March 31 1984

Outline of a seminar given in Cambridge[1] by H. Rouanet and J.-M. Bernard[2]

New ways of analysing sequences of actions
(with an application to the predatory behaviour of Eurobellia Moesta)

This talk is based on a paper by Bernard, Blancheteau and Rouanet (1984) [2] to appear shortly in the journal Biologie du Comportement (Biol. of Behaviour). The talk is intended to provide an introduction to the paper.

Only the statistical aspects will be discussed here. Detailed descriptions of the experimental situations that have been investigated and a discussion of substantive issues – especially the influence of environment on predatory behaviour – will be found in Blancheteau's paper [3, 4].

The plan of the talk will be as follows:

After a brief introduction we present Blancheteau's earwig data and discuss the descriptive analysis. Then we proceed to a Bayesian analysis.

Introduction

I suppose that there is no need for me, in front of this audience, to comment on the interest of refined studies of sequences of action for ethological research. In many circumstances a set of sequences is observed that is clearly neither of a 'fixed action pattern' type, nor 'completely random'. Then the problem is to search the sequential regularities of the behaviour under study, while allowing for its variability.

If we want to make an assumption-free analysis of a sequence of actions, the most straightforward way is clearly to start from the record of every single possible instance of a complete sequence of actions, with its corresponding number of occurrences. Then the basic object of study will be a tree-diagram of sequences of actions.

[1] On Wednesday, January 25, 1984

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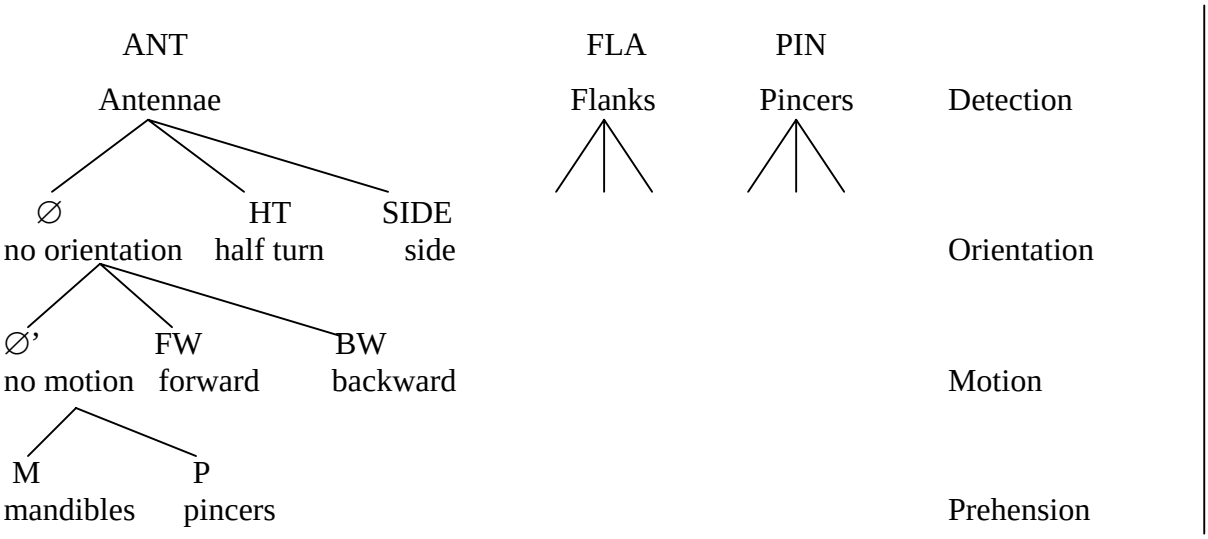
The overall pattern that emerges from the observed sequences of actions will then be found by simplifying the tree-diagram, or so to say, by 'pruning' it in order to bring out privileged transitions (whether of order 1 or higher). This in turn can be done using either descriptive methods or inferential ones. All these points will be exemplified by the analysis of the earwig data.

The earwig data

Earwig E. Moesta is shown on diagram #1. According to Marc Blancheteau, the predatory behaviour of this earwig can be decomposed into four phases:

detection, orientation, motion, prehension,

along the following scheme



This scheme shows a set of sequences of four actions (notice the ∅ and ∅' encodings). An example of a sequence is shown on diagram #2;

(Antennae, half-turn, Backward, Pincers)

Now for the results: in the table $1 are shown the basic data for two conditions which have been investigated – 'under shelter' and 'outside shelter'. A glance at the table shows that the predatory behaviour is neither of a 'fixed-action pattern' type, nor 'completely random'. A refined sequential analysis is in order. It will be done by decomposing sequences into transitions.

The concept of transition

Intuitively speaking, the general concept of transition is just that of an event, when envisaged conditionally upon the occurrence of some other event. Here an event will be an action or a succession of actions.

As a first example, consider – in the 'under shelter' condition – the Forward motion viewed conditionally on the successive detection by Antennae, the orientation to the Side; this transition will be denoted:

$$(\text{Antennae}, \text{Side}) \rightarrow \text{Forward}$$

For this transition we calculate a transition frequency as follows: we first compute the number of occurrences of the conditioning event, namely the succession (Antennae, Side); that is, the overall number of the sequences of four actions that started with these two actions; namely, as read from the table \$1, 6+6+8+3+1=24. Among these sequences, 8+3=11 were followed by a Forward motion. Therefore the frequency of the transition

$$(\text{Antennae}, \text{Side}) \rightarrow \text{Forward}$$

is 11/24. This transition frequency will be denoted

$$f^{\text{Antennae, Side}}_{\text{Forward}},$$

So we write $f^{\text{Antennae, Side}}_{\text{Forward}} = \frac{11}{24}$

(As a mnemonic for this notation, we may regard the transition as going 'from top to bottom'). We will also say that the transition (Antennae, Side) → Forward is of order 2, since its conditioning event involves two successive actions, namely Antennae and Side.

As another example, let us take the Forward motion again, but this time viewed conditionally on the Side orientation only; this new transition will be denoted Side → Forward. To compute the associated frequency, we count up the total number of sequences that comprise the Side orientation, that is 6+6+8+3+1+4+8+2+3+1+2+1+4=49. Then among these we look for those that comprise the Forward motion, that is: 8+3+2+1=14. Hence the transition frequency :

$$f^{\text{Side}}_{\text{Forward}} = \frac{14}{49}$$

This transition will be said to be of order 1, since its conditioning event involves a single event, namely Side.

