

## Typology of vigilance posture of wild boar (*Sus scrofa*): Descriptive and sequential approach

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**ABSTRACT.** *Typology of vigilance posture of wild boar (Sus scrofa): descriptive and sequential approach.*— A detailed description of the vigilance postures in the wild boar, based on the relative position of six body elements was made on animals in an enclosure. The analysis allowed five posture types, coinciding with various age and sex classes, to be identified. The average duration of certain types of posture varies significantly with respect to the mean for all postures. Sequential analysis shows that each type of posture depends on the behavioural context defined by the type of act preceding it and the act which follows. The variability of postures should correspond to different functions and involves to update the modelling of vigilance behaviour.

**KEY WORDS.** *Sus scrofa*, Vigilance, Typology, Multifactorial analysis.

### Introduction

The necessary preliminary work to any ethological study is the description of the behavioural flux. This description is an operation of discretisation of the phenomenological stream consisting of enumerating behaviour patterns, which are considered as classes «defined by regularities in one or more of five domains: location, orientation, physical topography, intrinsic properties, and physical effects» (Drummond, 1981). This behavioural catalogue can serve to order diversity and standardize data collection and allows comparisons to be made between animals of the same species or of different species. The behaviour patterns were often assumed to be «fixed action patterns» and regarded as essentially invariant (Schleidt, 1974). However, the stereotypy of behaviour is not the rule

and it was both empirically (Barlow, 1977; Slater, 1978, 1981) and theoretically (Maynard Smith, 1982) shown, that the extent of variability of different actions can vary a great deal.

Recently, vigilance behaviour has been the topic of numerous field studies (see reviews of Elgar, 1989; Lima 1990; Quenette, 1990) both on mammals and birds. In all these works, vigilance is characterized by a head lift or scan in which the animal swiftly raises its head and visually scans its surroundings. However no studies have finely described the phenotypic characteristics of this behaviour, although it appears important to assess its functions.

In this paper we focus on the description of vigilance postures in the wild boar. A typology of these postures is presented to distinguish behavioural categories on the basis of regularities of their physical

topography. Then, to examine the biological relevance of this classification it was decided to analyse the sequential relationship between the types of vigilance postures and the nature of the preceding and following act which determines their behavioural context (Morgan et al., 1974). The hypothesis that the type of posture depends upon the preceding act and affects the occurrence of the subsequent one is tested. This hypothesis underlies the implicit model that a behavioural unit corresponds to an unobservable state of the subject and that the temporal proximity between two behavioural units reveals a link of causality.

## Material and Methods

### Animals and environment

The study was carried out on a group of 62 captive wild boars from 14 April to 12 June 1987 which included six adult males more than two years old, 11 adult females, 18 subadults (age between 5-12 months) and 27 piglets. The observations were made from a hiding place either between 9.30-11.00 and 16.00-19.00 in an enclosure of 1.8 ha in size situated near Arles in the south-east of France. The wild boars were fed a standard full ration once every day at 8.30 at a feeding site. During each period of observation, as soon as a wild boar displayed a vigilance posture we noted its physical characteristics, the duration of the posture, the age and sex for adults (we distinguished four classes: adult male (AM), adult female (AF), subadults (S) and piglets (P)). Data were dictated into a portable cassette recorder for later transcription and the durations of vigilance postures were timed to the nearest s using a stopwatch. Preliminary observations made by «ad libitum» sampling allowed six body elements to be determined (fig. 1) for the description of the postures:

-Head: either in the body axis determined by vertebral spine (BH) or not (NH)

-Snout: three positions according to horizontal plan defined by abdomen, either horizontal (HS) or

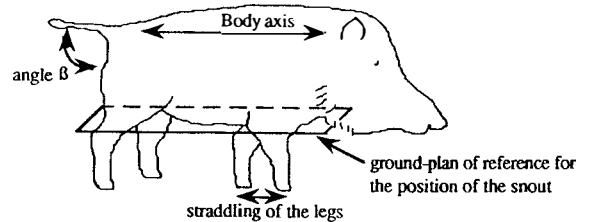


FIGURE 1. Schema of body elements chosen for the description of vigilance postures.

