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FLUCTUATIONS IN MORPH FREQUENCY IN CATCHES OF THE GROUND BEETLE PTEROSTICHUS OBLONGOPUNCTATUS F. AND ITS ECOLOGICAL SIGNIFICANCE

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When for many years I started to identify insects I wondered how it was possible that most characters on which insect species are separated taxonomically are so subtle. It was impossible to me to imagine that small differences in form and surface-structure of the clypeus, in the venation of wings, in the surface-structure of the elytra in beetles and of the scutellum in Hymenoptera, etc. could have any selective value. But at the same time selection must have worked highly on such characters, since most insect species can only be identified unmistakably with the help of these subtle characters. Hence, I concluded that selection must have worked indirectly on them and I expected these characters to be closely connected with important vital properties and in this way to be indicators for them. The indirect selective value of such indicators must even be more important than the direct value of many striking morphological properties, since the former generally are more rigidly separated in closely related species than the latter.

To be able to demonstrate the indirect selective value of such a character I had to look for an indicator which showed a measurable variation, since it might be expected that variations of such a character are correlated with different levels of the vital property, i.e. that these variations have different indirect selective values. Such an indicator was found in the number of pits on the elytra of the ground beetle Pterostichus oblongopunctatus F.

+ Afdeling van het Laboratorium voor Plantensystematiek en geografie van de Landbouwhogeschool, Wageningen.

The number of pits on each elytron is generally used as a character to separate the ground beetles (*Carabidae*) *Pterostichus oblongopunctatus* F.: 4-7(-12) pits (very rarely 3) and *P.angustatus* Dfts.: 3 pits (very rarely 2 or 4) (Figs.1 and 2). *P.oblongopunctatus* is an exclusive wood-species which, however, is found in many different types of wood. Early in spring the beetles leave their winter-shelters and reproduce. During about May-August the larvae develop in the litter of the woods and to start with August/September the young beetles emerge, which after some time are going to hibernate (Figs.3 and 4).

In the years 1959, 1960, 1961, 1962, 1963[*] large numbers of *P.oblongopunctatus* were caught in different types of wood with the help of catch-boxes. The number of pits on the left elytron of all hibernated specimens caught (March-August) was noted.

As is illustrated here by Habitat B (Fig.5) the greater part of specimens (80-90%) show 5 or 6 pits on each elytron, whereas also some specimens with 4, 7 or 8 pits and only very few specimens with 3, 9 or 10 pits on each elytron are found.

Since the quantitative distribution of "4-pitters" follows that of "5-pitters" and the quantitative distribution of "7-, 8-, etc.-pitters" follows that of "6-pitters" for the sake of simplicity in the following "4- and 5-pitters" are taken together as "low-pitters" and "6-, 7-, 8-, etc.-pitters" are taken together as "high-pitters". The Figure also shows that from 1959 to 1960 the percentages of "4- and 5-pitters" (the so-called "low-pitters") increased and the percentages of "6-, 7-, 8-, etc.-pitters" (the so-called "high-pitters") decreased; this shift is highly significant. From 1960 to 1961 the percentage of "low-pitters" somewhat decreased and the percentage of "high-pitters" somewhat increased; this shift, however, is only small and not yet significant. From 1961 to 1962 the percentage of "low-pitters" decreased again and the percentage of "high-pitters" increased again; this shift is significant.

Thus, from 1959 to 1960 selection has worked in favour of the "low-pitters" and from 1961 to 1962 and perhaps also

[*] Data of 1963 are afterwards added to the text of the paper and to the Figures (to the latter not in allcases).

from 1960 to 1961 selection has worked in favour of the "high-pitters". In all other habitats where the catches were continued during a number of years about the same phenomenon was observed (e.g. Fig.6). The statistical significances of these shifts are summarized in the Table (Fig.7). This Table shows that for all habitats taken together the shifts from 1959 to 1960 and from 1961 to 1962 are highly significant, whereas the shift from 1960 to 1961 is not significant. On the whole the percentage of "high-pitters" shows a rising trend in the order 1960 (30,3%), 1961 (33,4%), 1959 (38,6%), 1963 (43,8%), 1962 (44,3%), [*] which trend is highly significant (p= $0{,}0^{6}9$, trend-test of TERPSTRA); only the shifts from 1960 to 1961 and from 1962 to 1963 (not in the Table) obviously are too small to be statistically demonstrable, but they do not disturb the significance of the trend.

This trend in the percentage of "high-pitters" (or "low-pitters") appears to be correlated with a trend in the moisture condition of the substratum during the period of larval development, i.e.: between the top of the catches and the emergence of young specimens in the preceding year (about May-August: see Figs. 3 and 4). The moisture condition of the substratum (litter)is expressed in the form of the amount of precipitation during the months May-August (Fig.8): The summer of 1958 was very wet (38% of precipitation above normal) and this corresponds with 38,6% of "high-pitters" in 1959; the summer of 1959 was extremely dry (46% of precipitation below normal) and was followed by a significant decrease of the percentage of "high-pitters" (from 38,6% to 30,3%) in 1960. The dryness of the summer of 1959 held -although less severely- during the winter 1959/1960 and during the spring of 1960 until July-August and hence, the litter which was dried up during the summer of 1959 was not thoroughly wetted again before July-August 1960 (Fig.9). Thus, the larvae developed partly in dried up and partly in wetted litter and this inhomogeneous conditions could not be expected to result in a

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[*] Data of 1963 are afterwards added to the text of the paper and to the Figures (to the latter not in all cases)

distinct and significant shift of the percentage of "high-pitters". The summer of 1961 was very wet again (37% of precipitation above normal) and was followed by a highly significant increase of the percentage of "high-pitters" (from 33,4% to 44,3%) in 1962. The summer of 1962 had about the normal amount of precipitation (90% of normal) and was not followed by a shift in the percentage of "high-pitters". The resemblance between the trend in the percentage of "high-pitters" and the trend in the amount of precipitation during the period of larval development is summarized in Fig.8 (with the number of rainy days - $>$ 1 mm of precipitation- we should have reached about the same results).

If the sensibility of the larvae for the moisture condition of the litter really is genetically connected with the number of pits, each shift of the percentage of "high-pitters" starts from a level which is reached under the influence of the amount of precipitation during the preceding generation. Thus, in that case the influence of the amount of precipitation must be cumulative. If we compare (Fig.10) the trend in the cumulative deviation from the normal amount of precipitation with the trend in the percentage of "high-pitters" the resemblance indeed is very nice (τ = +1,00; p= 0,0163, n= 5). In Fig.11 the different expressions for the moisture condition of the litter during the larval period are plotted against the percentage of "high-pitters" to show the nearly complete correlation between the latter and the cumulative expressions for the moisture condition of the litter.

From the foregoing the hypothesis emerges: The number of pits on the elytra of the ground beetle P.oblongopunctatus is closely connected (genetically) with the sensibility of the larvae for the moisture condition of the litter, and thus: a shift in the frequency of the "pit-varieties" indicates the quantitative effect of a selection against moisture-sensibility which has occurred within the population.

The substratum in which the larvae develop, is the litter of the woods and since the structure of the layer of litter will influence its moisture condition, some relation between the structure of the layer of litter and the percentage of "low-pitters" (or "high-pitters") may be expected. In this strain obviously the correlation between the percentage of "low-pitters" and the thickness of the layer of litter (only broad-leaved woods) must be interpreted (Fig.12): In 1959 a correlation of $\tau = +0,600$ was found, in 1961 a correlation of $\tau = +0,524$ and in 1962 a correlation of $\tau = +0,429$ (these three years taken together gives: $\bar{\tau} = +0,518$; $p = 0,01016$)(1963 gave a correlation of $\tau = +0,469$). A thin layer of litter will more thoroughly be wetted by rain than a thick layer and hence, in a thick layer of litter "low-pitter"-larvae obviously will find relatively more suitable places than in a thin layer. This especially will occur of course during rainy summers, i.e.: during the summers of 1958, 1960 and 1961 (30-38% of precipitation above normal) and not during the summer of 1959 (46% of precipitation below normal). In accordance with this in 1960 no correlation ($\tau = +0,048$) was found.

Since in a thick layer of litter generally a more complete moisture-gradient will exist than in a thin layer, larvae with a different moisture-preferendum generally will have a greater chance to find suitable places in a thick layer than in a thin one and hence, in a thick layer of litter under normal or moist weather conditions larvae of *P.oblongopunctatus* on the whole will have a greater chance to survive than in a thin layer. In accordance with this a correlation is found (Fig. 13) to exist between the thickness of the layer of litter and catch-numbers (within one year a relative measure of effective density): In 1959 a correlation of $\tau = +1,00$ is found, in 1961 a correlation of $\tau = +0,810$ and in 1962 a correlation of $\tau = +0,810$ (these three years taken together gives: $\bar{\tau} = +0,873$; $p < 0,000066$) (1963 gave a correlation of $\tau = +0,867$). In 1960 no correlation was found ($\tau = -0,067$) because a difference in level is appeared between dry woods (on drift-sand) and moist woods (on loam or loamy sand): relative to the thickness of the layer of litter catch-numbers were much lower in the dry than in the moist woods (the same phenomenon can be observed in the data of 1959, 1961 and 1962, but here the differences in level are too small to disturb the correlations). Perhaps under the influence of the dry summer of 1959 conditions for the development of the larvae were less favourable in the litter of dry woods than in the litter of moist woods, e.g. because as a consequence of the severe dryness a greater part of the litter has become unhabitable for the larvae in the dry woods than in the moist woods (in this way the effective thickness of the layer of litter is more reduced in dry than in moist woods). If this is true one could expect to find a higher percentage of "low-pitters" in the catches of 1960 in dry woods than in moist woods (the "low-pitters" are relatively favoured by dry conditions). But this expectation is not realized (see Fig.12): in moist and in dry woods "low- and high-pitters" are influenced to the same extent by the measured thickness of the layer of litter, although catch-numbers are not so and perhaps are influenced by the effective thickness of the layer of litter. Obviously density is influenced by other environmental conditions than the frequency of the different "pit-varieties". The fact that in the different years catch-numbers are not correlated with the moisture condition of the litter during the larval period points into the same direction (Fig.14).