Incidentally, it will sometimes be found convenient to treat an event, when envisaged unconditionally, as a zero-order transition, and the corresponding relative frequency as a

transition frequency. Thus the detection by antennae may be denoted $\rightarrow$ Antennae, with the corresponding frequency

$$f_{\text{Antennae}} = \frac{65}{100}$$

A critical look at the conventional 'flow-diagram'

The sequential organization of a sequence of actions is often investigated by means of pictorial representations known as 'flow-diagrams'. In diagram #3 is shown the most familiar kind of flow-diagram for the earwig data, in the 'under shelter' condition; the thickness of a line representing a transition reflects the magnitude of the corresponding transition frequency.

The shortcomings of the conventional flow-diagram

As can readily be seen, the conventional flow-diagram only accounts for transitions of order 1. This in itself does not invalidate the representation, but it does constitute a limitation to the conclusions that can be drawn from the diagram.

So, to take an extreme example, the flow-diagram in diag.#3 might lead one to believe that the sequence

$$\rightarrow \text{Pincers} \rightarrow \varnothing \rightarrow \text{Forward} \rightarrow \text{Mandibles}$$

was observed a number of times, since it is composed of transitions with non-negligible – even important – frequencies, namely 16/100, 8/16, 15/24 and 25/29, whereas in fact this sequence is not realizable, since it cannot possibly lead to a capture. For if the earwig has detected the prey with its pincers, it necessarily moves away from it when it goes forward without having oriented itself toward the prey, therefore it cannot seize the prey with its mandibles.

The paradox can be resolved by the fact that transition frequencies of order 1 by themselves do not suffice, as a rule, to reconstruct the transition frequencies of order greater than 1. Consider by way of example the transition frequency

$$f^{\text{Side}}_{\text{Forward}} = \frac{14}{49} .$$

This frequency appears as a weighted average of three transition frequencies, namely

(Antennae, Side) $\rightarrow$ Forward with value 11/24 as we have seen,

(Flanks, Side) $\rightarrow$ Forward whose value is 0/17=0, and

(Pincers, Side) → Forward whose value is 3/8.

As can be seen, these 3 transition frequencies have quite different values. As a consequence, the first-order transition Side → Forward in itself carries but little information, as it is a mixture of quite heterogeneous transitions; in order to understand it properly we must take account of the reactional context, that is the 'past' – as constituted by the preceding actions (here the detection phase).

The tree-diagram

The most straightforward pictorial representation of the basic data is by means of a tree-diagram, as shown on figure $2. The tree-diagram is actually a sort of flow-diagram that makes no implicit assumptions about the orders of transitions, since all transitions are represented with their 'complete pasts'.

Notice that in the tree-diagram representation not all the 3x3x3x2=54 combinations of successive acts are represented. In fact, some combinations have been left out because they would refer to bio-mechanically unrealisable successions, given the relative locations and moves of prey and predator. An example of such an unrealizable sequence has already been seen, namely

Pincers → ∅ → Forward → Mandibles

(other deletions may result from logical constraints in the encoding rules).

Naturally, unrealizable sequences must be distinguished from sequences which were a priori regarded as realizable, but for which no occurrence was recorded; for instance

Antennae → Side → Backward → Mandibles

Such sequences do belong to the tree-diagram. The representations of this distinction, when it comes to the statistical analysis, will be commented on later.

The descriptive analysis of the tree-diagram and its shortcomings

The tree-diagram makes it immediately apparent which transitions are most frequently encountered. In order to 'prune the tree' we might simply keep the most frequently encountered transitions. If we do this kind of deleting operation, we get a schematic representation of the kind shown in diag.$2. In a descriptive sense, this procedure amounts to summarizing the original data ('descriptive filtering').

Yet, the descriptive analysis of the data is insufficient. Consider, for instance, the following three transitions:

i) (Antennae, Side) → ∅' with the transition frequency 12/24

ii) (Pincers) → Side with the transition frequency 8/16

iii) (Flanks, Half-turn) → Backwards with transition frequency ½.

The observed transition frequencies are all equal to .50, but they are based on different numbers of observations.

Now what is the researcher primarily interested in ? Presumably not in the observed frequencies themselves, rather he is interested in making statements about parent transition frequencies. That is: transition frequencies concerning the population from which the data is supposed to be a sample. From this inductive standpoint, the parent transition frequencies are unknown parameters, and the observed transition frequencies will be regarded as estimates of those parameters, whose reliability depends on the number of observations on which they are based.

In what follows, a population transition frequency – that is, a parameter – will be denoted like its corresponding observed frequency, using the letter φ instead of f. For instance, the population transition frequency connected with (Antennae, Side) → ∅' will be denoted

$$\varphi^{\text{Antennae, Side}}_{\varnothing'}$$

and it will be estimated by the corresponding observed frequency:

$$f^{\text{Antennae, Side}}_{\varnothing'} = \frac{12}{24}$$

Judgments about population transition frequencies based on observed transition frequencies will be more precise when the latter are based on larger number of observations. Here, for instance, the inference about

$$\varphi^{\text{Antennae, Side}}_{\varnothing'}$$

based on 24 observations will be more precise than the inference about

$$\varphi^{\text{Pincers}}_{\text{Side}}$$

based on only 16 observations, and much more precise than the inference about

$$\varphi^{\text{Flanks, Half-turn}}_{\text{Backward}}$$

based on only 2 observations.

Inferential analysis and Bayesian procedures; general considerations

In what follows, we present inferential results obtained through Bayesian procedures. The Bayesian approach of statistical inference constitutes, nowadays, a major branch of development for contemporary mathematical statistics which has come to supplement traditional significance and confidence methods.

A comprehensive introduction to the Bayesian statistical approach from a mathematical standpoint will be found in Lindley's (1965) classical textbook [5]. For a brief introduction to inference from observed frequencies, see Lindley and Phillips (1976) [6]. Some of the Bayesian procedures necessary for the analysis of sequences are new and have been worked out by Bernard (1983) [1].

In spite of the numerous mathematical developments of Bayesian Statistics, the Bayesian approach has remained largely under-used and neglected by experimenters.

For previous examples of detailed applications of the Bayesian approach to psychological data, see, for example, Rouanet, Lépine, Pelnard-Considère (1976) [9], Rouanet, Lépine, Holender (1978) [8], Rouanet, Lecoutre (1983) [7]. As far as we know, the paper by Bernard, Blancheteau, Rouanet (1984) [2] is the first application of the Bayesian approach to ethological data.

It should be emphasised that the choice of Bayesian methods for treating data is a methodological one. Bayesian methods will allow us to make statements not only about the existence of sequential dependencies – as traditional methods do – but also about their importance – which traditional methods do not (we might discuss Bayesian versus traditional approaches at the end of this talk).