[Esquema de los segmentos corporales elegidos para la descripción de las posturas de vigilancia.]

lowered (LS) or raised (RS)

-Ears: either raised and oriented (RE) or not (NR)

-Tail: either mobile (MT) or not (NT), it may have five positions according to the angle  $\beta$  (radians) between the tail and body axis: down (T1;  $\beta=0$ ), oblique down (T2;  $0<\beta<\pi/2$ ), horizontal (T3;  $\beta=\pi/2$ ), oblique up (T4;  $\pi/2<\beta\leq\pi$ ) and turned up (T5;  $\pi<\beta<3\pi/2$ ).

-Forelegs: either parallel (PF) or not (NF).

-Hind legs: either parallel (PP) or not (NP).

Although the determination of the body elements is arbitrary and not exhaustive, they were chosen because they were directly observable and recognizable and gave an analytic grid to collect our raw data. Moreover, the wild boar has great muscular control of these body elements so that they can move independently of each other.

The behaviour patterns were collapsed into four functional categories derived from the ethogram of Dardaillon & Teillaud (1987):

- 1) Foraging activity subdivided into two components: Feeding (F = ingestion of food) and Search (S = the snout is lowered near the ground and the wild boar is walking, presumably while looking for food);
- 2) Locomotion activity subdivided into two components: Slow displacement (SD = the head is in normal upright position and the wild boar walks, Fast displacement (FD = the animal is either trotting or galloping);
- 3) Social interaction (it includes any social behaviour obviously directed at another individual by

any subject); 4) Comfort activity (it includes self-centred behaviour, e.g. scratching, shaking, self-grooming and wallowing). These two last categories could not be considered in the sequential analysis for statistical reasons.

## Data analysis

### 1. Multiple correspondence analysis.

All the postures described by the presence (coded 1) or absence (coded 0) of the position of the body segments were grouped in a table which includes 22 columns (18 modalities of the variables of the body elements and four modalities of the age-sex variable). These data, considered as a contingency table, were subjected to a multiple correspondence analysis (MCA) which represents in the same space the row and column elements of the data table. This space is organized into a series of orthogonal factorial axes which bring out the maximum variance occurring in each case. This analysis allows unambiguous interpretations in terms of proximity, in the factorial space, of the row and column elements of the contingency table (Benzecri, 1973; Colgan & Smith, 1978).

### 2. Dynamic clouds and hierarchical cluster analysis.

The analysis was made from the table which included all the co-ordinates of the individual postures yielded by the MCA on the first 10 axes which sum up 84.7% of the total variance. In the first stage, we used a partitioning technique of the individual posture data based on the algorithm of the k-means or dynamic cloud type. This procedure along the «strong forms» method, allows significant classes to be isolated among a body data (Diday, 1982; Celeux et al., 1989). In the second stage, hierarchical cluster analysis was applied to the strong forms represented by their centre of gravity in order to examine the similarity between them and to determine clusters which could correspond to different types of vigilance postures. Within each cluster, we calculated the

hypergeometric probability  $p$  associated to each modality based on a random model. It represents the probability of obtaining the observed frequency in the case of random sampling without replacing: the lower the probability, the more characteristic the modality. Only the modalities with  $p \leq 0.025$  were considered as significant and were retained to describe the clusters (Molemar, 1973). The cluster criterion used in this algorithm was the Ward criterion. All the analyses were carried out with the SPAD.N program.

### 3. Sequential analysis.

For the sequential analysis, all the postures were assimilated to the cluster to which they belong. The frequencies of behaviour pairs defined as the transition from the preceding act to a type of posture, and also from a type of posture to the following, were computed and enabled to be constructed two contingency tables. Then, the hypothesis that the number of transitions between behaviour pairs is independent of the type of posture was tested. If this hypothesis was rejected the cells of each contingency table contributing to the heterogeneity were identified by comparing the observed and expected frequencies calculated on the independent occurrences of the two behaviours via the following formula (Slater & Ollason, 1972):

$$\text{Exp} = (\text{Row sum}) \times (\text{Column sum}) / (\text{Grand sum})$$

According to Haberman (1973) we computed for each cell:

-The standardized residual  $r$  and the variance  $v$  of this residual:

$$r = (\text{Obs} - \text{Exp}) / \sqrt{\text{Exp}}$$

$$v = (1 - \text{Row sum} / \text{Grand sum})(1 - \text{Column sum} / \text{Grand sum})$$

$$\text{-The corrected residual: } r_{\text{cor}} = r / \sqrt{v}$$

When rows and columns of the contingency table are independent, the  $r_{\text{cor}}$  fit a normal distribution with mean and standard deviation respectively equal to 0 and 1. Comparing the absolute value of the  $r_{\text{cor}}$  to the  $z_{\alpha/2}$  critical value of a normal law, the threshold of which is  $\alpha$ , we find the significant residuals (i.e. those with an absolute value  $\geq z_{\alpha/2}$ ).