Although many details are still obscure and most relations need experimental test, one point seems clear to me: a population of P.oblongopunctatus is able to cope with a continuously fluctuating environmental factor (moisture of the litter) by distributing sensibility for that factor over a range of phenotypes, the extent of the range being determined by the values of the factor reached in each habitat; in other words: the effect of the fluctuating environmental factor is continuously more or less intercepted by the ecological "polymorphism" of the population.

In my opinion this principle of "risk-distribution" by means of polymorphism to cope with continuously fluctuating environmental factors must be wide-spread among animal populations and it may underlie many other forms of polymorphism too.

Probably among students on polymorphism this principle is already well-known, but since I am not yet familiar with the literature on polymorphism it is new to me and in that case I hope that these data on P.oblongopunctatus will be of interest to you as another example of risk-distribution.

Of course this principle of "risk-distribution" also contributes to the quantitative stability of the population and in this way to its chance of survival and hence, the building up of forms of polymorphism based on this principle will be favoured by selection.

Fig. 1

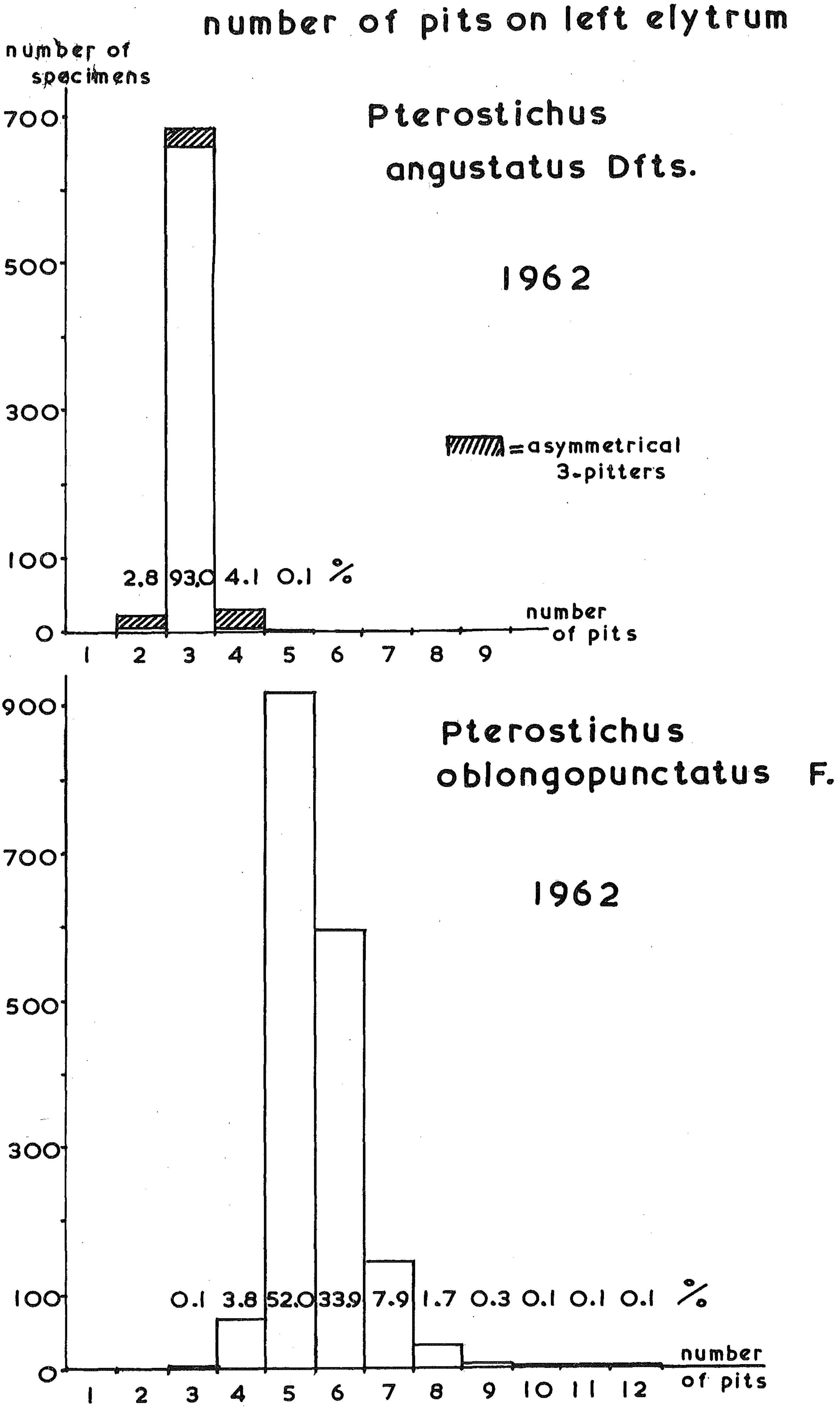
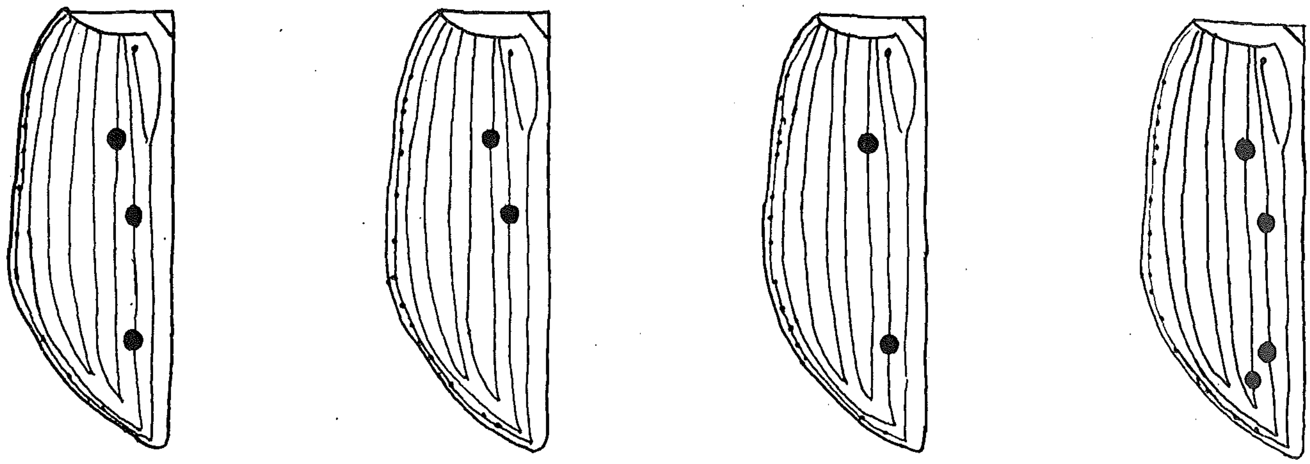
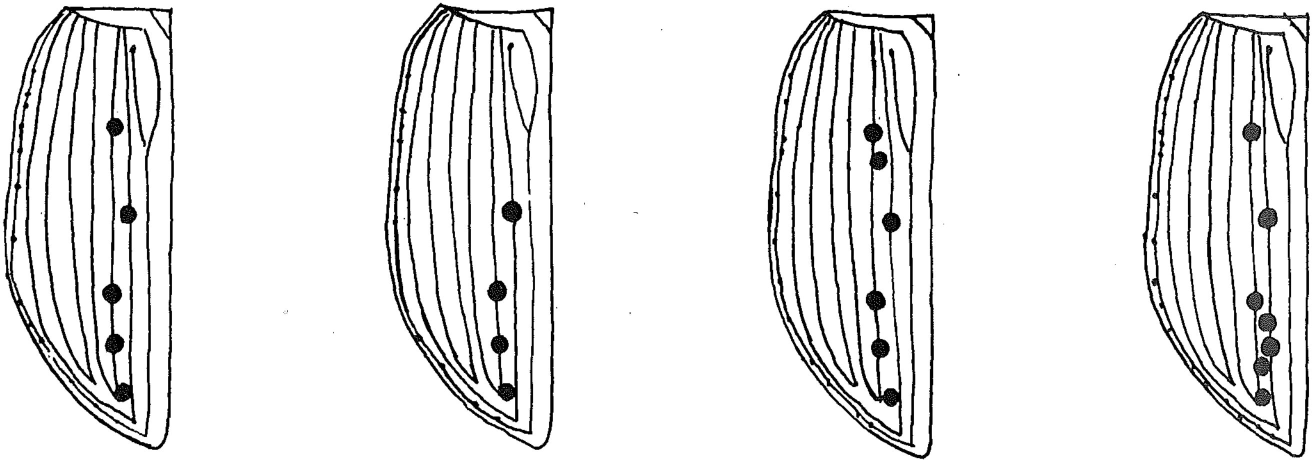

number of pits on left elytrum
number of specimens
Pterostichus angustatus Dfts.
1962
▨ = asymmetrical 3-pitters
700
500
300
100
0
2.8 93.0 4.1 0.1 %
number of pits
1 2 3 4 5 6 7 8 9
Pterostichus oblongopunctatus F.
1962
900
700
500
300
100
0
0.1 3.8 52.0 33.9 7.9 1.7 0.3 0.1 0.1 0.1 %
number of pits
1 2 3 4 5 6 7 8 9 10 11 12