Bayesian distributions

Through Bayes' theorem we derive, over every parent transition frequency φ of interest, a probability distribution that we call a Bayesian distribution. These distributions are obtained by standard Bayesian procedures that have been developed in Bernard (1983) [1]. The standard Bayesian distribution about φ can be regarded as merely expressing the information about the parent frequency contained in the data.

On diag.#4 are shown two examples of Bayesian distributions. As can be seen, the larger the number of observations on which a transition frequency is based, the more concentrated the distribution is about that frequency. For every parent transition frequency φ,

one can determine from the distribution the lower and upper Bayesian limits at a specified guarantee, just as one would determine critical values at a specified level for any probability distribution. As an example, for the distribution φ_{Ant}, the unconditional frequency of detection by antennae, the lower Bayesian limit is found to be equal to .567. This means that the Bayesian probability for φ_{Ant} to be greater than .567 is .95, which we write : $P(\varphi_{Ant}>.567)=.95$. We will also say that the statement "φ Ant>.567" holds at the Bayesian guarantee .95.

As another example, for the distribution of

$$\varphi^{\text{Pincers}}_{\text{Lateral}} ,$$

we find that

$$P(\varphi^{\text{Pincers}}_{\text{Lateral}} >.306) = .95$$

i.e.: the statement

$$\text{“}\varphi^{\text{Pincers}}_{\text{Lateral}} >.306\text{”}$$

is established with the guarantee .95.

Clearly, lower Bayesian limits allow inferential statements about the importance of every parent frequency of interest. The 'pruned tree' of fig. $3 has been constructed using this principle of 'inferential filtering'. It is similar to the tree of fig. $2 except that the thickness of lines now reflect the values of lower Bayesian limits (.95 guarantee).

It will be noticed that for some of the transitions – all pertaining to the last phase – the lower limit is equal to 1. This corresponds to the case where one of the two actions (prehension by Pincers or by Mandibles) could not possibly lead to a capture. Thus, for the transition (Flanks, Half-turn, Backward) $\rightarrow$ Pincers, one can state at once that

$$\varphi^{\text{Fla, HT, Bw}}_{\text{Pincers}} = 1.$$

But for the transition (Pin, Side, ∅') $\rightarrow$ P, with the same observed frequency

$$f^{\text{Pincers, Side, ∅'}}_{\text{Pincers}} =1/1$$

the prehension by Mandibles is another possible end to the sequence and, consequently, the data only allow the statement

$$\varphi^{\text{Pincers, Side, ∅'}}_{\text{Pincers}} >.173$$

at the guarantee .95.

The comparison of $2 and $3 points out the radical difference between inferential and descriptive filtering; the inferential filtering immediately eliminates those transitions that are more sensitive to sampling fluctuations, i.e. those based on a small number of observations.

Therefore it cannot possibly be equivalent to any descriptive filtering. For example, as we have seen, the three transitions (Ant, Side) → ∅', Pin → Side and (Fla, HT) → Bw, all have the same observed frequency – equal to .50 – but, since they are based on different numbers of observations, they are differentially treated by the inferential filtering; their lower Bayesian limits are respectively .332, .306, .097.

Privileged transitions for the 'under shelter' condition

Given the interest of inferential filtering, we may use it to operationally define the concept of a privileged transition. To fix ideas, let us define a transition to be privileged whenever its lower Bayesian limit, at the guarantee .95, is greater than .40. This will lead to a summary of privileged transitions that calls for a few remarks (we consider the 'under shelter' condition):

1) The frequency of detection by Antennae is privileged – reflecting the well-known functional predominance of antennae for sensory detection (in E. Moesta).
2) In successions such as → Ant → ∅ → Fw → M and → Ant → HT → Bw → P the first three phases entail the fourth one in a deterministic way: that is, a prehension by Mandibles always follows a Forward motion, and a prehension by Pincers a Backward motion. In other successions, especially those involving a Side orientation, there is a much greater variety of transitions between successive actions.
3) From the detection phase to the orientation phase, there are few privileged transitions; there are many more from the orientation phase to the motion phase, despite the decrease in the numbers of observations when descending the tree that makes it harder for a privileged transition to be established with a given guarantee. This shows that there is, from detection to orientation, a variety of behaviours used by the forficula, especially when the detection takes place by antennae.

Comment

Considering lower Bayesian limits is appropriate when we look for the most frequent (i.e.: privileged) transitions. It may be no less interesting to make statements about rare

transitions. In order to do so, one will naturally consider upper Bayesian limits. For example, the statement

$$\text{“ } \varphi^{\text{Fla, Side}}_{\text{Forwards}} < .065\text{”}$$

holds at the guarantee .90.

Comparison of the ‘under shelter’ and ‘outside shelter’ conditions

The comparison of the ‘under shelter’ and ‘outside shelter’ conditions was a paramount objective of the ethological research. As a first step towards this comparison, we may set up (see figure $4), for the ‘outside shelter’ condition, a drawing similar to that of $3 for the ‘under shelter’ condition.

The comparison of $3 and $4 reveals marked differences between the two processes. For instance, in the succession $\rightarrow$ Ant $\rightarrow$ Side $\rightarrow$ Fw $\rightarrow$ P, all transitions are privileged in the ‘outside shelter’ condition, whereas only $\rightarrow$ Ant is privileged in the ‘under shelter’ condition.

The comparison between the two conditions can be pursued by investigating in a direct way the differences between pairs of parent frequencies corresponding to the same transitions. As can be seen in fig. $5, the main difference concerns the actions following a detection by Antennae; if one compares the two parent frequencies relative to the transition Ant $\rightarrow$ HT, one can state with the guarantee .90, that the difference between these frequencies is greater than .24, with the larger frequency in the ‘under shelter’ condition.

Conclusions

The approach exemplified in this work readily applies to a wide range of sequences of actions. Let us summarize the key ideas:

1) The general concept of transition – not restricted to order 1 – is basic for the expression of the temporal structure of a process; the investigation should focus on the search for privileged transitions. In order to allow for transitions of order higher than 1, and provide assumption-free analyses, the tree-diagram representation of a process should be preferred to the usual flow-diagram.

2) Bayesian inference is a most appropriate inferential tool for the search for privileged transitions, since it permits statements about the magnitudes of parent transition frequencies, as well as differences between frequencies. The procedures illustrated here generalize to any linear combination of transition frequencies, for which specific standard Bayesian distributions have been derived; see Bernard (1983) [1].