## Results

Three hundred ninety eight postures which include 68 adult males, 141 adult females, 117 subadults and 72 piglets, were recorded. All the postures coded by the eight presence-absence variables were treated by Multiple Correspondence Analysis. On grounds of clarity, on the first three axes, which accounted respectively for 13.4%, 13.0% and 9.7% of the variance, only the 22 column-points of the column-variables are represented and not the lines-points (fig. 2).

Axis 1 and 2 oppose modalities of the variables «age-sex» (AM, FM, S, P), «snout position» (HS, RS,

LS) and «tail-position» (T1, T2, T3, T4, T5) which represent respectively 80.7% and 74.9% of the variance on the axes 1 and 2. These axes are therefore interpreted as representing change of the postures with the age and sex of the individuals and with the position of the tail and the snout. Axis 3 is essentially explained by the variables «head-position» and «age-sex» (58.0% of the variance of this axis) and opposes the points NH, S and AF to BH, P and AM. Another noticeable feature is the differential gathering of the items of «snout position» (LS, HS, RS) and «tail position» (T1, T2, T3, T4, T5) which reflects a clear association between these 2 body elements. The prox-

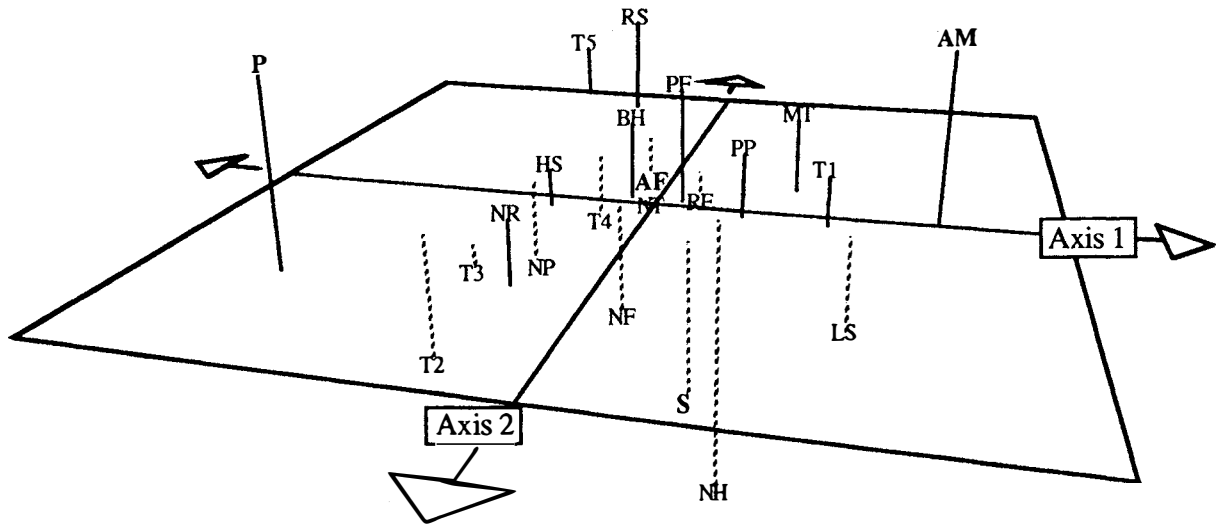


FIGURE 2. Plot of descriptive variables on the first 3 axis of multiple correspondance analysis of vigilance postures: AM, AF, S, P = age-sex class; BH, NH = head position; LS, HS, RS = snout position; MT, NT = tail mobility; T1, T2, T3, T4, T5 = tail position; PF, NF = forelegs position; PP, NP = posterior legs position; RE, NR = ears position.

