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ZOO-ECOLOGICAL RESEARCH AT THE BIOLOGICAL STATION
WIJSTER (DRENTE)

P.J. den Boer

(Communication of the Biological Station, Wijster, No.131).

When in 1959 the ecological work at the Biological Station was started I wondered why different species of carabid beetles generally live in different places or more exactly formulated: which are the most important factors that determine the fitting into and the distribution over a number of habitats in populations of carabid beetles? Since no species is wholly restricted to only one type of environment it was expected that the quantitative distribution of a species over a number of different types of environment would give a first indication towards the identity of the habitat-determining factors. Moreover it was expected that this quantitative distribution over different environments would shift under the influence of the different climatic conditions in different years, which would give a second indication. Hence, right away from the start it was evident that the working-method had to be a comparative one (completed with experiments): a comparison between different environments, different years and if possible between different species.

To get the desired information in a number of different environments there is uninterrupted trapping with the help of pitfalls: in each place a set of two pitfalls without fluid and one funnel with formalin from which catches are collected each week. All carabid beetles caught are identified, sexed, prepared and managed in prefabricated lists. Up till now more than hundred thousand carabid beetles are worked up in this way. In most places sampling is continued over a number of years: in some places it was already started in 1959 and is still continued. Sampling is concentrated in areas of heath and drift-sand and in remnants of the original wood. More incidentally there is also sampled in peat-moor and in different types of forest.

Like in each ecological investigation in the field after some years already it appeared that the question was posed too simple: the intensity of the habitat-determining factors varies from place to place and from moment to moment (especially meteorological and biotic factors) and within the population sensibility and behaviour vary from individual to individual and within each individual also in time (e.g. larval or beetle stage and inside or outside the reproducing period). Hence the problem of the most important factors which determine the fitting into and the distribution over a number of habitats is not a static or typological question but a statistical one: a problem of "ecological" variability in space and time within populations more or less replying to variability in space and time of habitat-determining factors. To get adequate information it is thus unescapable to sample statistically, i.e.: independent of the problem under consideration (random or in rows at equal distances, etc.). The results obtained in this field are not clear answers but statistic relations: probabilities and correlations on varying quantities. On the base of these results working hypotheses may be posed and it can be tried to prove the hypotheses with the help of experiments: if possible experiments from which the same kind of statistic relations can be expected as are found in the field.

I will not go with you through all or only part of the trials and errors, interesting and more or less adequate or inadequate suggestions of the past years, but only say - with all reserve - that for the moment we have the impression that the most important habitat-determining factors for most carabid populations in the neighbourhood of Wijster are: moisture condition of the substratum during critical periods of the life-cycle (often the larval stage) and structure of the habitat, especially of vegetation. By its very being a physical construction linked between the "weather measured by meteorologists" and the microweather at the soil, vegetation by its structure largely determines the relation between the "weather" and the physical conditions at the places where the carabid beetles move (microweather is a derivative of macroweather). By a shortage of "man-hours" at this institute in development the technics for measuring vegetation-structure are still in an early stage of growth. It is tried to photograph vegetation from above at a distance of some meters and it will be tried to measure the different components with a planimeter. Electronic technics

for continuous and adequate measuring and computing micrometeorological conditions in the field are developed within a group of "surface-zoologists" working at different universities within the Netherlands (Univ. of Leiden, Amsterdam (V.U.), Utrecht, and Nijmegen; I.T.B.O.N., Ecological Inst. Arnhem and Biological Station Wijster). For the moment it must be sufficient to compare the catches from adjacent places with evident differences in vegetation-structure and from years with evident differences in climatic conditions. Besides its influence on micro-meteorological conditions vegetation-structure may form a mechanical barrier for the movements of carabid beetles if a dense and rather voluminous and continuous structure covers the surface of the soil. This is especially the case if the heather is more or less shadowed by scattered trees and voluminous moss-layers develop within the Calluna-scrubs. Possibly the extensive Sphagnum-vegetation under Erica in peat-moor areas has a comparable mechanical effect. But instead of informing you with examples of habitat-selection in different species of carabid beetles - how interesting this may be - I will concentrate on what in my opinion is a more fundamental and more general aspect.

Every ecologist knows that in natural populations animal numbers fluctuate from generation to generation and that there is much discussion pro and contra the regulation of these numbers. It struck me that at the heath of Kralo where places with different structure are sampled simultaneously not only the numbers caught of each species differ from place to place within the same year, but also the fluctuations of catch-numbers from year to year are different places. This is illustrated by graph 1: especially the difference between M and N is evident, in M the greatest number in 1963, in N in 1962⁺. In other species than Calathus melanocephalus comparable phenomena are found. To be able to analyze this phenomenon, starting with 1963 the material of a number of species is collected in formalin in order to be able to dissect the females and to study the development of the ovaries and in this way the progress of the reproductive cycle in time. Especially of Calathus melanocephalus large numbers of females are studied

+ When this paper was read data from 1965 were only partly available; they were afterwards added to the text and to the graphs.

in this way and in the following I will restrict myself to this species. In the first place it appeared that early in spring only females without eggs but with "corpora lutea" (c.l.) in the ovaries were caught (a "corpus luteum" is a pigmented place in an ovariole which develops after the production of an egg). These females had reproduced in the foregoing year and survived winter ("spent" females). From June up to and including September mainly females with eggs and with or without c.l. are caught. Starting with October again "spent" females are caught (graphs 2 and 3). Hence, the general picture of this species is: reproduction between June and October, after which the "spent" females still move about, obviously until meteorological conditions become too unfavourable for activity; early in spring they reappear again. The larvae develop in winter and in early spring; young beetles are caught in June (soft with white ovaries without "corpora lutea"). The males show the same picture: part of the reproducing males can be recognized by protruding genitalia (4 + 5). The catches of still other places at the heath of Kralo are analyzed in the way shown in the graphs 2-5. For most places at Kralo the catches from 1963, 1964, and 1965⁺ can be divided now (all week-catches taken together) in "spring spent", "reproducers" and "autumn spent". Since "spring spent" and "autumn spent" generally can be easily recognized by a separate peak in the catches, also the catches from 1959, 1960, 1961, and 1962 could be divided in these three groups with an uncertainty of not more than a few percent (graph 6). From this graph it will be evident that the fluctuations in the numbers of "reproducers" from year to year are not the same at each place (only the reproducers are important for the future of the population): in M numbers decrease till 1961 and increase till 1963 and then decrease again; in N numbers increase till 1962 and then decrease again; in Z numbers are nearly constant between 1961 and 1963; etc. Only from 1963 to 1964 and from 1964 to 1965 there is a general trend to decrease, although not in each place to the same extent. To illustrate this more clearly in graph 7 the amount of change in the number of producers caught from one year to the following $\left(\frac{R_n}{R_{n-1}}\right)$ is plotted. It will be evident