References

[1] BERNARD J.-M. (1983), Inférence bayésienne sur des fréquences dans le cas de données structurées: méthodes exactes et approchées, Thèse de 3ème cycle, Université René Descartes, Paris.

[2] BERNARD J.-M., BLANCHETEAU M., ROUANET H. (1984), Le comportement prédateur chez un forficule, Eurobellia Moesta (Gene) : II. Analyse séquentielle au moyen de méthodes d'inférence bayésienne – to appear in Biology of Behaviour

[3] BLANCHETEAU M. (1981), Fixed and variablecomponents in the predatory behaviour of Eorobellia Moesta (Dermaptera, Labiduridae) – Biology of Behaviour, 6, 197-212.

[4] BLANCHETEAU M. (1983), Le comportement prédateur chez un forficule, Eurobellia Moesta (Gene) : I. Description et évaluation de la fréquence des principaux actes de capture, Biology of Behaviour.

[5] LINDLEY D.V. (1965), Introduction to Probability and Statistics from a Bayesian viewpoint, Vol. 2., Inference, Cambridge University Press.

[6] LINDLEY D.V. & PHILLIPS L.D. (1976), Inference for a Bernoulli process, a Bayesian view, The American Statistician, 30, 3, 112-119.

[7] ROUANET H., LECOUTRE B. (1983), Specific inference in ANOVA : from significance tests to Bayesian procedures, British Journal of Mathematical and Statistical Psychology, 36, 252-268.

[8] ROUANET H., LEPINE D., HOLENDER D. (1978), Model acceptability and the use of Bayes-fiducial methods for validating models, in REQUIN J. (Ed), Attention and Performance VII, Hillsdale: Lawrence Erlbaum Associates, Inc., 687-701.

[9] ROUANET H., LEPINE D., PELNARD-CONSIDERE J. (1976), Bayes-fiducial procedures as practical substitutes for misplaced significance testing : an application to educational data, In D.N.M. De Gruijter & L.J. Th. Van der Kamp (Eds), Advances in Psychological and Educational Measurement, Wiley & Sons, 33-50.