Fig. 2

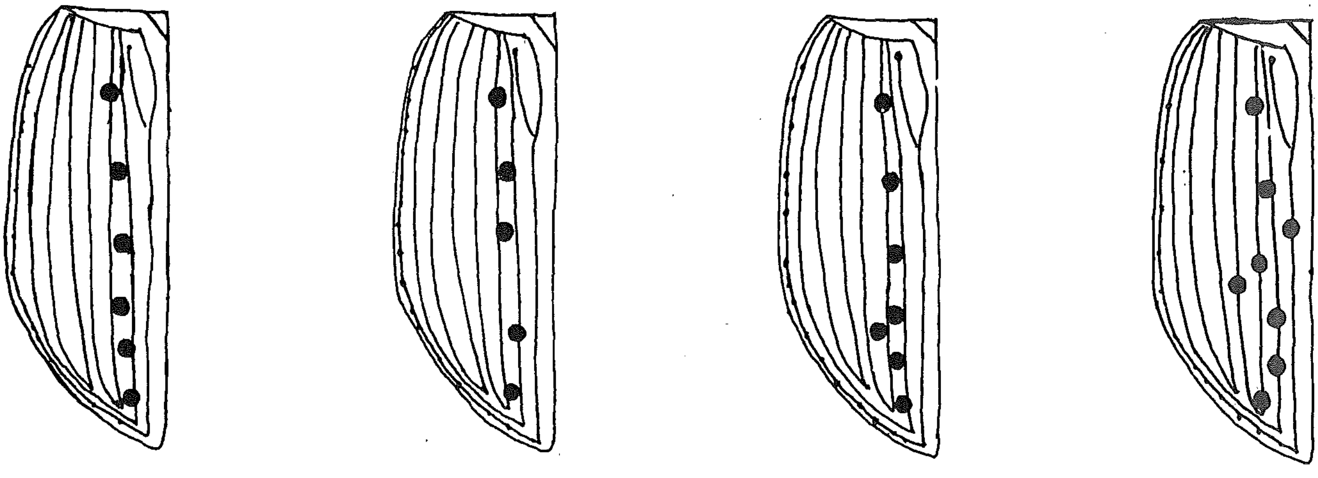
Pterostichus angustatus Dfts.



Pterostichus oblongopunctatus F.



pattern of 5-pitters



pattern of 6-pitters

Fig. 3

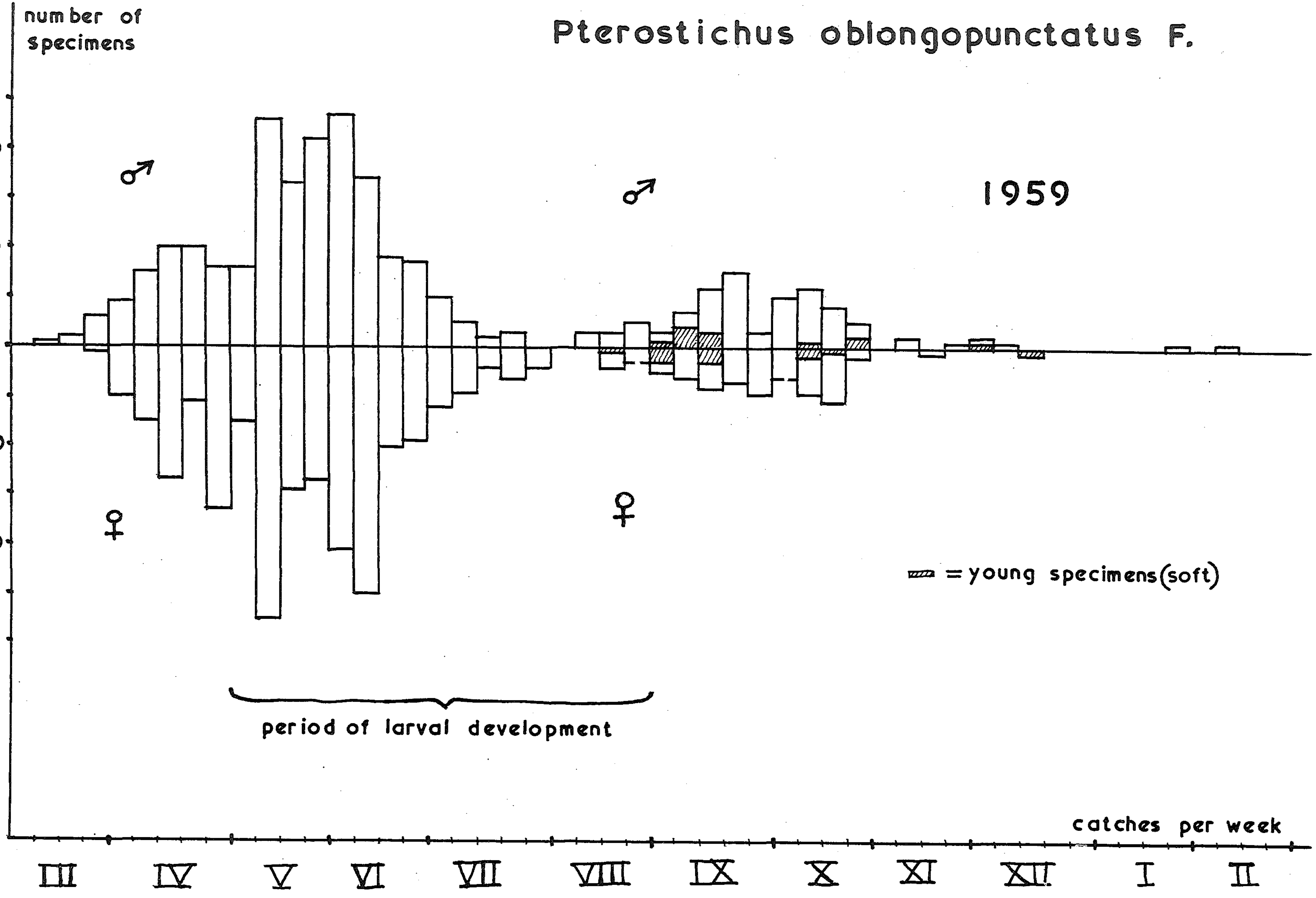

Pterostichus oblongopunctatus F.
1959
number of specimens
40
20
0
20
40
♂
♀
♂
♀
▨ = young specimens (soft)
period of larval development
catches per week
III
IV
V
VI
VII
VIII
IX
X
XI
XII
I
II

Fig. 4

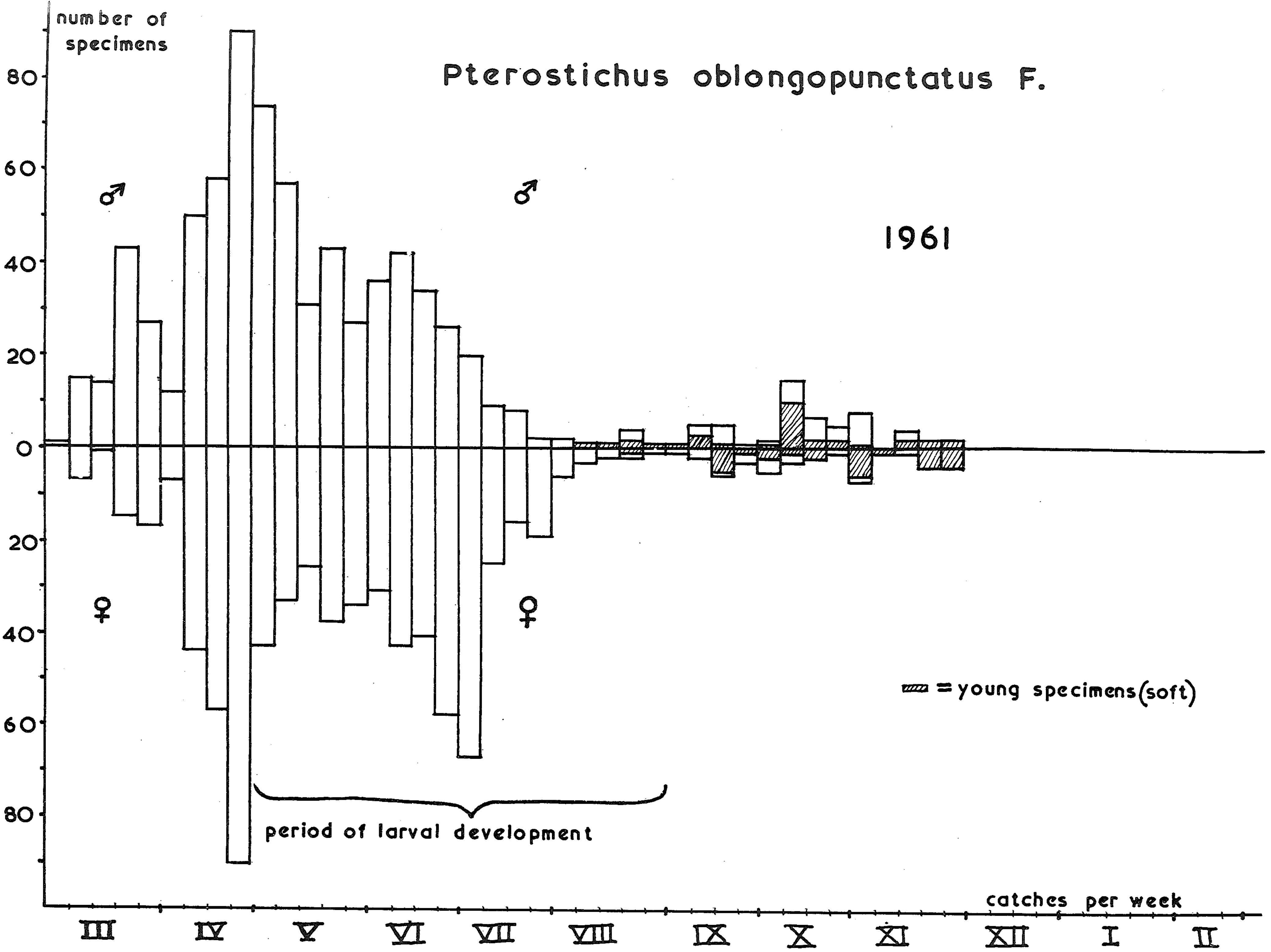

number of specimens
Pterostichus oblongopunctatus F.
1961
♂
♂
♀
♀
80
60
40
20
0
20
40
60
80
▨ = young specimens (soft)
period of larval development
catches per week
III
IV
V
VI
VII
VIII
IX
X
XI
XII
I
II