[Puntos de las variables descriptivas sobre los 3 primeros ejes de la una Análisis de correspondencias múltiples de las posturas de vigilancia: AM, AF, S, P = clases de edad y de sexo; BH, NH = posición de la cabeza; LS, HS, RS = posición de la jeta; MT, NT = movilidad de la cola; T1, T2, T3, T4, T5 = posición de la cola; PF, NF = posición de los anteriores; PP, NP = posición de los posteriores; RE, NR = posición de las orejas.]

imity of the point (NT) with the origin of the axes means that it contributes little to the inertia of each axis, so it is not relevant to distinguish between mobile tail or not for the description of the vigilance posture.

The dynamic cloud algorithm, applied to the coordinates on the first 10 extracted axes, yielded 26 strong forms which grouped individual postures of similar profiles. These stable classes were obtained by the crossing of two successive partitions and were constructed from six initial nuclei chosen at random among the initial data. Finally, a hierarchical cluster analysis expressed the degree of similarity between the strong forms and allowed them to be distributed into five clusters which will be assimilated to five types of vigilance postures. In order to define what these five large classes actually meant in terms of the descriptive variables the proportions of the more characteristic ( $p \leq 0.025$ , hypergeometric probability) modalities were calculated for each cluster (table I).

It is worth noting that each type of posture, except cluster 4, corresponds to a specific age and sex category, and is essentially characterized by the position of the snout and the tail. A lowered position of the snout is often associated with a lowered position of the tail. On the other hand the position of the forelegs and the distinction between mobile and not for the tail appear not to be relevant for the description of the postures, this is supported by the factorial analysis.

With a view to examine the biological validity of the classification into five large clusters we examined the frequencies of first order transitions between individual postures and the preceding and following behaviour (table II). For this analysis, the co-occurrences with social interaction and comfort activity were too small to be considered.

The postures of cluster 1 are preceded or followed more often by foraging activity (F and/or S) and less often than expected by displacements (SD and/or FD). The postures of cluster 2 are indifferently preceded by any behavioural category and followed more often by a slow displacement and less often than expected by a fast displacement. The postures of cluster 3 are preferentially preceded by a slow displacement, rarely by feeding, and followed by any behaviour. The postures of cluster 4 are especially preceded and fol-

lowed by fast displacement and rarely followed by foraging activity. Finally the postures of cluster 5 did not occur in a particular behavioural context, except for slow displacement (table II).

Finally the duration of some posture types can vary significantly: the mean duration (second +/- SE) of postures of cluster 2 (13.4 +/- 1.8 ) and 5 (3.8 +/- 0.2) differ significantly from the main mean (6.6 +/- 0.3) calculated for all the postures (t test,  $p < 0.01$ ).

TABLE I. Characteristic modalities of each class of postures. Class/Mod = percentage of the class for the modality, Mod/Class = percentage of the modality in the class; p = hypergeometric probability associated to each modality.

[Modalidades características de cada clase de posturas. Class/Mod = porcentaje de la clase para la modalidad, Mod/Class = porcentaje de la modalidad en la clase; p = probabilidad hipergeométrica asociada a cada modalidad.]






Class of postures (size)	Modality	Class/Mod	Mod/Class	p	
P1 (119)	S	84.6	83.1	0.000	
	LS	51.1	54.6	0.000	
	NH	58.0	39.5	0.000	
	T3	44.9	26.0	0.003	
	T1	36.4	55.4	0.006	
P2 (61)	AM	89.7	100.0	0.000	
	T1	32.0	95.0	0.000	
	PP	22.0	83.6	0.000	
	LS	25.2	52.4	0.001	
P3 (110)	AF	74.4	95.4	0.000	
	T5	93.7	40.9	0.000	
	RE	38.9	97.2	0.000	
	RS	55.0	20.0	0.000	
	BH	30.9	89.0	0.002	
P4 (38)	T4	100.0	100.0	0.000	
	RS	22.2	21.05	0.021	
	HS	12.2	73.7	0.025	
P5 (70)	P	90.2	92.8	0.000	
	NR	45.5	80.0	0.000	
	HS	27.7	91.4	0.000	
	T2	45.1	40.0	0.000	
	T3	33.3	32.8	0.000	
	BH	20.2	91.4	0.003	
	NP	23.3	55.7	0.008	

TABLE II. Observed and expected values for behaviour pairs between type of posture and preceding or following act.

[Valores observados y esperados para los pares de comportamiento entre el tipo de postura y el acto que precede o que sigue.]

