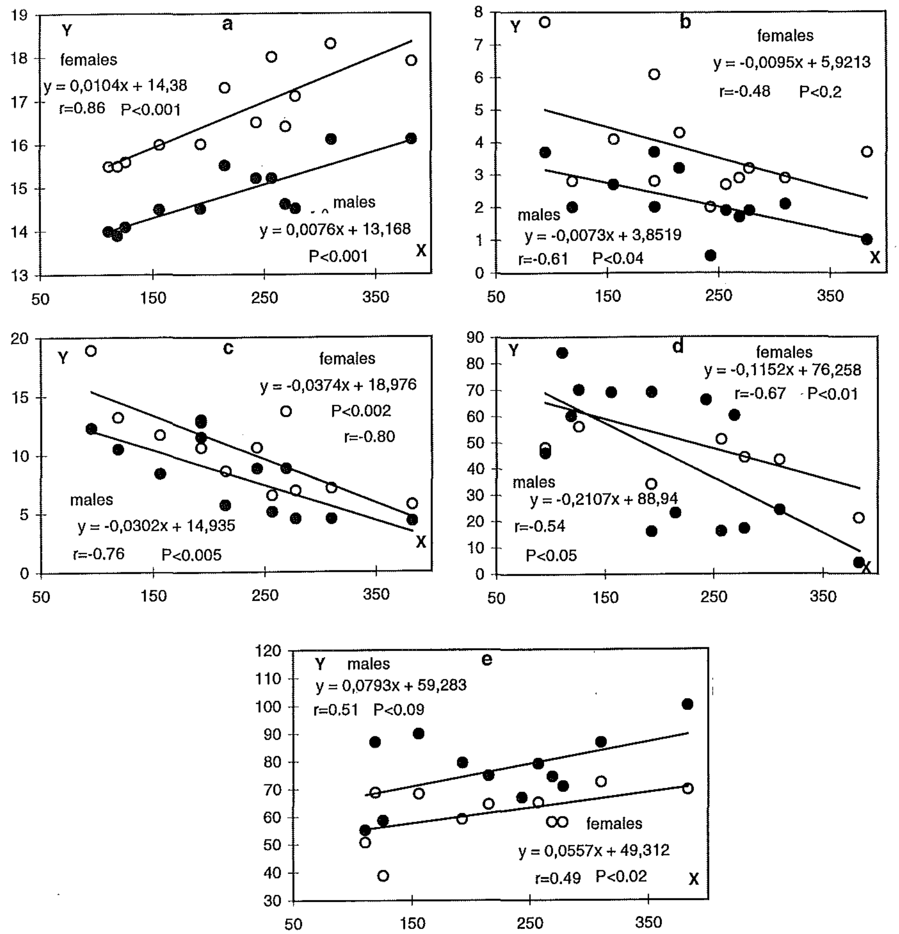


**Fig. 2.** Relationship between MIB (X) and the species characteristics (Y) obtained for groups of males (black circles) and females (open circles) of *P. oblongopunctatus* from various stands in Germany, Holland and Poland. a - surface area of elytra, b - respiration, c - consumption, d - period of activity in days, e - percentage contribution of young individuals.

from four stands in Germany. These results are interesting as *P. oblongopunctatus* had previously been considered to be usually unable to fly (Den Boer, 1987), while Nematoda parasitism of the species had not been mentioned sofar in ecological papers.

MIB values calculated for the different stands (Table 2) show that the interaction groups of *P. oblongopunctatus* examined were part of various faunas. Differences were high with values ranging from 63 to 383 mg, and with these extreme values again being recorded in German stands. The faunas of the other stands also showed large differences in MIB values, albeit within this interval. It must be noted, however, that it was difficult to catch a representative sample of individuals in the stands with the highest and lowest MIB values respectively.

The material above indicates that groups of *P. oblongopunctatus* differ from one another, and that the differences probably are not due to climatic conditions, since the characteristics of neighbouring stands frequently differed much more than those of widely-separated ones in different countries. Thus, other factors must have played a role and had similar effects on both males and females, since high correlation coefficients were found between females and males from the stands concerning size, biomass, respiration, consumption, the contribution of young individuals and the time of activity (Fig. 1). If this argument is correct, the causes of the observed differences should be in the habitat of the particular interaction groups, and to get a first indication correlation coefficients were calculated for the relationship between MIB and the size of elytra, consumption, sex ratio and the number of eggs in ovaries (Fig. 2). Lower correlation coefficients, (but usually above 0.5) were found in relation to respiration, the contribution of young individuals and the activity period. The correlations showed that the higher the MIB value, the larger the dimensions of the adults, the higher the number of eggs in the ovaries, the higher the proportion of young individuals, the lower the contribution of males in traps, the lower the respiration and consumption and the shorter the activity period.