- EUBORELLIA MOESTA -

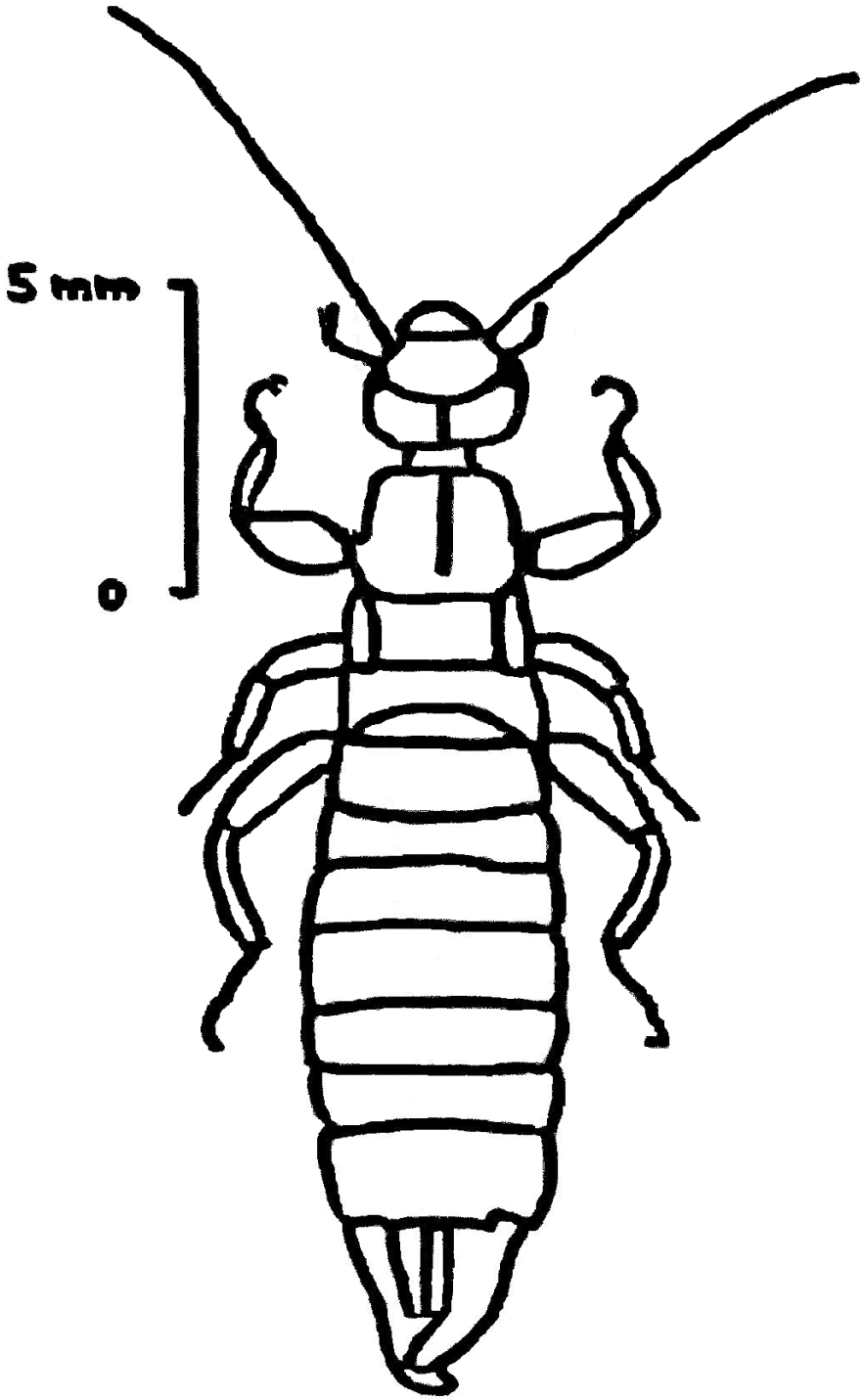


Diagram #1

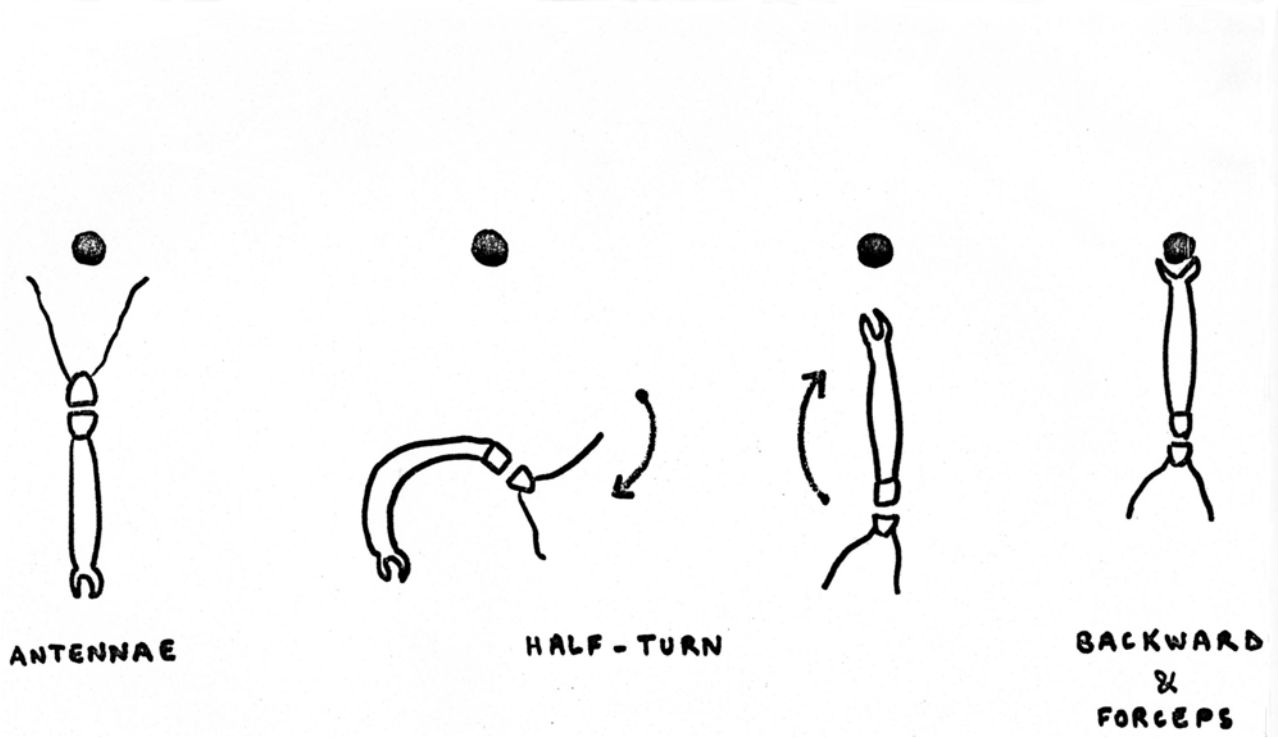


Diagram #2

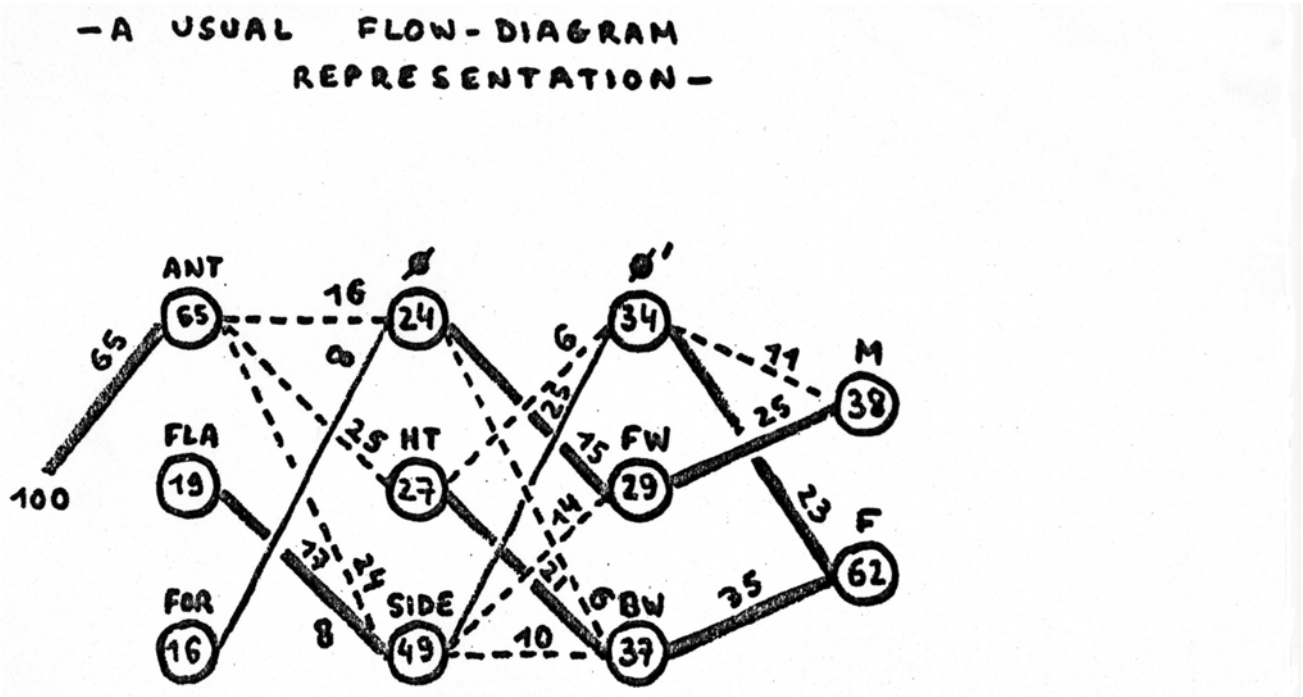


Diagram #3

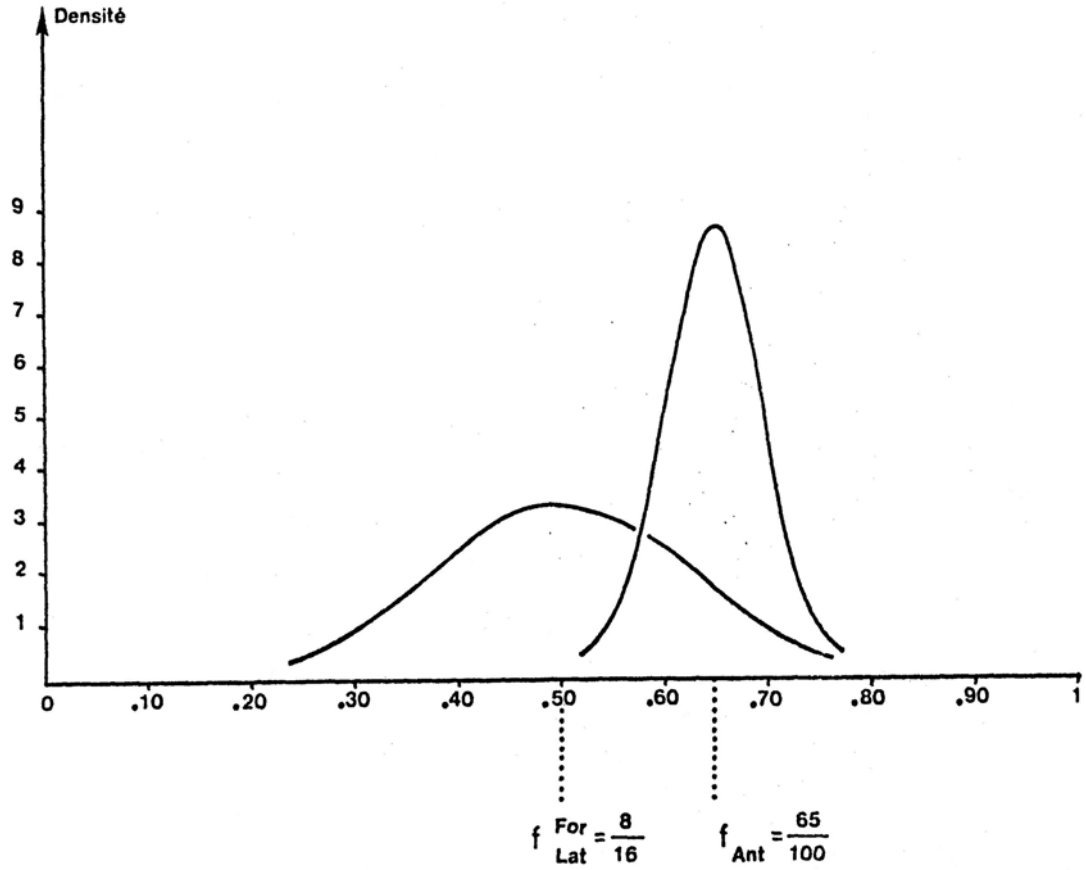

Densité
9
8
7
6
5
4
3
2
1
0
.10
.20
.30
.40
.50
.60
.70
.80
.90
1
f For Lat = 8/16
f Ant = 65/100

Diagram #4

Application to the capture behaviour of Euborellia Moesta)
by H. ROUANET and J.-M. BERNARD (& M. BLANCHETEAU)

Basic data : sequences of actions

and their numbers of occurrences

				UNDER SHELTER	OUTSIDE SHELTER
Ant	ϕ	ϕ′	M	1	1
"	"	Fw	M	15	6
"	Side	ϕ′	M	6	1
"	"	"	F	6	9
"	"	Fw	M	8	12
"	"	"	F	3	22
"	"	Bw	F	1	0