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that in this respect there are great differences between the different places: from 1960 to 1961 M decreased with a factor 0.4 and N with a factor 0.7, whereas Z increased with a factor 2; from 1962 to 1963 N decreased with a factor 0.5, Z remained the same and M increased with a factor 1.8; from 1963 to 1964 and from 1964 to 1965 in all places numbers decreased (graph 7). Since most of these places are adjacent and not separated from each other (they are all parts of the same heath of Kralo) in fact our information is drawn from different parts of the same population of Calathus melanocephalus. Since the animals obviously can live in all these places and since the beetles are continuously moving about, there will be a significant exchange between the different places (although there are no indications for directed migration). It may seem a rather trivial thing to calculate the amount of change for all places together which are sampled in two succeeding years and to show that in that case the change is smaller than in most separate places : for N in all pairs of years (6), for AG in 3 out of 4 pairs, for Z in 2 out of 5 pairs, for M in 3 out of 6 pairs (graph 7). But in connection with the theories on the regulation of animal numbers it is important to demonstrate that if the habitat of a population consists of a mosaic of different structured places (and this will generally be the case in nature) the chance to reproduce and to survive will be different in these different places and for the population as a whole this means that extreme conditions in one place will be buffered by less extreme conditions in other places. Moreover, an extreme place in one year often will become a more or less normal place in a year with other climatic conditions. In other words: if within a population the chance to survive and to reproduce is unequally distributed over a number of different places which more or less replace each other in years with different climatic conditions, the fluctuation of numbers of the population as a whole will be relatively stabilized: the losses in one place will more or less be compensated by the gains in another place. This principle of "risk distribution" is the base on which insurance companies are able to survive (and perhaps animal populations too). In the case of Calathus melanocephalus this principle of "risk distribution in space" is demonstrated here with places of about a thousand quadrat meters or more (a rough estimation of the minimal catch-range of a set of traps). But within such a place there will again be inhomogenities in structure the influence of which generally can not be separated

from the catches (indications of such influences are obtained by considering the catches of the separate traps of a set). In general: the complicated variability in the structure of natural habitats on a small as well as on a large scale via all kinds of "risk-distributions in space" in my opinion must importantly contribute to the stabilization of the fluctuations in animal numbers. Of course it will be necessary to study these things more in detail and to bring many refinements into the frame (e.g. by sampling with many small traps in the different components of a mosaic). This can only be broached when more "man-hours" are available.

But let us return to Calathus melanocephalus. We may wonder whether the hibernated spent females again take part in reproduction or that the group of reproducers only consists of young animals. Although we are able to divide the females with eggs in females without and females with corpora lutea and can divide the latter group in "c.l. above eggs", "c.l. below eggs" and "c.l. between eggs" and although especially my co-worker Sanders studied great numbers of females in this way, the problem is not yet solved. The difficulties are caused by the fact: 1st that females which develop eggs generally are not active and consequently not caught and 2nd that soon after an egg has leaved its ovariole a corpus luteum becomes increasingly visible, so that young and hibernated females become increasingly difficult to distinguish when reproduction goes on. Nevertheless there are indications that the hibernated females again take part in reproduction: 1st a few of such females of which we are sure and 2nd dissection of marked hibernated females from Schiermonnikoog by VLIJM and from Denmark by SCHJØTZ-CHRISTENSEN (1965). We are pretty sure, however, that at Kralo the reproducing group mainly consists of young females, whereas Vlijm is sure that at Schiermonnikoog an important part of the reproducing group consists of hibernated females. Both opinions may be right in which case an interesting example of geographical variation over short distance is found. If it is true that hibernated females reproduce again it is important to compare the survival of beetles and larvae in winter. Spent-survival in winter is indicated by the quotient $\frac{\text{spring spent } n}{\text{autumn spent } n-1}$. Since graph 6 shows that in 1959, 1960 and 1961 in most places only very small numbers of spent animals were caught the most reliable results are obtained from 1962 and following years. Graph 8 shows that in difficult places there are no important differences in spent-survival, with the remark-

able exception of AT (and perhaps AY), where spent-survival is very low. Between different years spent-survival does not show great differences too. Although hibernated females apparently reproduce again, at Kralo they generally will form only a small part of the total group of reproducers (perhaps not at Schiermonnikoog) and thus, the quotient $\frac{\text{reproducers } n}{\text{reproducers } n-1}$

may be considered a rough measure for larval (and pupal) survival in winter and early spring. If we plot $\frac{R_n}{R_{n-1}}$ against $\frac{S \text{ spring } n}{S \text{ autumn } n-1}$

for the year-pairs 1962/'63, 1963/'64 and 1964/'65 graph 9 illustrates that the differences in larval (+ pupal) survival are much greater than those in spent survival with again the exception of AT (and perhaps AY) with a lower spent survival than all other places in the winters 1963/'64 and 1964/'65. Possibly this difference between AT (and perhaps AY too) and all other places has something to do with the fact that AT and AY are the only sampled places at Kralo where the ground-water level in winter never reaches the surface; in all other sampled places at Kralo the ground-water level in most winters sometimes will reach the surface. One point, however, is clear from a comparison of the graphs 7 and 8: larvae generally are more sensible for conditions in winter than beetles and hence, the hibernation of beetles may be important for the survival of the population during winters in which conditions are very unfavourable for larvae. This situation nicely illustrates another kind of risk-distribution, risk-distribution in time: by distributing the risks of perishing during winter over different stages of development with different sensibility the effect of winter on numbers is buffered, especially if it is combined with a risk-distribution in space (as in the case of Calathus melanocephalus). It will be necessary to bring many refinements into this picture: biology and habitat-selection of the larvae, experiments on tolerance and preference of hibernating larvae and beetles, etc. This can only be started when more "man-hours" are available.

Risk-distribution in time by the hibernation of different stages of development appears to be very common among carabid beetles: up till now it was found in each species of which females were dissected. In Calathus erratus (graph 10) spent females hibernate and reproduce and larvae hibernate giving young females in spring which reproduce too. The same phenomenon is found in Pterostichus coerulescens (graph 11) with the difference that spent females and newly hatched females appear at the same time. The same is found in the wood species

Pterostichus oblongopunctatus. Another kind of "risk-distribution in time" probably is illustrated by Amara lunicollis (graph 12), where in M most specimens are caught in May and June and in AG in July, August and September. These data suggest that reproduction takes place much earlier in M than in AG. Only after having dissected the caught females we will be sure about this. A nice example of a risk-distribution of this kind is found by A. Daanje in the weevil Rhynchitus cupreus where in the same place different reproducing groups only partly overlap each other in time.

Another kind of risk-distribution is found in the wood-species Pterostichus oblongopunctatus, where the larvae of different morphological forms apparently show a different sensibility for the moisture condition of the litter: the larvae of the form with 5 or less pits on the elytra are relatively favoured by dry conditions and the larvae of the form with 6 or more pits on the elytra by moist conditions of the litter. Consequently the percentage of "high"- and "low-pitters" in the population shifts from year to year parallel with the deviation from the normal amount of precipitation during the period of larval development (May-August) (see: Comm. of the Biological Station, Wijster, No. 103a, 1962). Experiments on the terrain of the Biological Station are going on now to prove this form of "genetic-risk-distribution". From our data it is clear that populations of Pterostichus oblongopunctatus will be able to cope with a continuously fluctuating environmental factor like the moisture condition of the substratum by distributing sensibility for that factor over a number of genotypes, or in other words: the effect of the fluctuating environmental factor is continuously more or less intercepted by the "genetic variability" of the population and hence, fluctuations of numbers will be relatively stabilized. In his book of 1963 also MAYR points to the important "survival value" of genetic variability, which is a common feature of natural populations.