Fig. 5

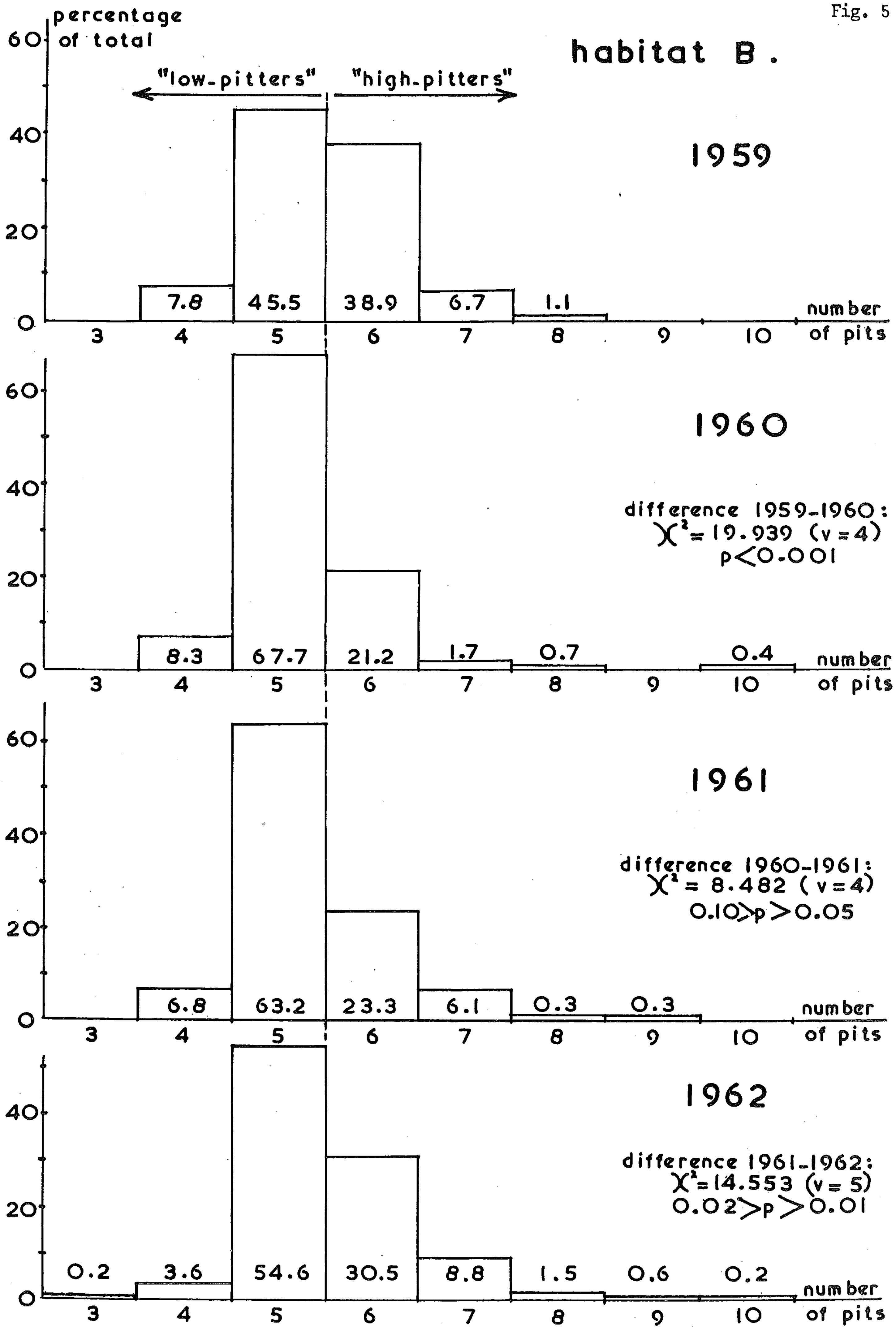

habitat B.
percentage of total
"low-pitters"
"high-pitters"
1959
7.8
45.5
38.9
6.7
1.1
number of pits
3
4
5
6
7
8
9
10
0
20
40
60
1960
difference 1959-1960:
$\chi^2 = 19.939$ (v = 4)
$p < 0.001$
8.3
67.7
21.2
1.7
0.7
0.4
1961
difference 1960-1961:
$\chi^2 = 8.482$ (v = 4)
$0.10 > p > 0.05$
6.8
63.2
23.3
6.1
0.3
0.3
1962
difference 1961-1962:
$\chi^2 = 14.553$ (v = 5)
$0.02 > p > 0.01$
0.2
3.6
54.6
30.5
8.8
1.5
0.6
0.2

Fig. 6

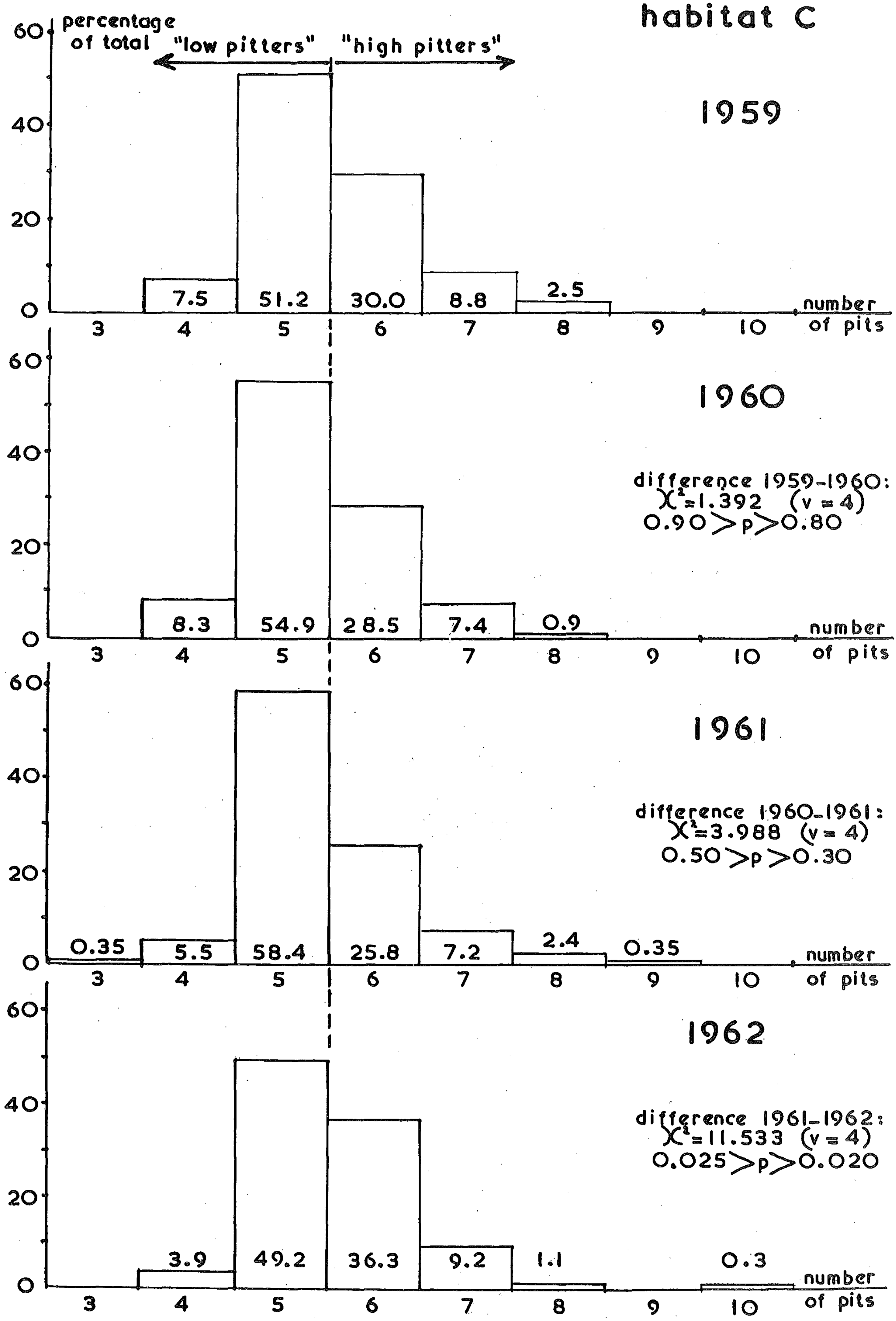
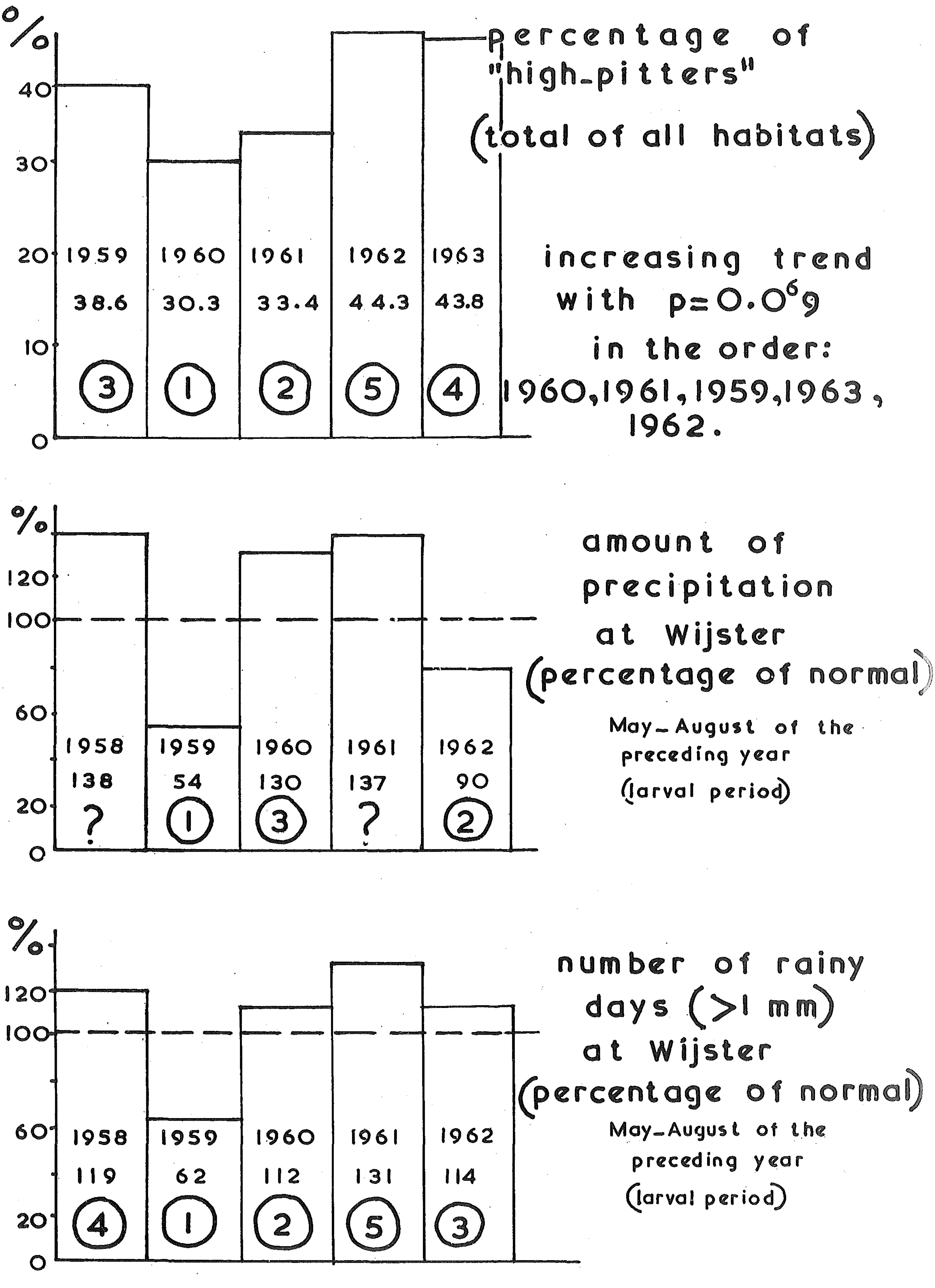