## Discussion

According to the suggestion of Szyszko (1987, 1990), each species would occur in a definite interval of successional development, as indicated by MIB values in the case of Carabids. This suggestion seems to be supported by the materials presented here, because *P. oblongopunctatus* was difficult to catch when MIB was low or high respectively (Tables 1,2). The correlation coefficients calculated for the relationship between MIB values and the studied characteristics in the different interaction groups from various stands seem to indicate that changes occurring in a habitat along with successional development are accompanied not only by changes in the abundance of species but also by changes in special characteristics of populations also.

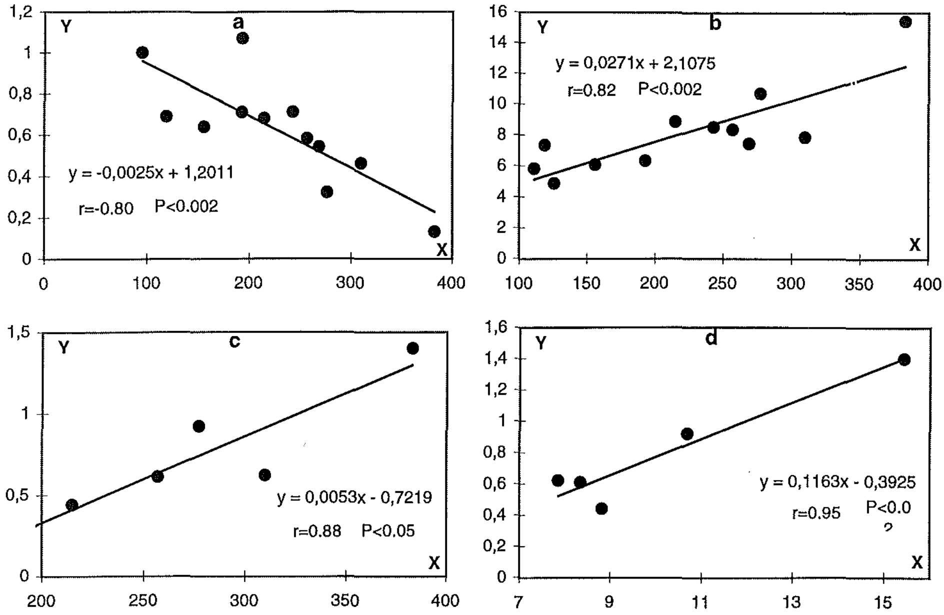


**Fig. 3.** Relationship between MIB (X) and particular characteristics estimated for samples pf *P. oblongopunctatus* individuals (Y) from various stands in Germany, Holland and Poland, a - sex ratio, b - number of eggs in ovaries, c - number of eggs laid in laboratory in relation to the numbers of eggs in the ovaries (X) and d - numbers of eggs laid in laboratory in periods of starvation and of feeding combined (Y).

The positive correlation found between MIB and the dimensions of elytra (Fig. 2) would seem to suggest that, with successional development, the adult of *P. oblongopunctatus* becomes larger and larger. Assuming that abiotic factors did not play a significant role in the data presented here, it may be supposed that it is the feeding situation for the larvae that plays the main role, since it has been demonstrated that better nutritional situations for larvae are associated with larger adults (Nelemans 1987a, Van Dijk 1984). If this is true then the size of the adult may be a simple indicator of the food situation for larvae in previous years. The positive correlation found between MIB and the percentage contribution of young individuals indicated that in the course of succession, the mean life period of the adults becomes shorter, or to put it in another way, the mortality of old individuals increases. It may be that some role here is played by parasites which have been detected in small numbers,

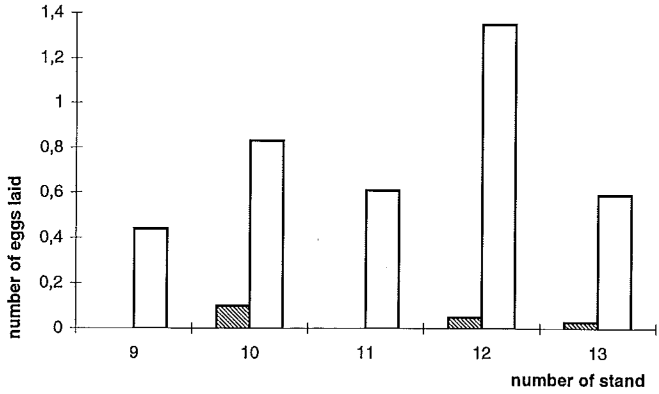


**Fig. 4.** Mean number of eggs laid in laboratory in periods of starvation (black bars) and feeding (open bars) by samples of females from various stands in Germany. Number indication of stands as in Table 1.

but especially in the stands where the MIB value was high. However,it was also shown, that the beetles were capable of flying giving the possibility that some individuals disperse by flying away from this habitat.