It will be clear now that the fact, that the intensity of the habitat-determining factors varies from place to place and from moment to moment and that within the population sensibility and behaviour vary from individual to individual and within each individual also in time, must not merely be considered a inconvenientness of field data which must be neglected or got round by retreating into the laboratory being only "deviations" from the "typical" or "representative"

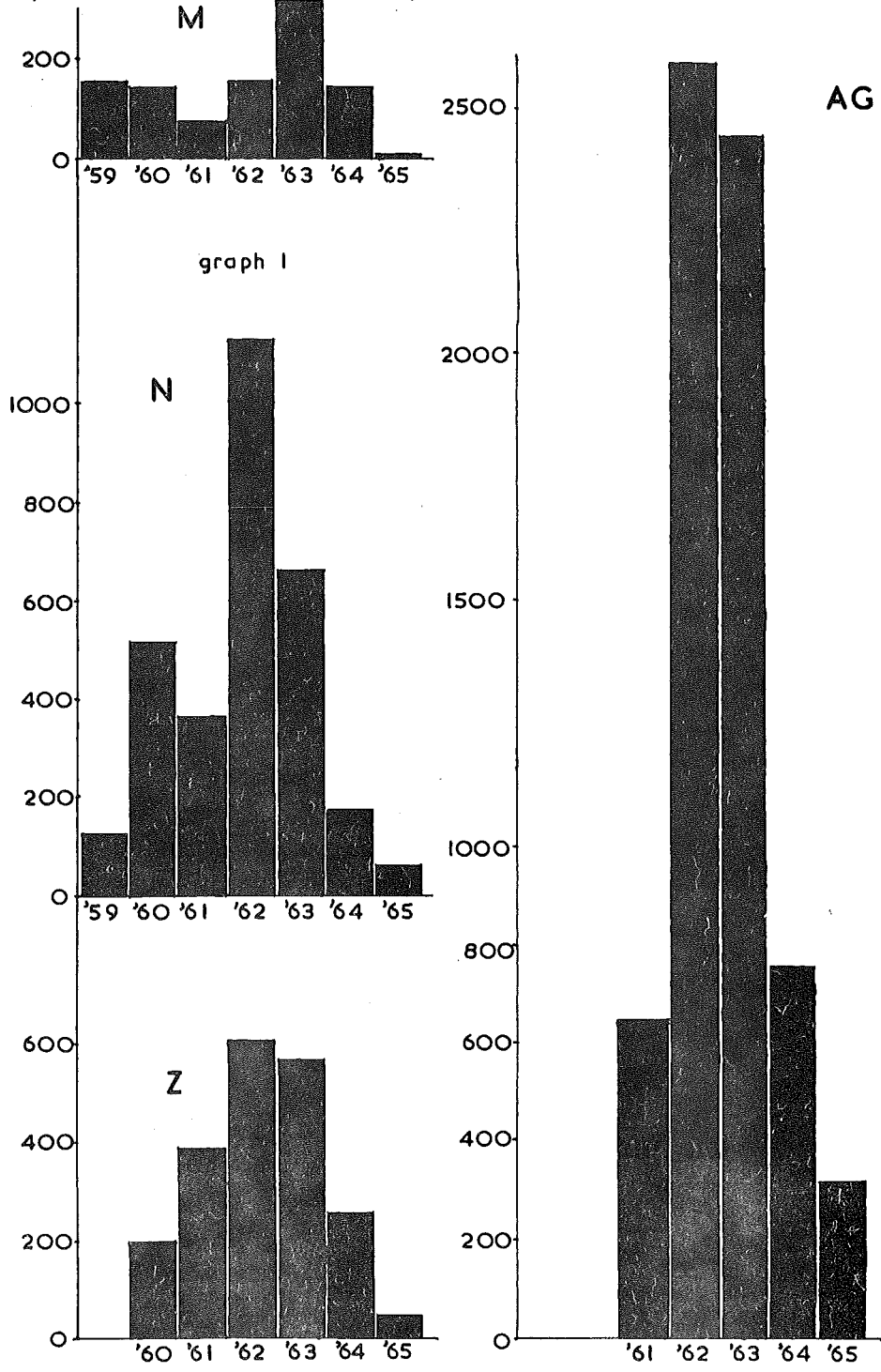
case or even "noise", but rather must be considered a fundamental feature of the natural situation. In this connection the discussions pro and contra "the regulation of animal numbers" in my opinion largely are premature (which does not mean of course that I should deny the possibility of the existence of real regulatory "mechanism" in some natural populations). As long as we do not quantitatively know the stabilizing effect of the many kinds of risk-distribution which are at work in each natural population we do not know how to think about the fluctuations of numbers as they are found in natural populations and we are not able to predict how long a population which is "only" stabilized by a number of risk-distributions (by chance) may survive. As a first trial to fill up this gap I have constructed a simple mathematical model which demonstrates the stabilizing effect of risk-distributions on the fluctuations of numbers and which I hope to publish soon. This trial is regularly discussed with: KLOMP, Wageningen, BAKKER, Leiden and REDDINGIUS, Groningen.

Not only within the populations of one species risk-distributions play an important part, but also in the relations between species: a monophageous predator often will be forced more or less to follow the fluctuations in numbers of his prey, a polyphageous predator has "distributed" this "risk" over a number of different prey-species; the same can be said about monophageous and polyphageous parasites and perhaps about other groups of species which more or less depend upon each other. Not only the numbers of predator-populations are relatively stabilized by distributing the risk over a number of prey-species, but also the numbers of a prey-population are relatively stabilized by distributing the risk of "being eaten" over a number of different predator-species. To risk a speculation: the greater the number of species which live together in one place (biotope), the greater the chance that risk-distributions of this kind play a significant part and the more the numbers of each separate population will be stabilized. In my opinion this may be the base of the much-discussed "biological equilibrium" (balance of nature), which is so "easily" and so frequently destroyed by man. Hence the richer a "community" in species, the more stable; note, that it is not the quality of the species, but rather the quantity, which seems to be important in this view. But now I must stop in order to prevent still more speculation.

Calathus melanocephalus L.

number of specimens

catch-numbers per year in different places at Kralo





Calathus melanocephalus L.

number of specimens
(females)

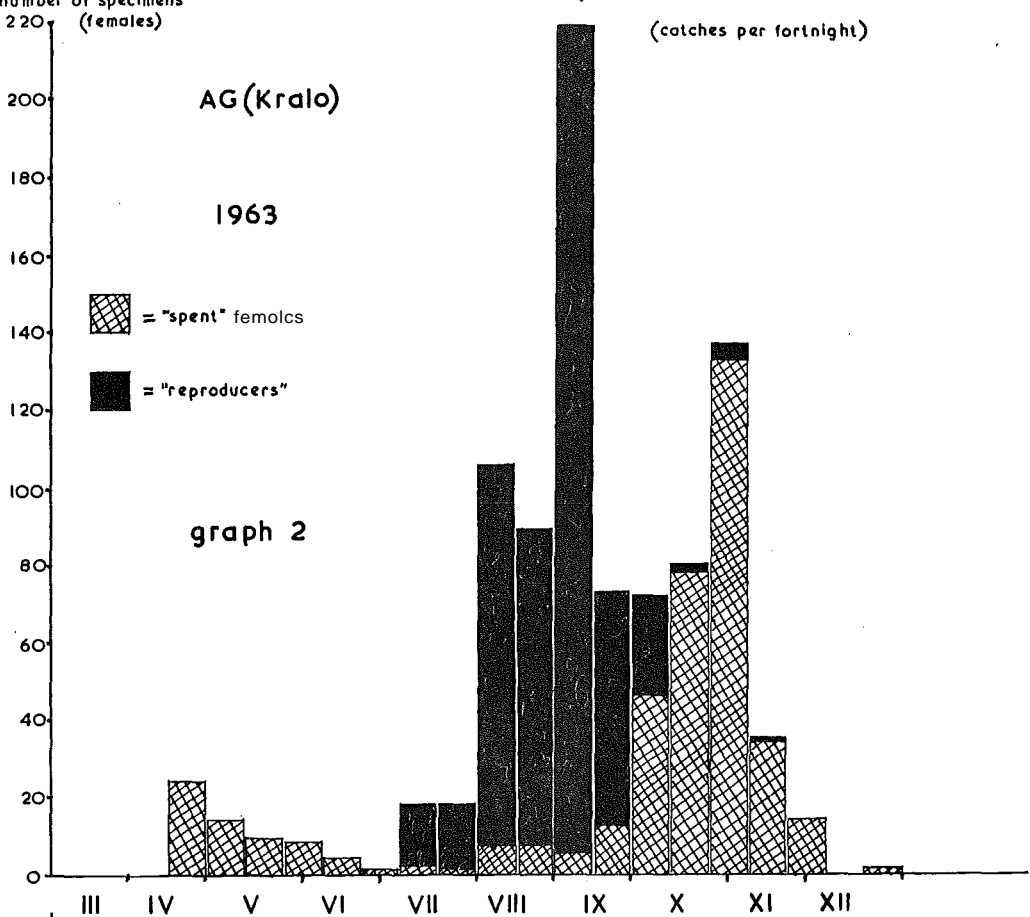
(catches per fortnight)