habitat C
percentage of total
"low pitters"
"high pitters"
1959
60
40
20
0
7.5
51.2
30.0
8.8
2.5
3
4
5
6
7
8
9
10
number of pits
1960
difference 1959-1960:
$\chi^2 = 1.392$ ($v = 4$)
$0.90 > p > 0.80$
60
40
20
0
8.3
54.9
28.5
7.4
0.9
3
4
5
6
7
8
9
10
number of pits
1961
difference 1960-1961:
$\chi^2 = 3.988$ ($v = 4$)
$0.50 > p > 0.30$
60
40
20
0
0.35
5.5
58.4
25.8
7.2
2.4
0.35
3
4
5
6
7
8
9
10
number of pits
1962
difference 1961-1962:
$\chi^2 = 11.533$ ($v = 4$)
$0.025 > p > 0.020$
60
40
20
0
3.9
49.2
36.3
9.2
1.1
0.3
3
4
5
6
7
8
9
10
number of pits

Fig. 7

statistical significance of the snift from one year to another of the quantitative distribution of catched specimens of Pterostichus oblongopunctatus Fbr. over different "pit-variations"

habitat	from 1959 to 1960	from 1960 to 1961	from 1961 to 1962
B	$\chi^2 = 19.939$ $P < 0.001$	$\chi^2 = 8.482$ $0.10 > P > 0.05$	$\chi^2 = 14.553$ $0.02 > P > 0.01$
C	$\chi^2 = 1.392$ $0.90 > p > 0.80$	$\chi^2 = 3.988$ $0.50 > p > 0.30$	$\chi^2 = 11.533$ $0.025 > P > 0.02$
G	$\chi^2 = 5.511$ $0.20 > P > 0.10$	$\chi^2 = 2.086$ $0.70 > P > 0.50$	
C + G	$\chi^2 = 3.651$ $p \approx 0.30$		
X		$\chi^2 = 0.164$ $0.99 > P > 0.95$	$\chi^2 = 15.101$ $P \approx 0.005$
B+C+G	$\chi^2 = 17.665$ $P \approx 0.001$	$\chi^2 = 5.573$ $0.30 > p > 0.20$	
B+C+X		$\chi^2 = 5.875$ $0.50 > P > 0.30$	$\chi^2 = 31.13$ $P < 0.001$
all habitats together	$\chi^2 = 24.241$ $P < 0.001$	$\chi^2 = 7.356$ $p \approx 0.20$	$\chi^2 = 46.84$ $P < 0.001$

Fig. 8


percentage of "high-pitters" (total of all habitats)

increasing trend with $p = 0.0^{6}9$ in the order: 1960, 1961, 1959, 1963, 1962.

amount of precipitation at Wijster (percentage of normal)

May-August of the preceding year (larval period)

number of rainy days (>1 mm) at Wijster (percentage of normal)

May-August of the preceding year (larval period)

Fig. 9

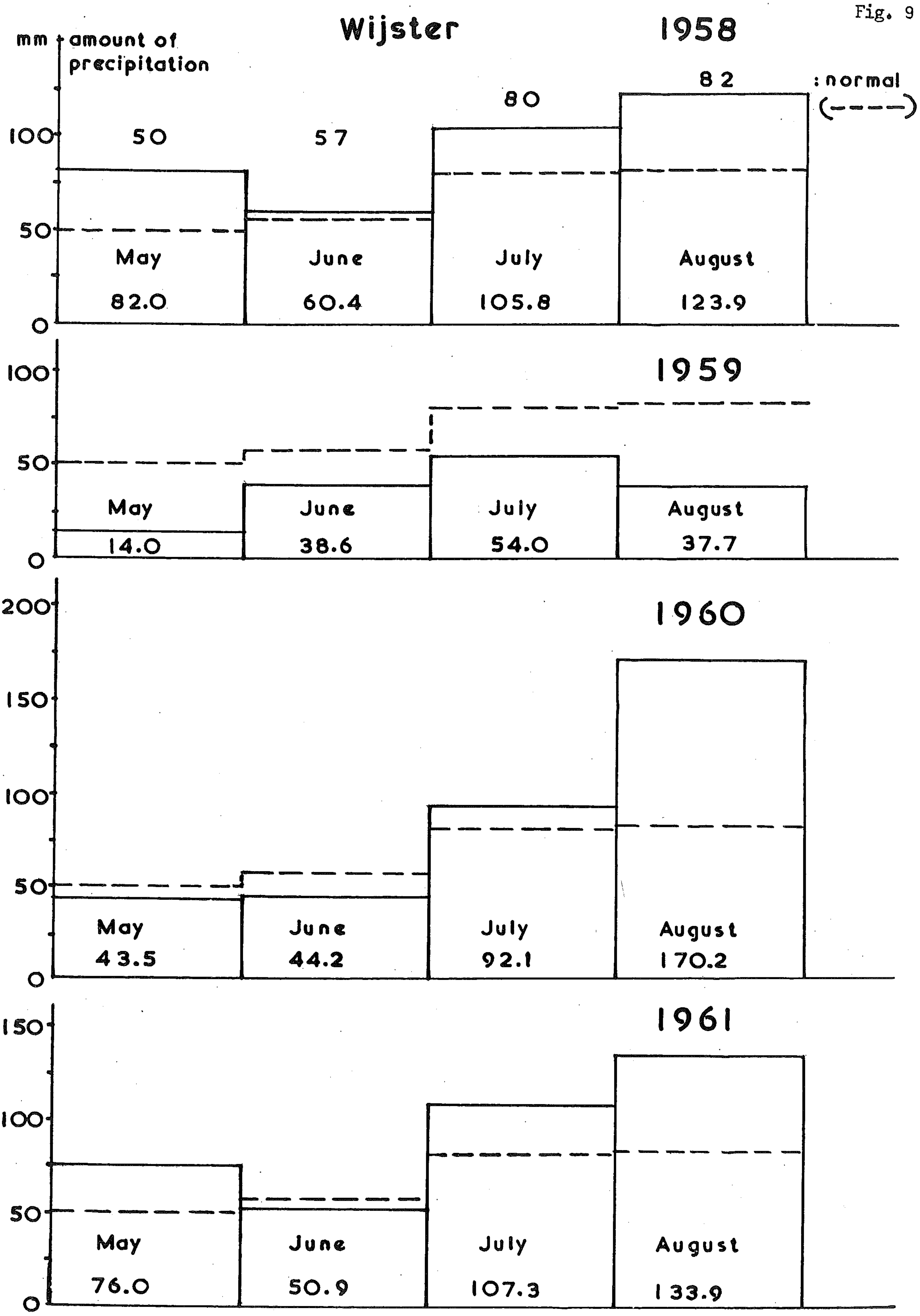
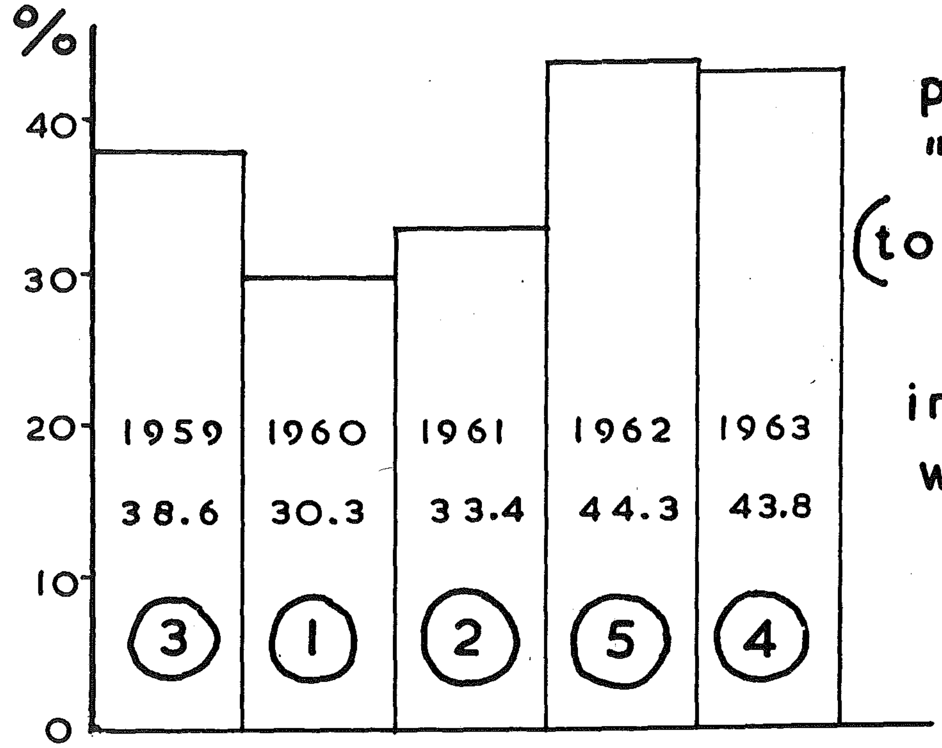
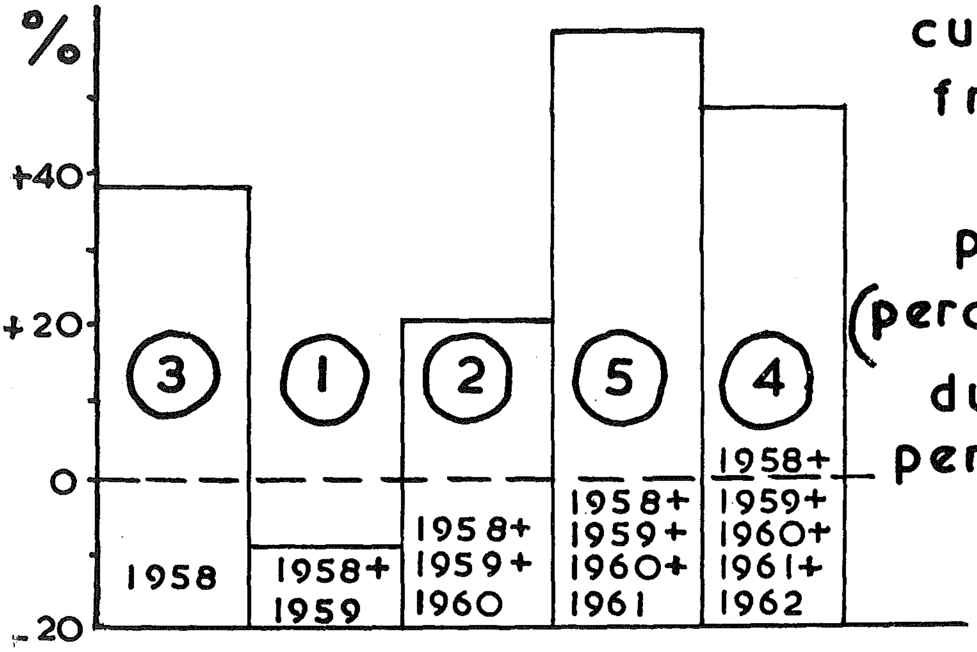