Assuming with Makowski & Szyszko (1986) that in the laboratory consumption by insects is inversely related to the degree of satiation of individuals, it may be said that the better the food situation in the habitat for the adult the more advanced the succession in the habitat. This is suggested by the negative correlation found between MIB and consumption by the imago (Fig. 2). A similar conclusion may be reached when considering the number of eggs in ovaries as an estimate of the food situation, since a positive correlation was found between MIB and the values for this estimate (Fig. 3). This was confirmed additionally, though only in relation to five stands, by a positive correlation between the number of eggs laid in laboratory conditions and the number of eggs in the ovaries (Fig. 3). Since the number of eggs laid may be considered a good indicator of the food situation, the presented data would seem to indicate unequivocally that the more advanced the developmental stage of the habitat in which the *P. oblongopunctatus* adult lives the better the situation for the adult.

However, this argument raises some doubts because of a negative correlation found between MIB and respiration (Fig. 2), (indicating that the higher the MIB value, the smaller the decrease in individual biomass in the starvation period). According to Makowski and Szyszko (1986) this would seem to be evidence of a deteriorating nutritional situation, since under constant laboratory conditions low respiration characterizes hungry individuals and high respiration those that are satiated (Makowski & Szyszko 1986). Also the fact that females with a large number of eggs in the ovaries, (originating from stands with a high MIB value) laid practically no eggs during the starvation period in laboratory conditions (Fig. 4) and only laid after food had been supplied (Fig. 4), might point in this direction. This

**Table 3.** Schematic representation of changes occuring in *Pterostichus oblongopunctatus* with changes in its habitat.

| low state of development of fauna | | high state of development of fauna |
|---|---|---|
| -high number of species | ---> | -low number of species |
| -small species | ---> | -big species |
| -small MIB | ---> | -big MIB |
| | Interaction group of *Pterostichus oblongopunctatus* | |
| -long activity period | ---> | -short activity period |
| -long survival of adult | ---> | -short survival of adult |
| -complicated age structure | ---> | -simple age structure |
| -small individuals (adult) | ---> | -large individuals (adult) |
| -large proportion of males in pitfall traps | ---> | -large proportion of females in pitfall traps |
| -low number of eggs in ovaries | ---> | -high number of eggs in ovaries |
| -high number of eggs laid ? | ---> | -low number of eggs laid ? |
| -good food conditions for adults ? | ---> | -bad food conditions for adults ? |
| -bad food conditions for larva ? | ---> | -good food situation for larva ? |
| -not able to fly ? | ---> | -able to fly ? |
| -uneconomic way of life ? | ---> | -economic way of life ? |

Population of *Pterostichus oblongopunctatus*

| | | | | |
|---|---|---|---|---|
| -asynchronously fluctuating interaction groups | → | -synchronously fluctuating interaction groups | → | -asynchronously fluctuatig interaction groups |
| -small probability of high fluctuation of population size | → | -high probability of high fluctuation of population size | → | -small probability of high fluctuation of population size |
| -resistant population | → | -not resistant population | → | -resistant population |

seems to indicate that the females from habitats advanced in succession have a large number of eggs in their ovaries, because they had accumulated these and a shortage of food in the field prevented them laying these.

If the latter argument is correct, then the negative correlation with MIB shown for the sex ratio in the traps (Fig. 3) can be a simple indicator of the food situation for the adult. The worse the food situation for the adult the greater the domination of females in the traps. this suggestion is confirmed by the paper of Szyszko & Gryuntal (in preparation), which for *Carabus hortensis* shows that well-nourished males are more active than females in the same situation, and, conversely, the hungry females are more active than hungry males. Such a situation will influence the ratio of males to females in traps.

The materials and suppositions presented here suggest that changes in the overall food situation for the larvae and adults of *P. oblongopunctatus* arise in the course of successional changes occurring in the habitat. The situation for larvae would improve with increasing MIB while for the adult it deteriorates. This seems to be confirmed by the fact that only young individuals possess functional wings in habitats with high MIB values, a fact that Nelemans (1987b) considered to indicate a good feeding situation for the larvae. the absence of flight muscles in old individuals from this these habitats may be the result of their disappearing with time because of a poor feeding situation for the adult.

In spite of the exact, but unknown, causes of the observed phenomena, it may be safely stated that successional changes in the habitat are accompanied by modifications in the life-history pattern of *P. oblongopunctatus*. In environments with more advanced stages of succession, lower respiration and consumption, shorter activity times, larger numbers of eggs in ovaries and probably smaller numbers of eggs laid, with larger dimensions of adults would all seem to be evidence of a much more economical way of life, which contrasts with that in habitats with less advanced stages of succession.

The discussion presented aand additional suggestions of Szyszko (1987, 1990), led to the scheme for changes in interaction groups and populations of *P. oblongopunctatus* in connection with the successional changes occurring in its habitat (Table 3). This scheme should be considered a working basis for further study which suggests, as announced in the paper by Den Boer et al. (1993) a necessity for genetic research in this species in habitats differing in their state of successional development. It can easily be imagined that *P. oblongopunctatus* may be present for no more than a dozen years in young forest plantations (after clear cut, Szyszko 1990) out of the thousands of years in natural stands.

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