AG (Kralo)

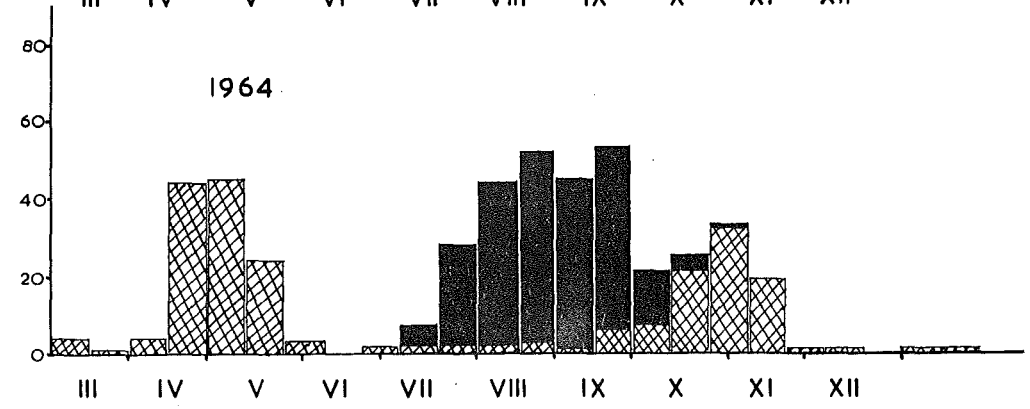
1963

 = "spent" females
 = "reproducers"

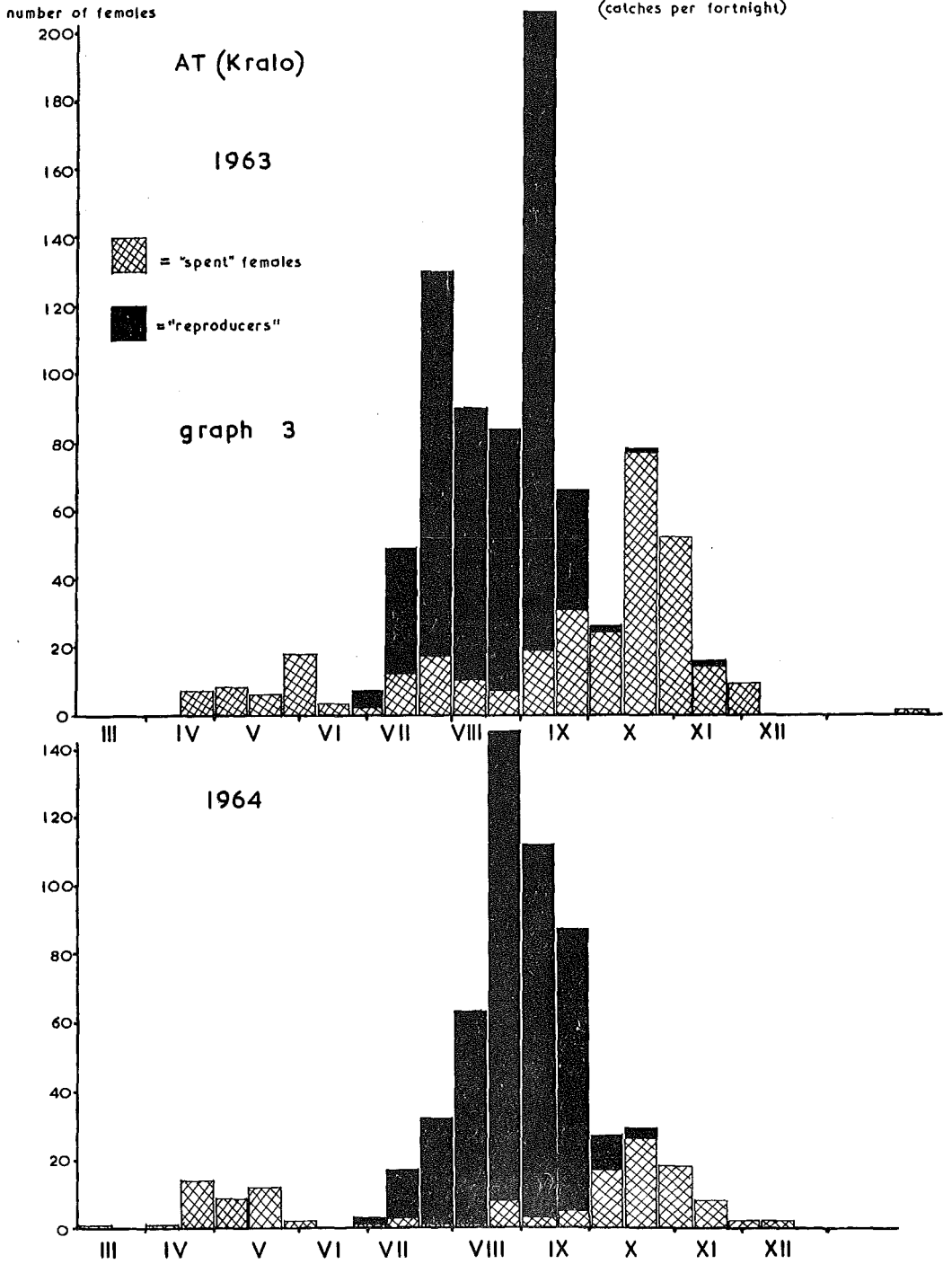
graph 2



1964



Calathus melanocephalus L.



Calathus melanocephalus L.

(catches per fortnight)

males

AG (Kralo)