"	HT	ϕ′	F	5	1
"	"	Bw	F	20	2
Fla	Side	ϕ′	M	4	3
"	"	"	F	8	5
"	"	Bw	M	2	0
"	"	"	F	3	0
"	HT	ϕ′	F	1	0
"	"	Bw	F	1	0
For	ϕ	ϕ′	F	2	3
"	"	Bw	F	6	1
"	Side	ϕ′	F	1	4
"	"	Fw	M	2	1
"	"	"	F	1	0
"	"	Bw	M	0	1
"	"	Bw	F	4	3
				100	75

Table $1

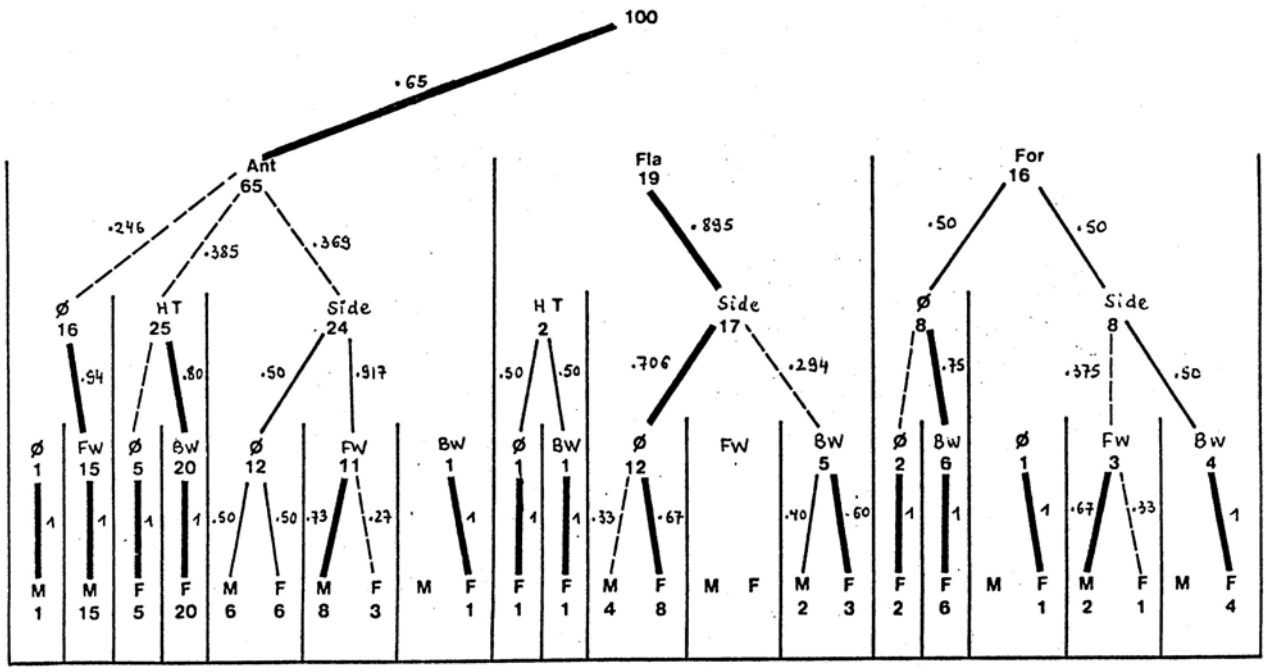

– Descriptive filter ; under shelter condition –
100
.65
Ant
65
.246
.385
.369
Ø
16
.94
HT
25
.80
Side
24
.50
.917
Ø
1
FW
15
Ø
5
BW
20
Ø
12
FW
11
BW
1
M 1
M 15
F 5
F 20
M 6
F 6
M 8
F 3
M
F 1
HT
2
.50
.50
Ø
1
BW
1
F 1
F 1
Fla
19
.895
Side
17
.706
.294
Ø
12
FW
BW
5
M 4
F 8
M
F
M 2
F 3
For
16
.50
.50
Ø
8
Side
8
.75
.375
.50
Ø
2
BW
6
Ø
1
FW
3
BW
4
F 2
F 6
M
F 1
M 2
F 1
M
F 4