Behaviour pair <sup>a</sup>	Relative Frequency <sup>b</sup>	Observed/Expected	Corrected residuals <sup>c</sup>
F-P1	>	38/26.4	3.1
S-P1	>	17/9.5	3.0
SD-P1	<	51/59.9	-2.0
FD-P1	<	7/17.2	-3.2
F-P2	<	13/12.6	0.1
S-P2	=	5/4.5	0.2
SD-P2	=	32/28.6	1.0
FD-P2	=	4/8.2	-1.7
F-P3	<	15/25.7	-2.9
S-P3	=	5/9.2	-1.7
SD-P3	>	71/58.3	2.9
FD-P3	=	19/16.7	0.7
F-P4	=	4/8.9	-2.0
S-P4	=	0/3.2	-
SD-P4	=	21/20.1	0.3
FD-P4	>	13/5.8	3.4
F-P5	=	19/15.4	1.1
S-P5	=	5/5.5	-0.3
SD-P5	<	27/35.0	-2.2
FD-P5	=	15/10.0	1.9
P1-F	>	26/17.5	2.6
P1-S	=	19/13.8	1.7
P1-SD	=	48/53.1	-1.2
P1-FD	<	13/21.5	-2.4
P2-F	=	5/9.3	-1.6
P2-S	=	10/7.2	1.2
P2-SD	>	36/28.0	2.3
P2-FD	<	5/11.4	-2.3
P3-F	=	15/17.8	0.9
P3-S	=	12/14.0	-0.7
P3-SD	=	54/54.1	0.0
P3-FD	>	29/21.9	2.1
P4-F	<	2/6.3	-2.0
P4-S	<	0/4.9	-2.5
P4-SD	=	20/19.0	0.3
P4-FD	>	16/7.7	3.5
P5-F	=	13/10.1	1.1
P5-S	=	7/7.9	-0.4
P5-SD	=	27/30.6	-1.0
P5-FD	=	14/12.4	0.6

<sup>a</sup> P1, P2, P3, P4, P5 = Postures of clusters 1, 2, 3, 4, 5. F = feeding, S = searching for food, SD = slow displacement, FD = fast displacement.

<sup>b</sup> Relative frequency indicates whether a given behavior pair occurs more often than (>), as often as (=), or less often than (<) expected based on the independent occurrences of the two behaviours involved.

<sup>c</sup> For absolute values of corrected residuals  $\geq 1.96$ ,  $P < 0.05$ .

[<sup>a</sup> P1, P2, P3, P4, P5 = Posturas de los grupos 1, 2, 3, 4, 5. F = alimentarse, S = buscar alimento, SD = desplazamiento lento, FD = desplazamiento rápido.

<sup>b</sup> La frecuencia relativa indica si un comportamiento se produce más a menudo (>), igual (=), o menos (<) frecuentemente que el otro, que si los dos se sucedieran de forma independiente.

<sup>c</sup> Para los valores absolutos de los residuos corregidos  $\geq 1,96$ ,  $P < 0,05$ .]

## Discussion

Our results obviously reflect the method of classification to some extent, but this would have been so whatever procedure we used. Nevertheless analysis allowed the determination of typical configurations of the vigilance postures which emphasize two processes.

The first one corresponds to a sensorimotor coordination of the movements of body elements that confirms previous studies on other ungulate species (Kiley-Worthington, 1976 ; Von Czehak & Altmann, 1983). This coordination is the strongest for the position of the snout, the tail and the ears. Because of their motor characteristics, each type of posture is then associated to a differential activation of sensory systems (e.g. smelling, sight and hearing). So, the postures P3 and P4 are associated to a multi-sensory exploration of the surroundings which privileges especially the smelling. On the other hand, the postures P1 and P2 does not indicate a preferential activation of a sensory system. The second is the influence of age and sex. Adult females are characterized by tonic posture with head and tail up when adult males display relaxed posture. The subadults and piglets show an intermediate state. Moreover the duration of the postures for the different age classes can vary significantly according to the cluster to which they belong.