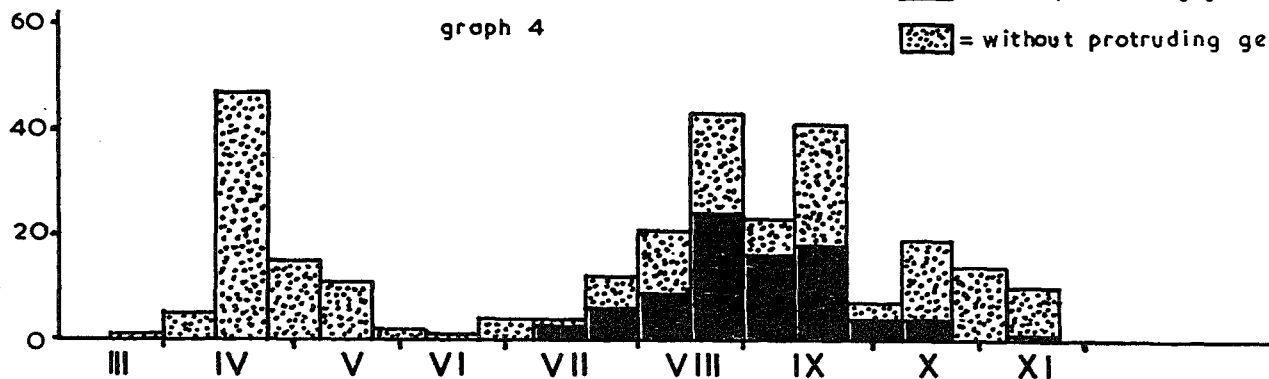
1964

number of males

graph 4

■ = with protruding genitalia

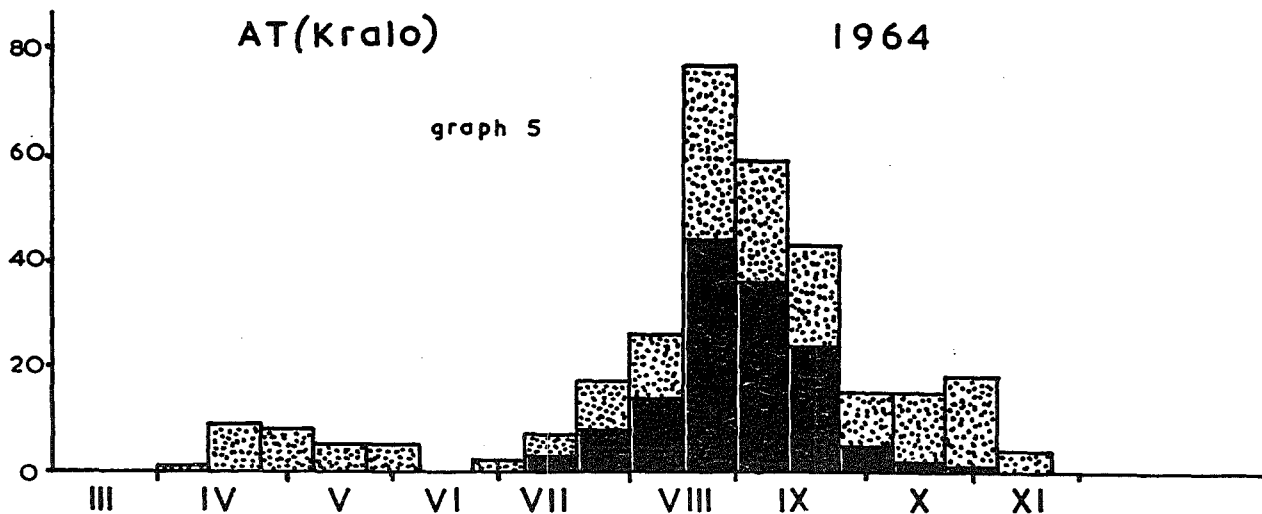
▨ = without protruding genitalia

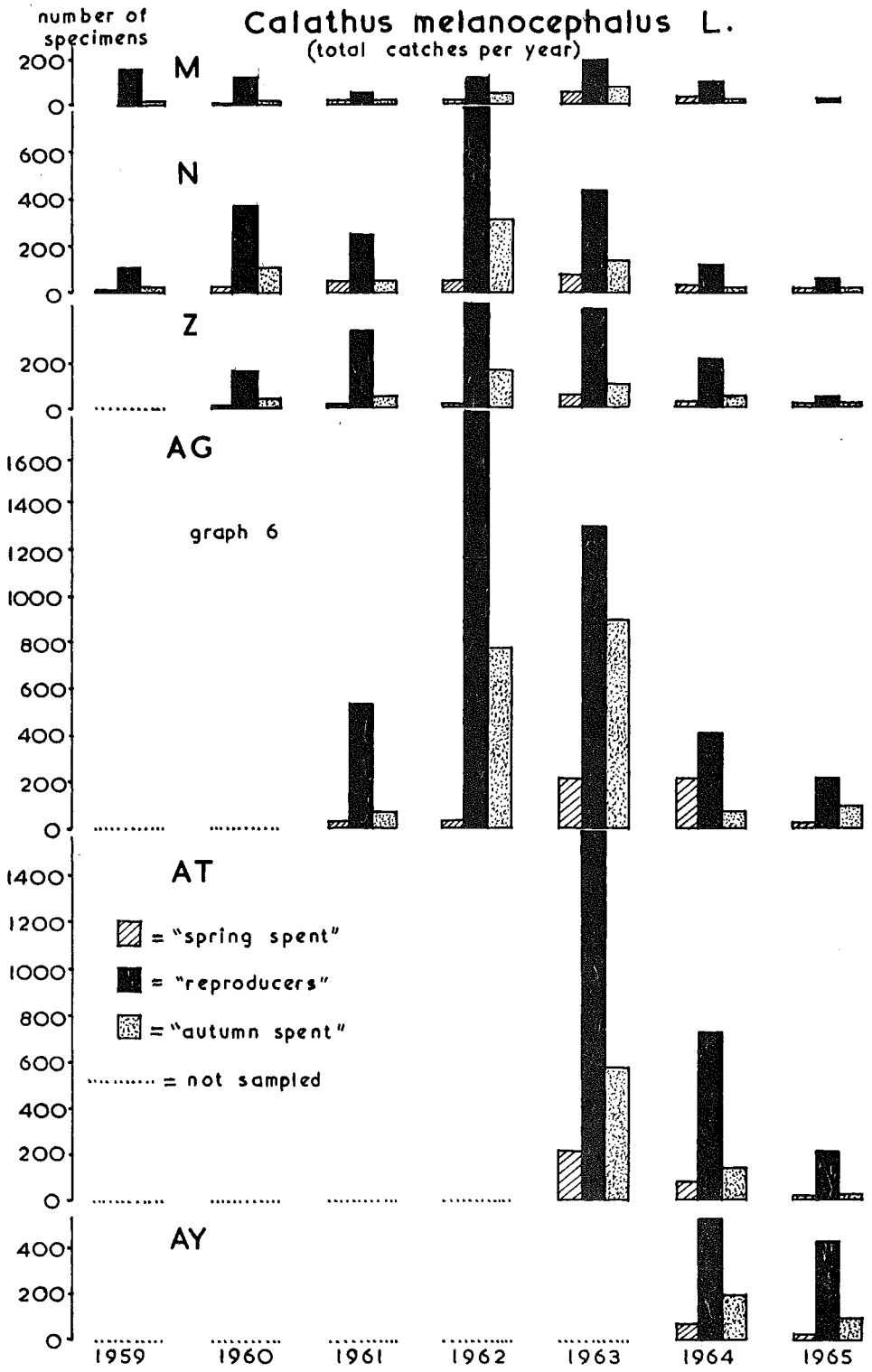


AT (Kralo)