Wijster
1958
mm
amount of precipitation
: normal (----)
0
50
100
50
57
80
82
May
82.0
June
60.4
July
105.8
August
123.9
1959
0
50
100
May
14.0
June
38.6
July
54.0
August
37.7
1960
0
50
100
150
200
May
43.5
June
44.2
July
92.1
August
170.2
1961
0
50
100
150
May
76.0
June
50.9
July
107.3
August
133.9

Fig. 10

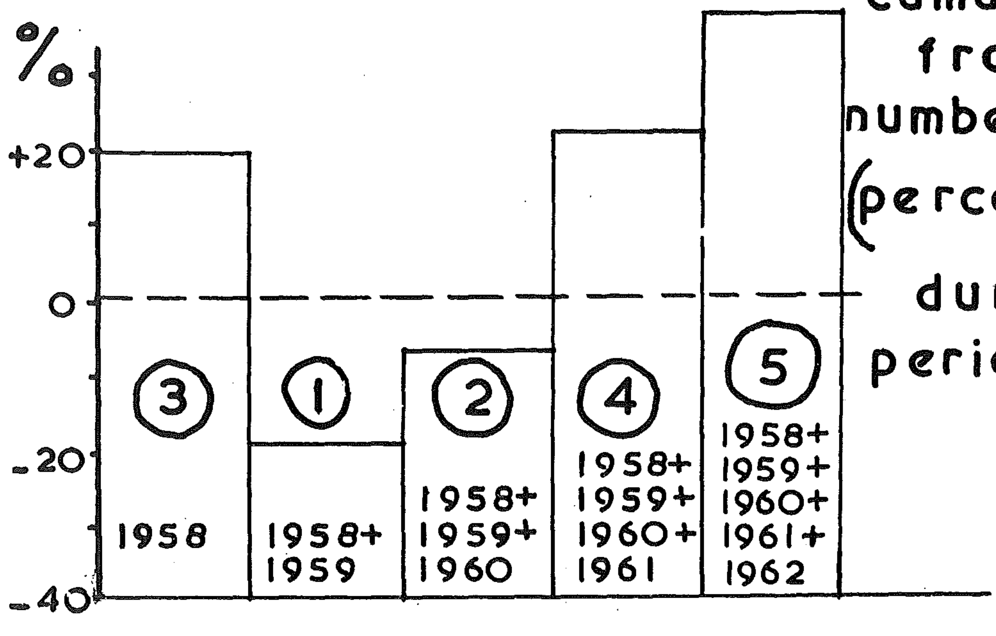


percentage of "high-pitters" (total of all habitats)

increasing trend with $p=0.0^{6}9$ in the order: 1960, 1961, 1959, 1963, 1962.

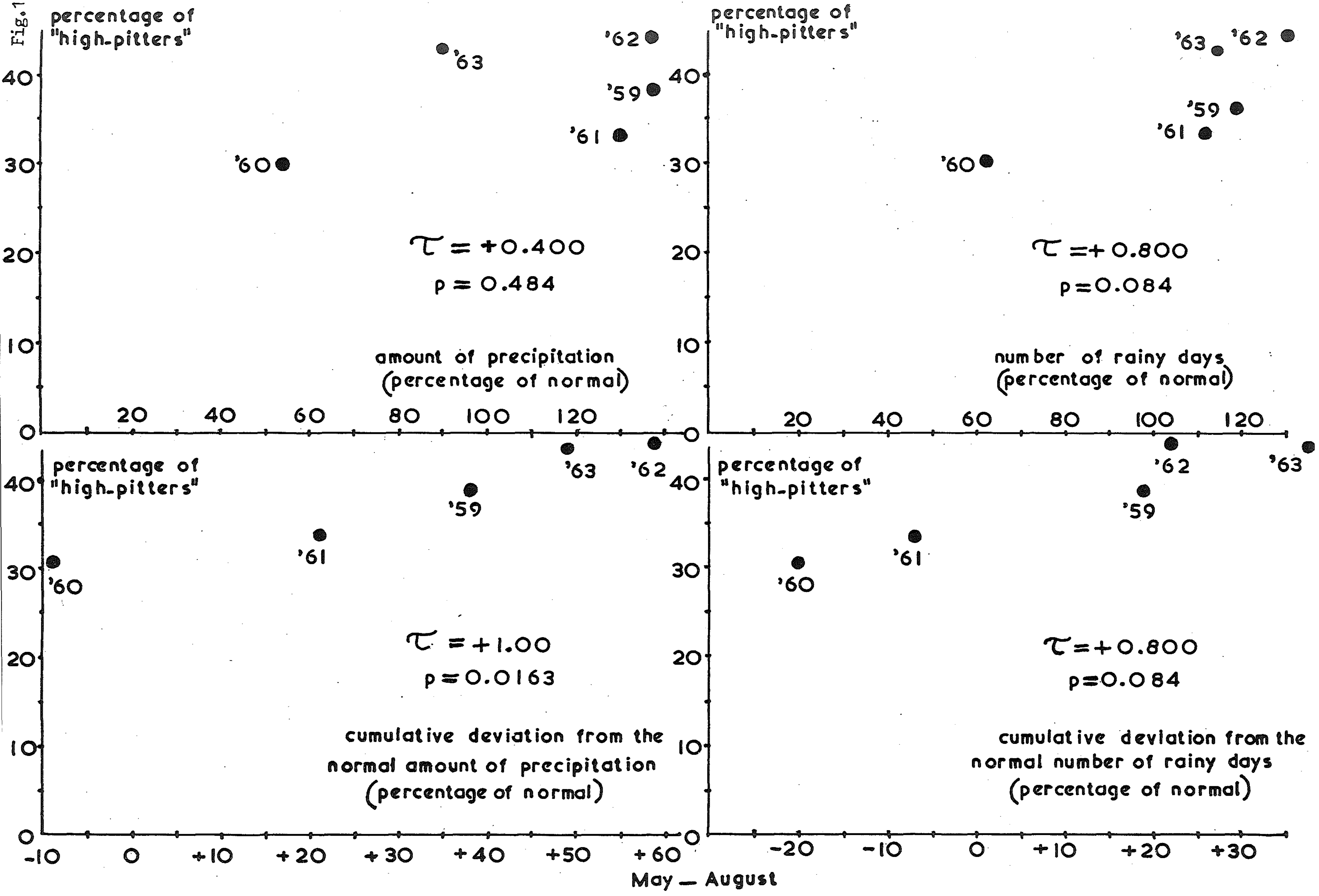


cumulative deviation from the normal amount of precipitation (percentage of normal) during the larval period (May-August)



cumulative deviation from the normal number of rainy days (percentage of normal) during the larval period (May-August)