Vigilance behaviour has been the topic of numerous field studies and modelling both on birds and mammals, and the main functions attributed to this behaviour were the detection of predators, observation of conspecifics, avoidance of kleptoparasitism and searching for food (Bertram, 1980; Elgar, 1989; Quenette, 1990). Among these, authors have especially stressed the antipredator function at the expense of others. More generally, this behaviour can be considered as a phenotypic expression of a general endogenous mechanism regulating the levels of vigilance for the perception of the environment. Recent studies made on mammals or birds support the hypothesis of such endogenous processus able to produce periodic fluctuations of the durations of the observed vigilance events (Desportes et al., 1989, Quenette, 1992). It seems that the existence of such endogenous rhythms independent of any external con-

trol is a fundamental characteristic of living systems (Connor, 1985; Jacklet, 1985). They correspond to a temporal self-organizing phenomenon whose amplitude and periods of oscillation depend on the functioning of the whole system (Goldbeter, 1990).

So, from a functional point of view, we may distinguish predictive vigilance behaviour from responsive acts, in that the former involves attention to an unspecified exploration of the environment whilst the latter involves attention for the detection of a determined perturbation from the environment (Dimonds & Lazarus, 1974; Craig, 1985). In this situation the postures of clusters 3 and 4, especially characterized by the higher positions of the snout and the tail, are probably associated to a high level of vigilance and they may correspond either to the detection of a disturbance for any age and sex class (cluster 4) or for the females to a component of maternal behaviour (cluster 3) because the period of observation took place just after the birth of the young. On the other hand, the postures of clusters 1 and 2 are related to a lower level of vigilance and coupled with an unspecified scanning of the surroundings.

The sequential analysis strengthens this interpretation insofar as the vigilance postures occur in different behavioural contexts (defined by the nature of the preceding and subsequent behaviour) which correspond either to a slow or fast locomotion bout (P3 and P4) or to a quiet foraging bout (P1 and P2). Jarman (1987) and Alados (1985) have already mentioned that the different postures of vigilance indicate various levels of arousal according to the context. For the postures of cluster 5, which essentially contains piglets, there is not an obvious interpretation because they did not occur in a specific behavioural context.

This fine description of vigilance postures which reveals the motor diversity of this behaviour appears to be a prerequisite for functional studies. According to the morphology and duration of a posture, the capacity to perceive any perturbation from the environment is strongly altered and then the function of the behaviour can change. Such results involve to update the most models on vigilance behaviour which assume implicitly or explicitly that the vigilance behaviour is negligible duration and uniform and is only concerned with predators detection.

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## Resumen

*Tipología de la postura de vigilancia en el jabalí (Sus scrofa): aproximación descriptiva y secuencial.*

Una descripción detallada de la postura de vigilancia en el jabalí ha sido realizada sobre animales en cautividad utilizando la posición relativa de seis partes del cuerpo. El análisis ha permitido determinar cinco tipos de postura que se diferencian ampliamente según la posición de la jeta, la cabeza y la cola.

Esta tipología pone de manifiesto la existencia de dos procesos que corresponden a la coordinación sensora-motriz de los segmentos corporales asociados a cada tipo de postura y a un proceso que traduce la influencia de la edad sobre la morfología de la postura. Las hembras adultas manifiestan sobre todo una postura tónica (P3) con la cabeza y la cola en posición alta cuando los machos adultos presentan un tipo de postura más relajada (P2). Los jabatos y los subadultos se caracterizan por posturas (P1 y P5) asociadas a posiciones intermediarias de los segmentos corporales. Además ciertas clases de postura varían de forma significativa en referencia a la media del conjunto de las posturas.

El análisis secuencial muestra también que cada tipo de postura depende de su contexto comportamental definido por la naturaleza del acto que lo precede o que lo sigue. Las posturas P3 y P4 se observan preferencialmente durante las fases de desplazamiento rápido o lento y las posturas P1 y P2 en fase de alimentación. Las posturas P5 no se manifiestan en un contexto comportamental específico.

Estos resultados sugieren que estos tipos de posturas, por sus duraciones y su morfologías, correspon-

den verosímilmente a diferentes funciones de la actividad de vigilancia asociadas a diferentes niveles de vigilancia. Esta observación subraya la necesidad de tener en cuenta esta variabilidad para modelizar el comportamiento de vigilancia.