1964

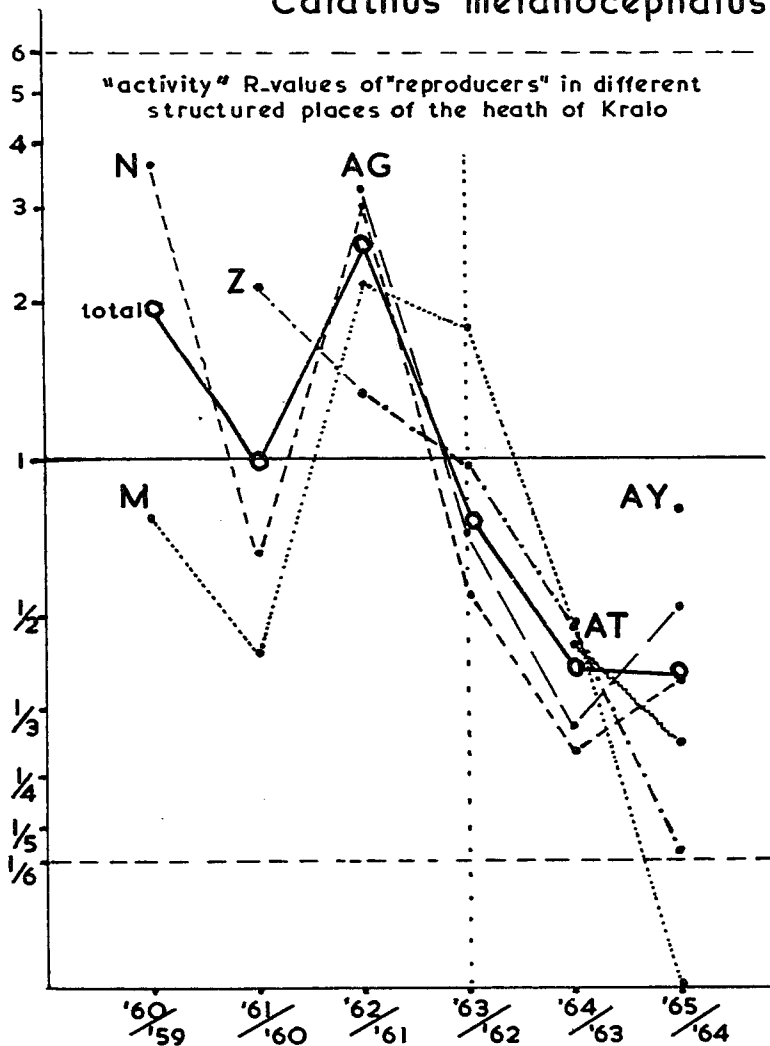
graph 5





Calathus melanocephalus L.

R

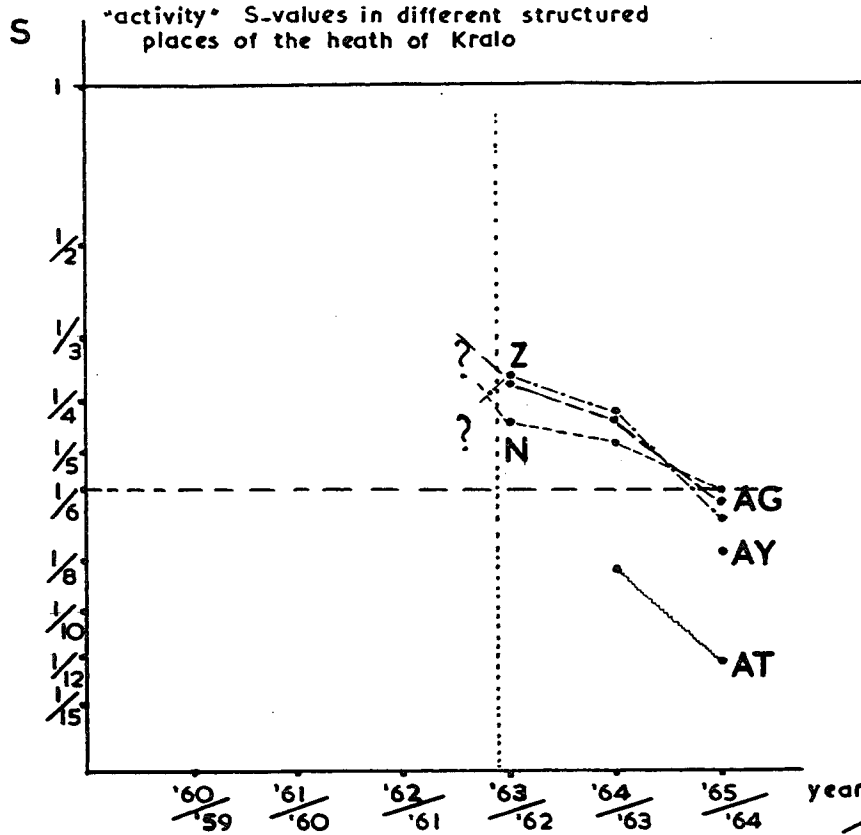


"reproducers" caught in year n
 "reproducers" caught in year n-1
 (= "activity" R-values)

'60/'59	'61/'60	'62/'61	'63/'62	'64/'63	'65/'64	
3.70	0.67	3.06	0.55	0.28	0.38	N
0.78	0.43	2.14	1.78	0.49	0.10	M
	2.13	1.33	0.97	0.48	0.18	Z
		3.30	0.73	0.31	0.52	AG
				0.45	0.29	AT
					0.80	AY
2	3	4	4	5	6	number of places sampled
1.95	0.98	2.64	0.75	0.40	0.38	total

graph 7

Calathus melanocephalus L.



"spring spent" caught in year n
 "autumn spent" caught in year n-1
 (= "activity" S-values)

'63/'62	'64/'63	'65/'64	
0.23	0.21	0.17	N
0.28	0.24	0.15	Z
0.27	0.23	0.16	AG
	0.12	0.08	AT
		0.13	AY

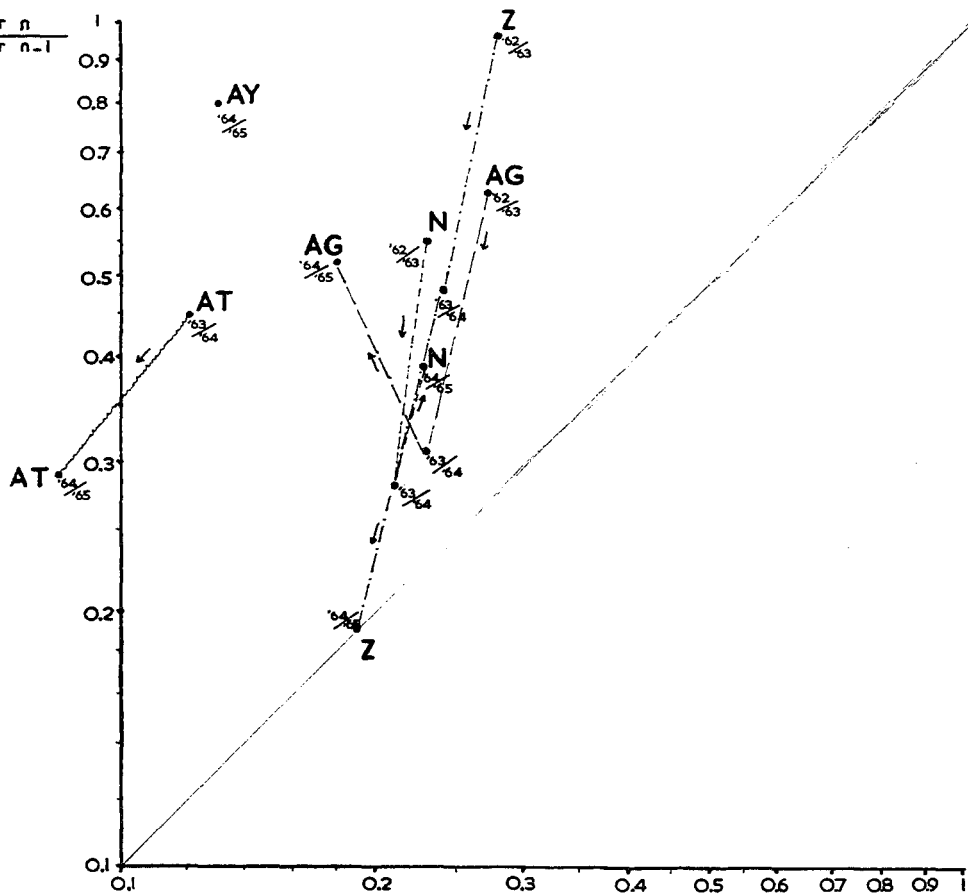
graph 8

Calathus melanocephalus L.