Fig. $2

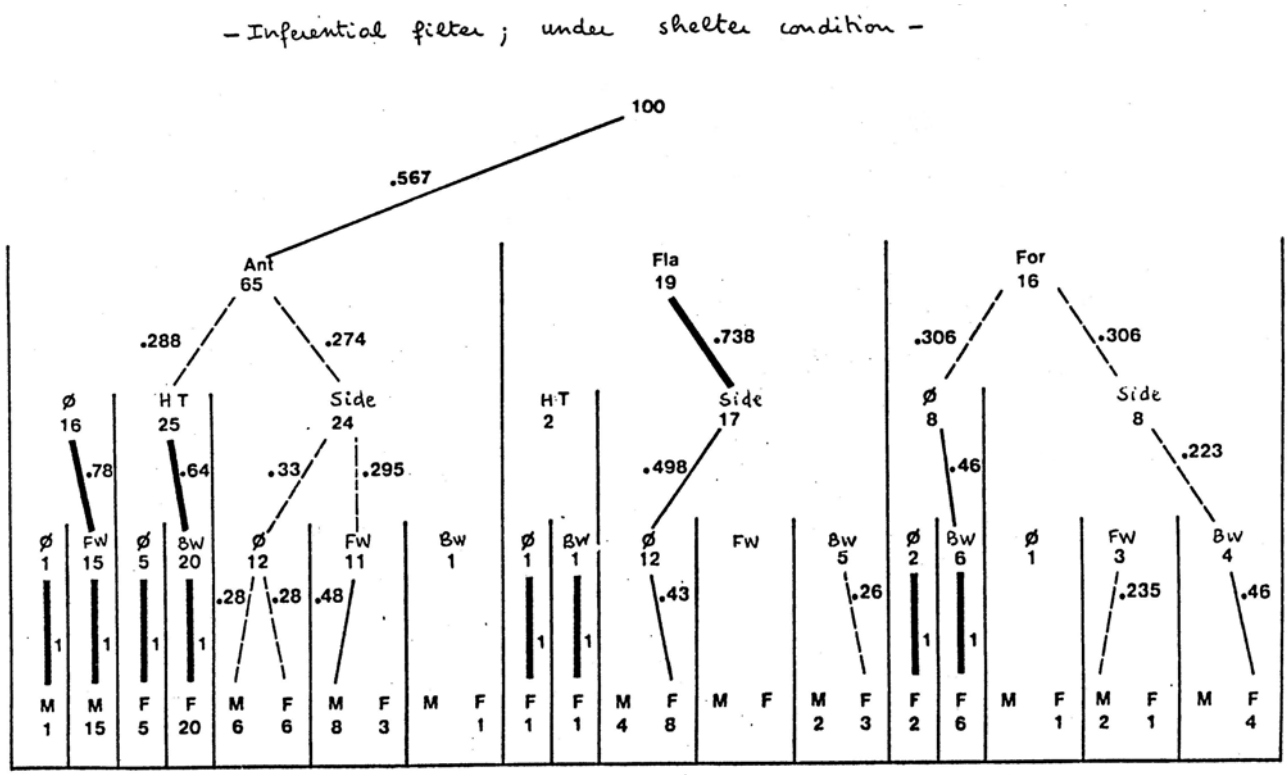
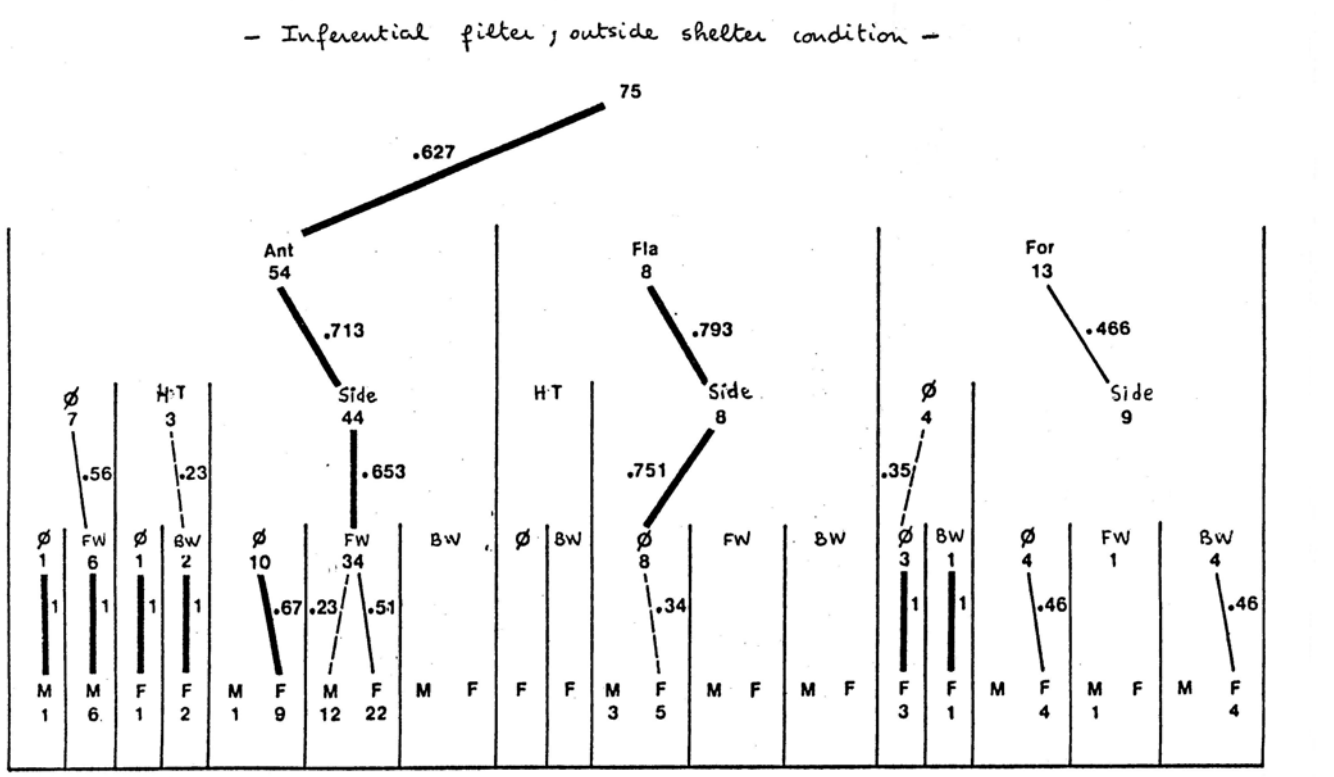