Fig. 11



percentage of "high-pitters"
40
30
20
10
0
'62
'63
'59
'61
'60
τ = +0.400
p = 0.484
amount of precipitation (percentage of normal)
20
40
60
80
100
120
percentage of "high-pitters"
'63
'62
'59
'61
'60
τ = +0.800
p = 0.084
number of rainy days (percentage of normal)
percentage of "high-pitters"
'63
'62
'59
'61
'60
τ = +1.00
p = 0.0163
cumulative deviation from the normal amount of precipitation (percentage of normal)
-10
0
+10
+20
+30
+40
+50
+60
percentage of "high-pitters"
'62
'63
'59
'61
'60
τ = +0.800
p = 0.084
cumulative deviation from the normal number of rainy days (percentage of normal)
-20
-10
0
+10
+20
+30
May — August

Fig. 12

broad-leaved woods

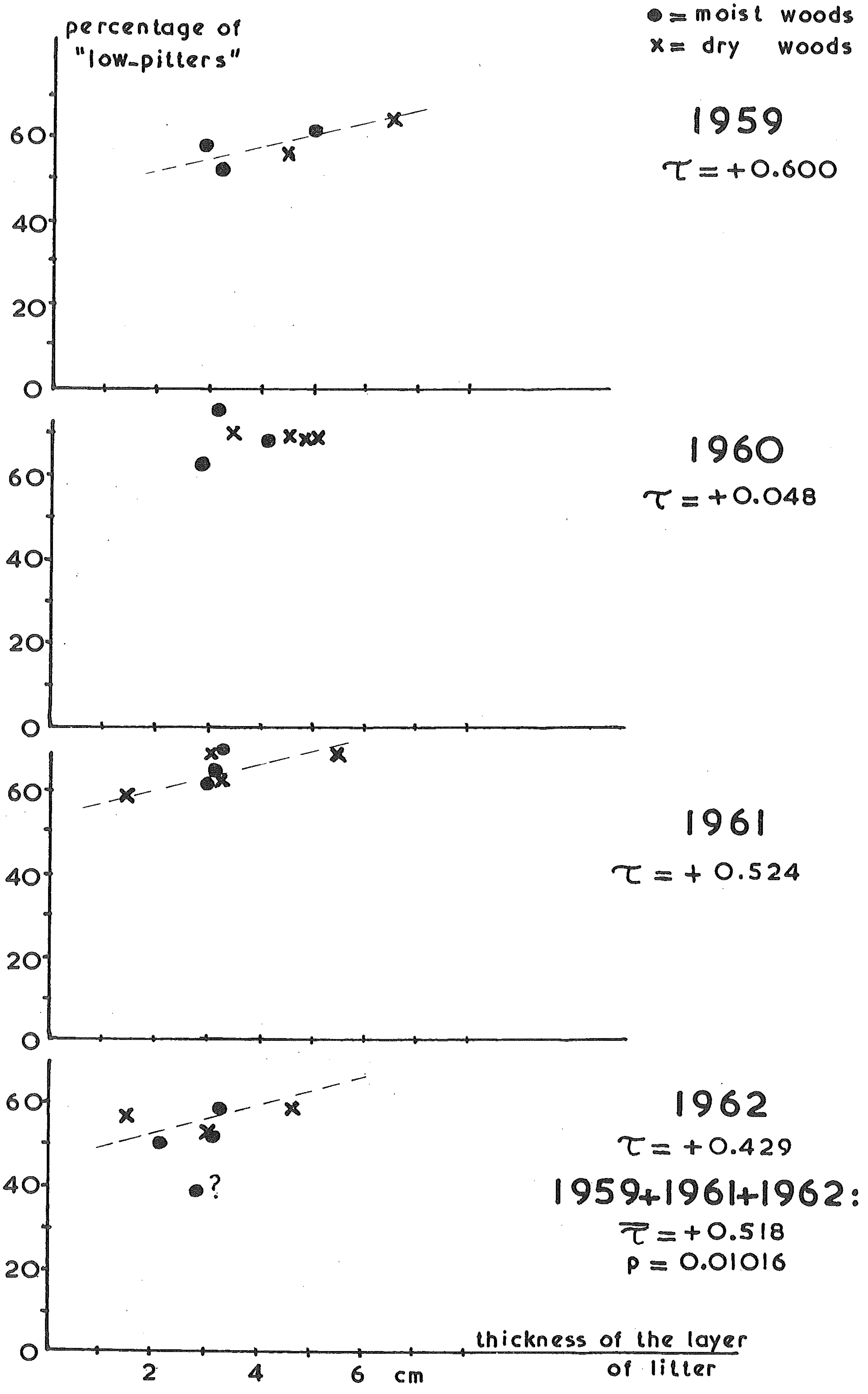
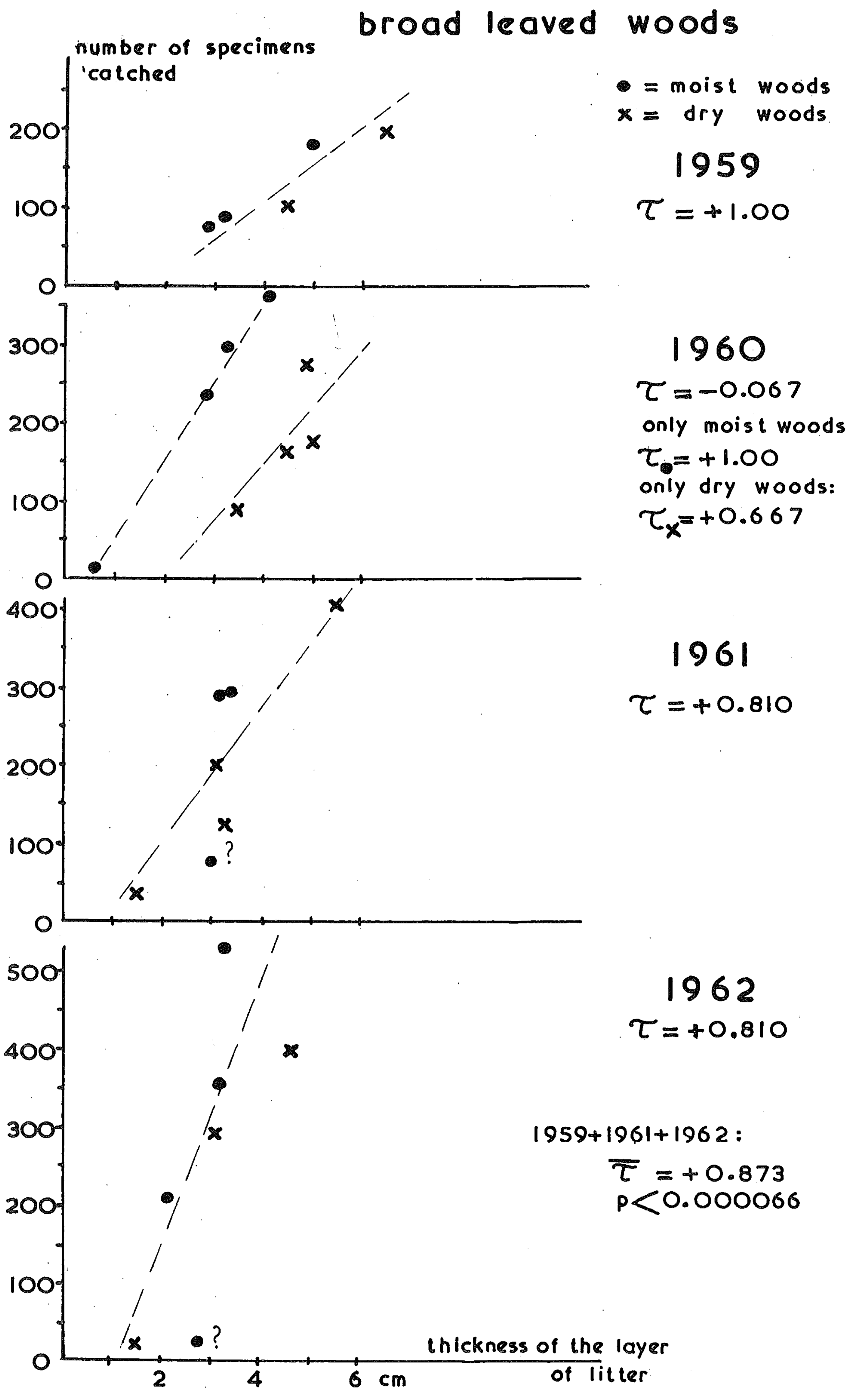
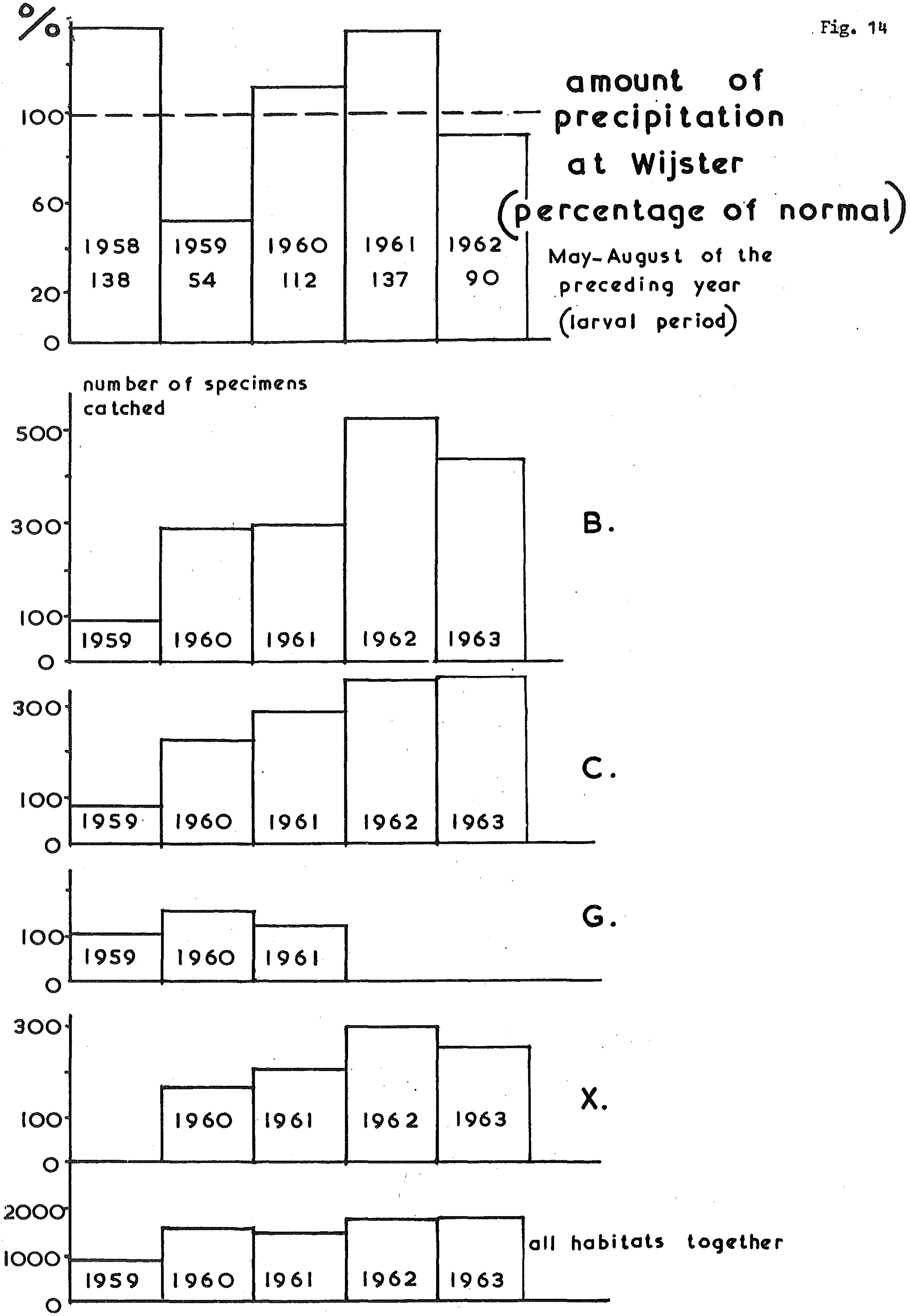