$$R = \frac{\text{"reproducers" year } n}{\text{"reproducers" year } n-1}$$

(graph 7)
 (= larval + pupal survival)

graph 9



$$S = \frac{\text{"spring spent" year } n}{\text{"autumn spent" year } n-1}$$

(graph 8)
 (= spent survival)

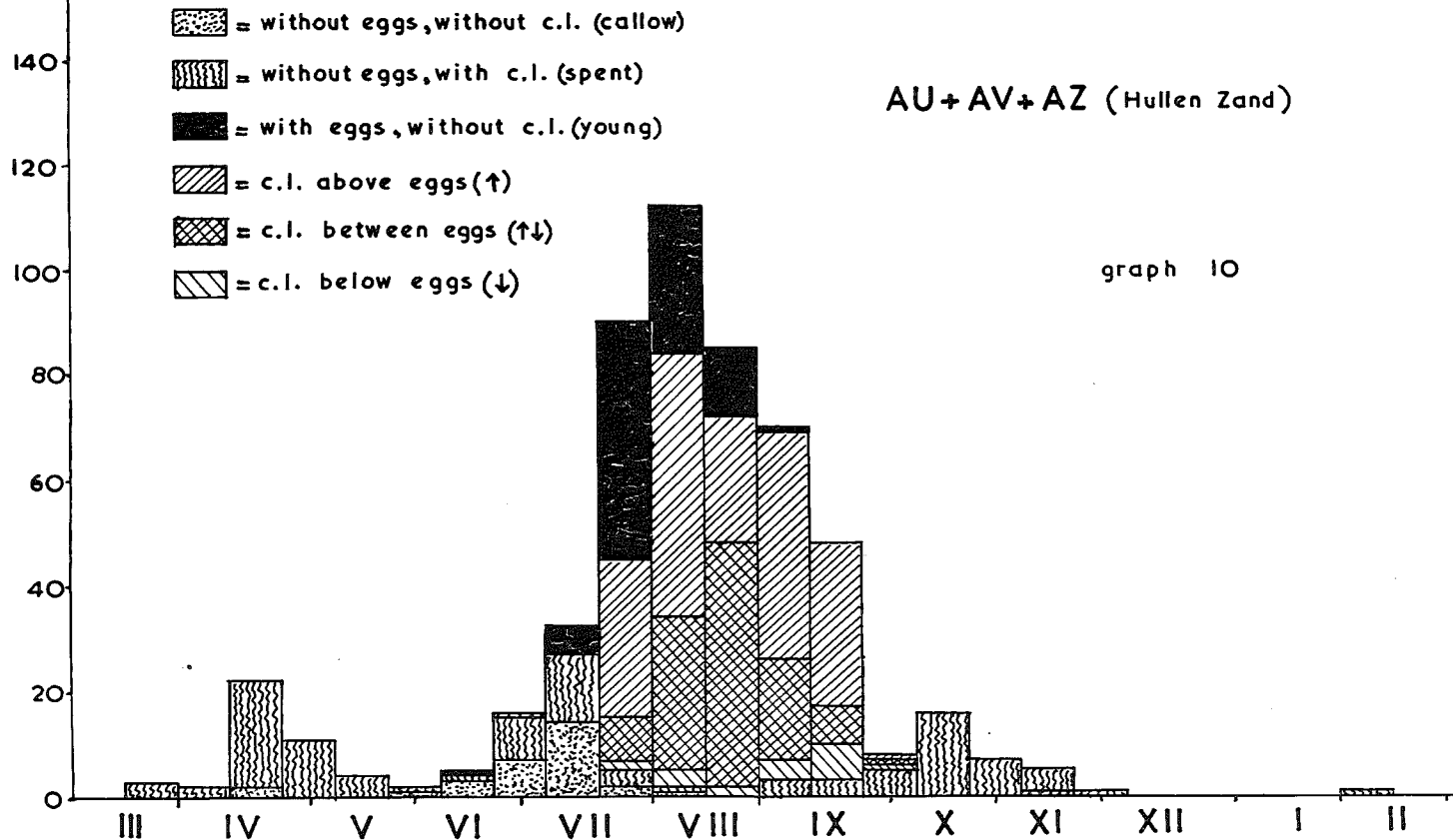
Calathus erratus Sahlb.
(catches per fortnight)

540 females

1964

AU+AV+AZ (Hullen Zand)

number of females



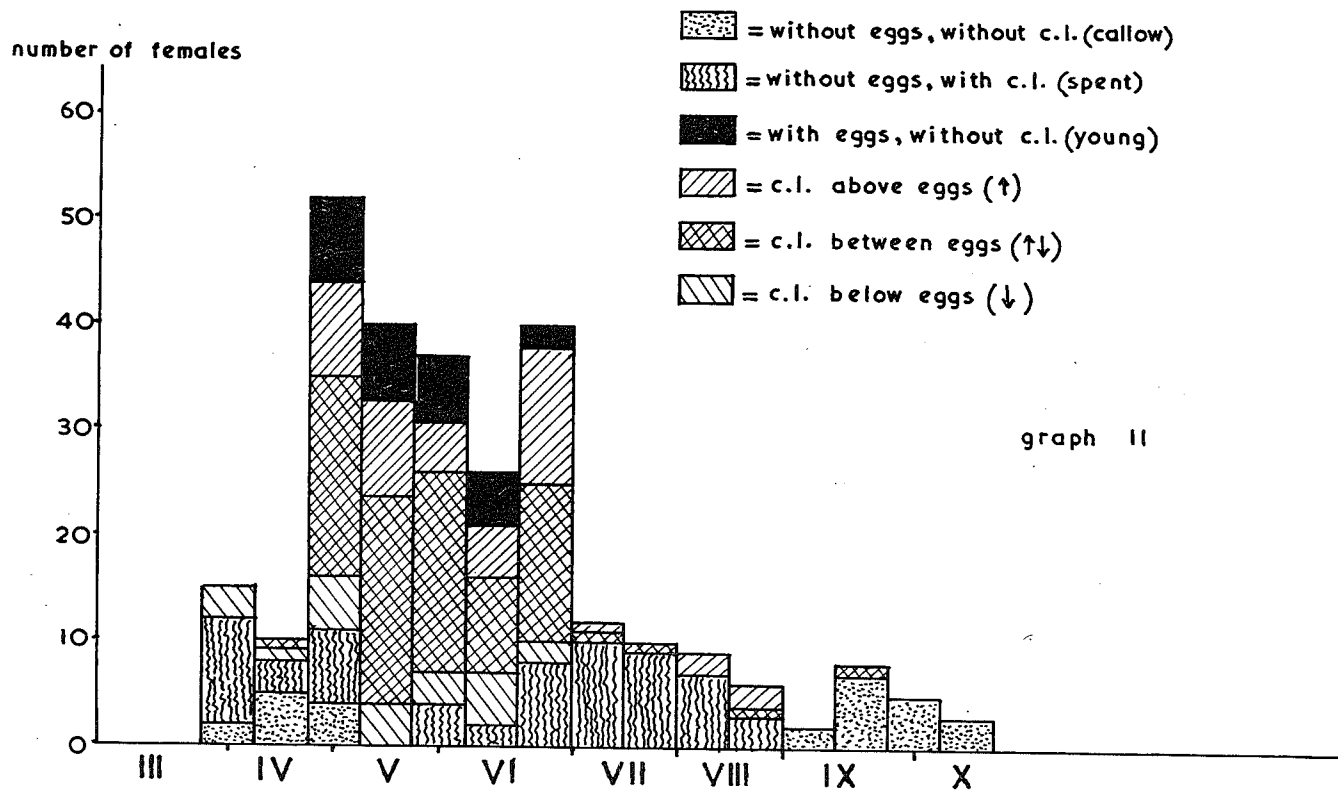
graph 10

Pterostichus coeruleus L.
(catches per fortnight)