– Inferential filter ; under shelter condition –
100
.567
Ant
65
.288
.274
Ø
16
.78
HT
25
.64
Side
24
.33
.295
Ø
1
FW
15
Ø
5
BW
20
Ø
12
FW
11
BW
1
.28
.28
.48
M 1
M 15
F 5
F 20
M 6
F 6
M 8
F 3
M
F 1
HT
2
Ø
1
BW
1
F 1
F 1
Fla
19
.738
Side
17
.498
Ø
12
FW
BW
5
.43
.26
M 4
F 8
M
F
M 2
F 3
For
16
.306
.306
Ø
8
Side
8
.46
.223
Ø
2
BW
6
Ø
1
FW
3
BW
4
.235
.46
F 2
F 6
M
F 1
M 2
F 1
M
F 4

Fig. $3


– Inferential filter, outside shelter condition –
75
.627
Ant
54
.713
Side
44
.653
Ø
7
.56
H·T
3
.23
Fla
8
.793
Side
8
.751
H·T
For
13
.466
Side
9
Ø
4
.35
Ø
1
FW
6
BW
2
Ø
10
.67
.23
FW
34
.51
BW
Ø
BW
Ø
8
.34
FW
BW
Ø
3
BW
1
Ø
4
.46
FW
1
BW
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.46
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F 2
M 1
F 9
M 12
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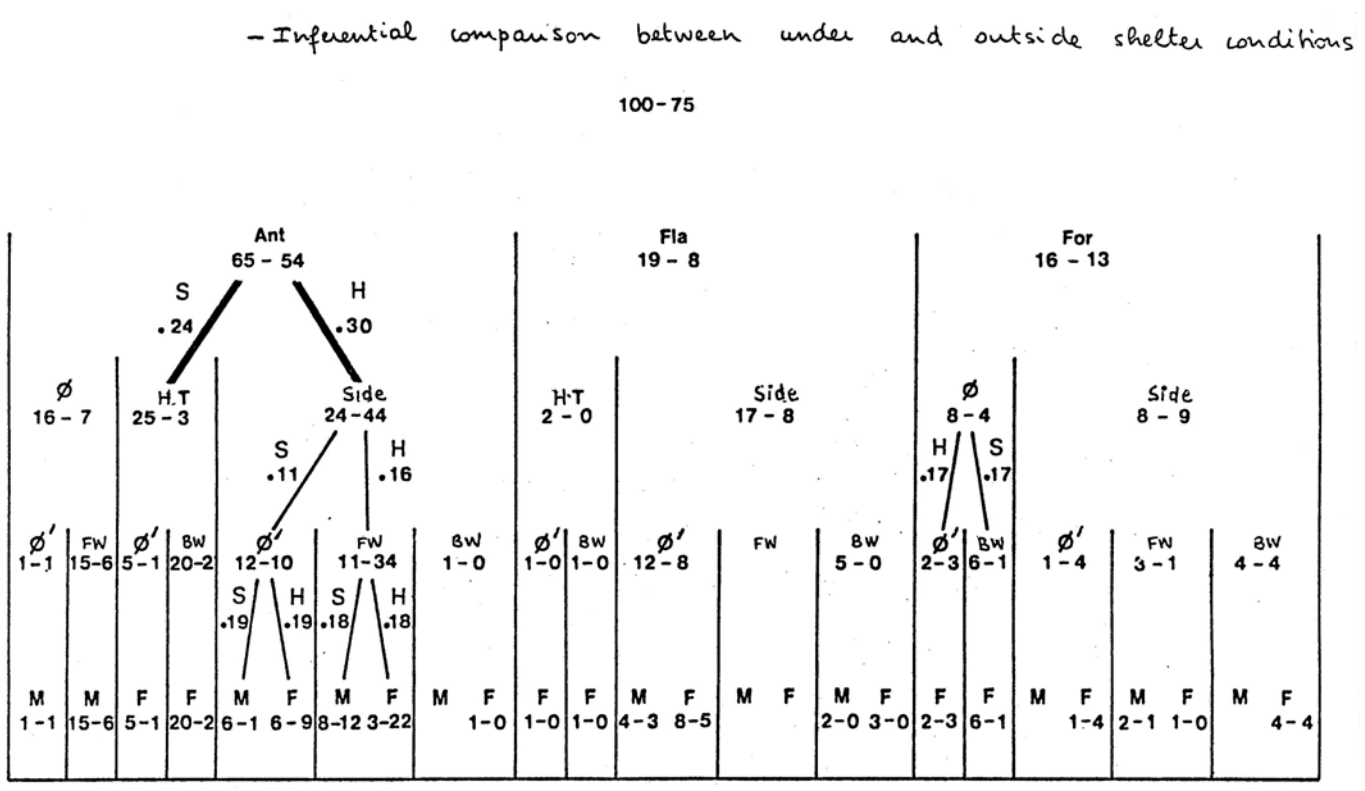
M F
M F
F 3
F 1
M F
M 1
F 4
M F
F 4

Fig. $4


– Inferential comparison between under and outside shelter conditions
100-75
Ant
65 – 54
S
.24
H
.30
Fla
19 – 8
For
16 – 13
Ø
16 – 7
H.T
25 – 3
Side
24 – 44
S
.11
H
.16
H·T
2 – 0
Side
17 – 8
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8 – 4
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.17
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.17
Side
8 – 9
Ø′ 1–1
FW 15–6
Ø′ 5–1
BW 20–2
Ø′ 12–10
FW 11–34
BW 1–0
S .19
H .19
S .18
H .18
Ø′ 1–0
BW 1–0
Ø′ 12–8
FW
BW 5–0
Ø′ 2–3
BW 6–1
Ø′ 1–4
FW 3–1
BW 4–4
M 1–1
M 15–6
F 5–1
F 20–2
M 6–1
F 6–9
M 8–12
F 3–22
M F 1–0
F 1–0
F 1–0
M 4–3
F 8–5
M F
M 2–0
F 3–0
F 2–3
F 6–1
M F 1–4
M 2–1
F 1–0
M F 4–4

Fig. $5