Fig. 13



broad leaved woods
number of specimens 'catched
● = moist woods
x = dry woods
1959
$\tau = +1.00$
1960
$\tau = -0.067$
only moist woods:
$\tau_{\bullet} = +1.00$
only dry woods:
$\tau_{x} = +0.667$
1961
$\tau = +0.810$
1962
$\tau = +0.810$
1959+1961+1962:
$\bar{\tau} = +0.873$
$p < 0.000066$
?
?
0
100
200
300
400
500
2
4
6 cm
thickness of the layer of litter

Fig. 14


%
100
60
20
0
1958
138
1959
54
1960
112
1961
137
1962
90
amount of precipitation at Wijster (percentage of normal)
May-August of the preceding year (larval period)
number of specimens catched
500
300
100
0
1959
1960
1961
1962
1963
B.
300
100
0
1959
1960
1961
1962
1963
C.
100
0
1959
1960
1961
G.
300
100
0
1960
1961
1962
1963
X.
2000
1000
0
1959
1960
1961
1962
1963
all habitats together

Reprint of the Abstract circulated among the members of the Conference.

THE SHIFT FROM YEAR TO YEAR OF THE PROPORTION OF DIFFERENT MORPHOLOGICAL FORMS IN CATCHES OF THE GROUND-BEETLE PTEROSTICHUS OBLONGOPUNCTATUS F. AND ITS ECOLOGICAL SIGNIFICANCE.

P.J. den Boer

Many characters by which insect species are separated taxonomically are thought, by some, not to have a direct selective value (e.g.: form and surface-structure of the clypeus, venation of wings, surface-structure of the elytra in beetles and of the scutellum in Hymenoptera, etc.). But such characters must have an important indirect selective value, since in separating the species selection must have worked highly on them. Thus, such characters (indicators) generally will be connected with important vital properties of the organism.

If such a character shows variability it may be expected that the different variats are correlated with different levels of this vital property, i.e. that the variats have different indirect selective values.

The number of pits on each elytron is generally used as a character to separate the ground-beetles (Carabidae) Pterostichus angustatus Dfts. (3 pits) and P.oblongopunctatus F. (4-7(-10) pits). In the years 1959, 1960, 1961 and 1962 a total of 5620 individuals of Pterostichus oblongopunctatus F. were trapped in different types of woods. The number of pits on the left elytron of each specimen caught was noted.

Most of the specimens (80-90%) show 5 or 6 pits on each elytron. Since the quantitative distribution of "4-pitters" follows that of "5-pitters" and the quantitative distribution of "7-, 8-, etc.-pitters" follows that of "6-pitters" for the sake of simplicity in most calculations "4- and 5-pitters" are taken together as "low-pitters" and "6-, 7-, 8-, etc.-pitters" are taken together as "high-pitters".

In this way the quantitative relations between the different "pit-variations" can be shortly characterized in the form of the percentage of "low-pitters" (or "high-pitters") for each habitat and for each year separately.

This percentage of "low-(or high-)pitters" shows a characteristic and highly significant ($p= 0,008$, trend-test of TERPSTRA) trend in the order: 1960, 1961, 1959, 1962. To give an example: wood-habitat B: 1960, 76% (288 ind.); 1961, 70% (296 ind.); 1959, 53,3% (90 ind.)and 1962, 58,4% (531 ind.); all habitats taken together: 1960, 69,7%(1564 ind.); 1961, 66,6% (1432 ind.); 1959, 61,4% (855 ind.) and 1962, 55,7% (1763 ind.)"low-pitters".

This shift of the percentage of "low-pitters" seems to be correlated with a shift of the moisture condition of the substratum during the period of larval development (May-August of the preceding year) expressed in the form of the amount of precipitation (or the number of rainy days): this moisture condition (especially in the form of a cumulative trend) follows the same trend as the percentage of "low-(high-)pitters": 1960, 1961, 1959, 1962. Thus, e.g. the dry summer of 1959 is followed by a general increase of the percentage of "low-pitters" in 1960, whereas the wet summer of 1961 is followed by a general decrease of the percentage of "low-pitters" in 1962, etc. (these shifts are significant with the exception of the shift from 1960 to 1961, which exception, however, fits the picture and contributes to the reliability of the trend).

The substratum in which the larvae develop, is the litter of the woods and since the structure of the layer of litter will influence its moisture condition some relation between the structure of the layer of litter and the percentage of "low-pitters" may be expected. The observed correlations between the percentage of "low-pitters" and the thickness of the layer of litter (only broad-leaved woods) must be interpreted in this way (1959: τ = +0,600; 1961 τ = +0,524; 1962: τ = +0,429; these 3 years together: τ = +0,518, $p= 0,01016$): a thin layer of litter will more thoroughly be wetted by rain than a thick layer and hence, in a thick layer of litter "low-pitter"-larvae will find relatively more suitable places than in a thin layer; this is especially true of course during rainy summers (1958, 1960, 1961) and thus, it is clear that in 1960 no correlation could be expected: τ = +0,048 (the summer of 1959 was extremely dry).

Since in a thick layer of litter generally a more complete moisture-gradient will exist than in a thin layer, larvae with a different moisture-preferendum generally will find suitable places more easily in a thick layer than in a thin one and hence, a thick layer of litter under normal or moist weather conditions will be generally more favourable for the development of larvae of *P.oblongopunctatus* than a thin layer. In accordance with this a correlation is found to exist between the thickness of the layer of litter and catch-numbers (within one year a relative measure of effective density): 1959, τ = +1,00; 1961, τ = +0,810; 1962, τ = +0,810; these 3 years together: $\bar{\tau}$ = +0,873, $p < 0{,}000066$. In 1960 no correlation (τ = -0,067) was found because during the dry summer of 1959 even in a thick layer of litter the moisture-gradient undoubtedly was nullified.

Although many details are still obscure and most relations need experimental test, one point seems clear to me: a population of *Pterostichus oblongopunctatus* is able to stand up to a continuously fluctuating environmental factor (moisture of the substratum) by distributing the risk of perishing over a range of phenotypes which seems to be controlled by the particular habitat.

The effect of the fluctuating environmental factor is continuously more or less intercepted by the ecological "polymorphism" of the population.

In my opinion this principle of "risk-distribution" to accomodate continuously fluctuating environmental factors must be wide-spread among animal populations and it may underlie many forms of polymorphism. Of course this principle of "risk-distribution" also contributes to the quantitative stability of the population and in this way to its chance of survival and hence, the building up of forms of polymorphism based on this principle will be favoured by selection.