275 females

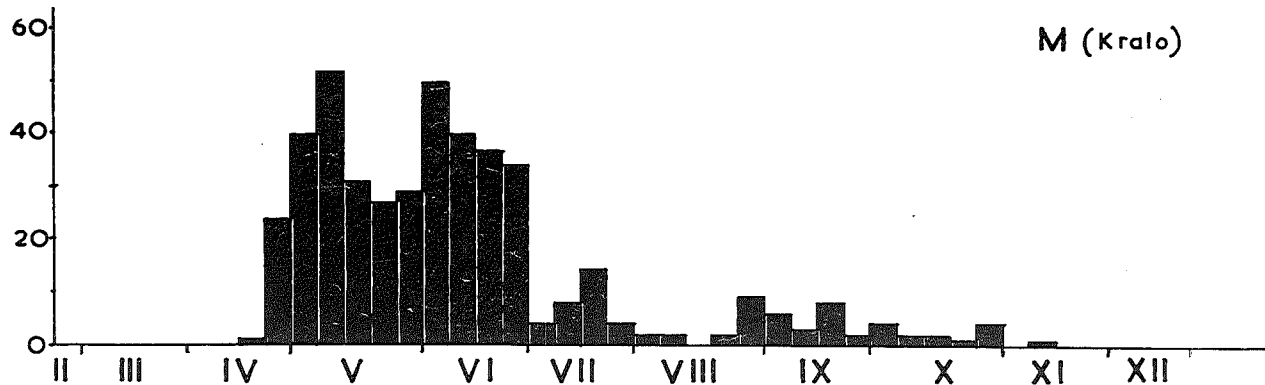
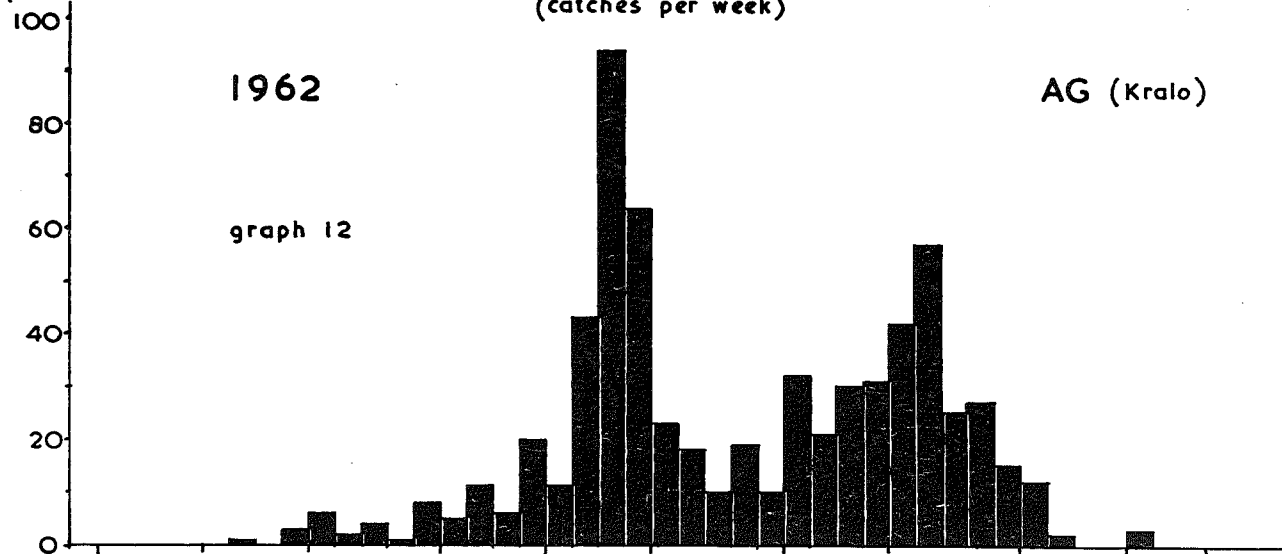
1965

BB (Kralo)



number of
specimens

Amara lunicollis Schödte
(catches per week)



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ZOO-ECOLOGICAL RESEARCH AT THE BIOLOGICAL STATION
WIJSTER (DRENTE)

P.J. den Boer

(Communication of the Biological Station, Wijster, No.131).

The problem of the current zoological work can be formulated as follows: "which are the most important factors that determine the fitting into and the distribution over a number of habitats in the populations of carabid beetles?" The relation between these habitat-determining factors and a population will not be a static one: the intensity of the factors generally will vary from place to place and from moment to moment (especially meteorological and biotic factors); within the population sensibility and behaviour will vary from individual to individual and also in time. Hence, the problem formulated above is a statistic one: a problem of "ecological" variability in space and time within populations in relation with variability in space and time of the habitat-determining factors.

To get information about the distribution of populations of carabid beetles in space in a number of environments there is uninterrupted trapping with the help of pitfalls (the samples are collected each week). By continuing trapping over a number of years (in some environments it was already started in 1959) information about shifts of the quantitative distribution over a number of environments of some carabid populations may become available, and may be compared with changes in the (micro) climatic conditions from year to year. After a number of years it will be possible in some cases to make suggestions on the identity of the habitat-determining factors, after which experiments must be carried out to prove the concerning working hypothesis. By working in this way during six years I got the impression that the most important habitat-determining factors for most carabid species in the neighbourhood of Wijster are: moisture condition of the substratum during critical periods of the life-cycle (e.g. the larval stage) and structure of the habitat (especially vegetation). Not only habitat-selection in particular species and its shifts from year to year but also the

"suitability" of some environments for carabid species as a whole can be "understood" with the help of these factors: some examples will be shown and discussed at the "Kralose Veld" (Heath of Kralo). Technics for estimating these factors as quantitatively as possible - including their variability in space and time - are being developed. Large numbers of stomach-contents are collected on slides in order to learn something about the possible part played by food in habitat-selection.

The greater the individual variability in timing of the life-cycle and in tolerance for factors which fluctuate continuously in intensity (e.g. moisture conditions and other (micro) climatic factors) the greater the probability that the population will survive periods with extreme conditions. This principle of "risk-distribution" is no doubt an important factor in the "stabilization of animal numbers" (a paper on the theoretical significance of "risk-distribution" in population dynamics is in preparation). Some populations of carabid beetles in the investigated area show interesting forms of "risk-distribution", e.g. the wood-species Pterostichus oblongopunctatus F. in which different morphological forms show a different sensibility for the moisture condition of the litter ("genetic risk-distribution"). With this species experiments are going on to prove this working-hypothesis. At the "Kralose Veld" Calathus melanocephalus L. lives in a number of different types of vegetation: in some years the subpopulations in "dense" vegetations (e.g.: Molinia), in other years the subpopulations in more "open" vegetations, (e.g.: mosaics of Calluna, Erica, Empetrum, Nardus, Festuca, etc. etc. with many "open" places more or less covered with Cladonia-species), are relatively favoured ("risk-distribution" in space). In populations of Calathus melanocephalus a group of individuals hibernates in the larval stage and another group in the beetle stage. There are strong indications that in a "closed" vegetation of Nardus the survival of hibernating larvae is much greater than in an "open" mosaic-vegetation, whereas the survival of hibernating beetles should just be the other way round ("risk-distribution" in time). By studying the ovaria of the caught females (with or without developing eggs, with or without "corpora-lutea", "spent", reproducing for the first or for the second time, etc.) we try to disentangle the different reproducing groups which compose the population in varying proportions. These problems on Calathus melanocephalus will be discussed more fully at the Biological Station, Wijster and as far as possible be demonstrated in the field.