## References

- Alados, C.L., 1985. An analysis of vigilance in the spanish ibex (*Capra pyrenaica*). *Z. Tierpsychol.*, 68: 58-64.
- Barlow, G.W., 1977. Modal actions patterns. In: *How animals communicate?*: 98-136 (T.A. Sebeok, Ed.). Indiana University Press: Bloomington.
- Benzecri, J., 1973. *L'analyse des données. II. L'analyse des correspondances*. Dunod: Paris.
- Celeux, G., Diday, E., Govaert, G., Lechevalier, Y. & Ralambondrainy, H., 1989. *Classification automatique des données*. Paris: Dunod.
- Colgan, P.W. & Smith, J.T., 1978. Multidimensional contingency table analysis. In: *Quantitative Ethology*: 145-174 (P.W. Colgan, Ed.). Wiley and sons: New York.
- Connor, J.A. 1985. Neural pacemakers and rhythmicity. *Ann. Rev. Physiol.*, 47: 17-28.
- Craig, A., 1985. Vigilance: theories and laboratory studies. In: *Hours of work*: 107-121 (S. Folkards & T.H. Monk, Eds.). Wiley and sons: New York, Brisbane, Toronto, Singapore.
- Dardaillon, M. & Teillaud, P., 1987. Ethogramme du sanglier adulte et du marcassin (*Sus scrofa L.*). *Monitore zool. ital.*, 21: 41-68.
- Desportes, J.P., Metcalfe, N.B., Cezilly, F., Lauvergeon, G. & Kervalla, C., 1989. Tests of the sequential randomness of vigilant behaviour using spectral analysis. *Anim. Behav.*, 38: 771-777.
- Diday, E., 1982. *Elements d'analyse des données*. Paris: Dunod.
- Dimond, S. & Lazarus, J., 1974. The problem of vigilance in animal life. *Brain Behav. Evol.*, 9: 60-79.
- Drummond, H., 1981. The nature and description of behavior patterns. *Perspect. Ethol.*, 4: 1-33.
- Elgar, M.A., 1989. Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biol. Rev.*, 64: 13-33.
- Goldbeter A., 1990. *Rythmes et chaos dans les systèmes biochimiques et cellulaires*. Paris: Masson.
- Guttinger, H.R., Wolffgramm, J. & Thimm, F., 1978. The relationship between species specific song programmes and individual learning in songbirds: a study of individual variation in songs of canaries, greenfinches, and hybrids between the two species. *Behaviour*, 65: 241-262.
- Jacklet J.W., 1985. Neurobiology of circadian rhythms generators. *Trends Neurosci.*, 8: 69-72.
- Jarman, P.J., 1987. Group size and activity in eastern grey kangaroos. *Anim. Behav.*, 35: 1044-1050.
- Kiley-Worthington, M., 1976. The tail movements of ungulates, canids and felids with particular reference to their causation and function as displays. *Behaviour*, LVI: 69-115.
- Lima, S.L., 1990. The influence of models on the interpretation of vigilance. In: *Interpretation and explanation in the study of animal behavior: comparative perspectives* Vol. 2: 448 (M. Bekoff & D. Jamieson, Ed.), Westview Press, Boulder, Colorado.
- Maynard Smith, J., 1982. *Evolution and the theory of games*. Cambridge University Press: Cambridge.
- Molemar, W., 1973. Simple approximations to the poisson, binomial and hypergeometric distributions. *Biometrics*, 29: 403-407.
- Morgan, B.J.T., Simpson, M.J.A., Hanby, J.P. & Hall-Craggs, J., 1974. Visualising interaction and sequential data in animal behaviour: theory and application of cluster-analysis method. *Behaviour*, 56: 1-43.
- Quenette, P.Y., 1990. Functions of vigilance behaviour in mammals: a review. *Acta Oecologica*, 11 (6): 801-818.
- Quenette, P.Y. & Desportes, J.P., (in press). Temporal and sequential structure of vigilance behaviour of wild boar (*Sus scrofa*). *J. Mammal.*
- Schleidt, W., 1974. How fixed is the fixed action pattern. *Z. Tierpsychol.*, 36: 184-211.
- Slater, P.J.B., 1978. Data collection. In: *Quantitative Ethology*: 7-24 (P.W. Colgan, Ed.), Wiley Interscience New York.



Slater, P.J.B., 1981. Individual differences in animal behavior. *Perspect. Ethol.*, 4: 35-49.

Slater, P.J.B. & Ollason, J.C., 1972. The temporal pattern of behaviour in isolated male zebra finches:

transition analysis. *Behaviour*, 42: 248-269.

Von Czehak, E. & Altmann, D., 1983. Audio-visual orientation responses in zoo animals. *Zool. Jb. Physiol.*, 87: 231-239.

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