

**THE ORGANISATION OF PERCEPTUAL PROCESSING IN  
SIKA DEER (*Cervus Nippon Nippon Temminck 1838*)**

By  
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In the last century, there has been a shift in the biological and psychological literature from seeing deer as biological entities, to seeing them more as social individuals within a larger group or society. Despite the increasing volume of literature, however, the visual perception of deer and the factors mediating their flight response have remained virtually unstudied. It is to these areas of behaviour, as well as to the sexual and aggressive behaviour of deer, that this paper addresses itself.

Darling (1937) discusses the visual perception of the Red deer in his typically anecdotal style and raises some interesting points in the process. Despite noting the deers' large lack of stereoscopic vision, he states, "The sight of deer is exceedingly acute to movement up to long distances, and in this way they are superior to most men." Darling also makes the slightly surprising claim that at 60-70 yards, the movement of an observer's eyes is detectable. This would require detecting a change in the visual field in the order of 2-3 microns at the retina. He adds, "The eye and its movements are quite enough to shift deer. They do not like being looked at even if they are tame". Darling's final comment of interest here is in connection with specific predator stimuli. "Human beings in certain places, in certain positions, and gently moving on their way, are harmless creatures, it seems, but highly dangerous under other sets of conditions." Underlying his words is the assumption that human being are recognised by the deer as a specific predator stimulus. Pleasant reading though this makes, Darling's approach unfortunately leads to a somewhat muddy picture, more suited to the arm-chair romantic than the scientist. We can, however, draw out our first set of null-hypotheses from these observations.

- H:1.1 The presentation of a figure containing features characteristic of a predator figure elicits the same order of fear response as does the presentation of a simple non-predator figure.
- H:1.2 The presentation of a figure with eyes elicits the same order of fear response as does presentation of the same figure without eyes.
- H:1.3 The presentation of a moving figure elicits the same order of fear response as does the presentation of the same stimulus when it is stationary.

The work of Curio (1975) provides scope for a more detailed analysis of the organisation of the perceptual capabilities of deer. In his study of Pied Flycatchers, Curio coins the term "sign-stimuli" by which he means any features of a natural stimulus (such as, in this study, another deer or a human) which produce a reaction in the deer that can be altered by changing the feature involved. This change might be a change in the intensity or a change in the nature of the response. For instance, if a deer with 3-point antlers produces a different reaction from a female deer to that produced by an identical deer with 4-point antlers in an identical situation, then the antler size can be termed a sign-stimulus.

Curio proposes that there exist at least two independent perceptual channels, each of which separately deals with a specific predator figure (such as a human). He demonstrates this by **combining** sign-stimuli from two different predator figures and observing how the Pied Flycatchers' reactions are altered by different combinations. Put simply, Curio's "two-channel" hypothesis would predict that such a combination of predator sign stimuli would produce a reaction which was either the same as, or less intense than the reaction produced by either of the contributory sign-stimuli. This should still be true if the features are altered in some way. Curio's model seriously challenges the conventional and widely accepted concept of perceptual organisation hitherto developed (e.g. Tinbergen, 1951; Schleidt, 1962; 1964).

According to this model, then, one would not expect to find a predator sign-stimuli (PSS) combination (with features from two predator figures) producing either a stronger response than its contributory figures or a novel response. This enables us to propose our second set of hypotheses:

- H:2.1 Presentation of a stimulus constructed from sign stimuli taken from two contributing figures elicits the same **quantitative order** of response as one or other of the two contributing figures.
- H:2.2 Presentation of a stimulus constructed from sign stimuli taken from two contributing figures elicits the same **qualitative type** of response as one or other of the two contributing figures.

In addition, the effects of group size and membership on behaviour remains almost completely unresearched and this study provides an ideal opportunity to further research this area. Hence, our final set of hypotheses:

- H:3.1 The fear response of individual deer is unaffected by group size.
- H:3.2 The fear response of individual deer is unaffected by the number of stags in the group.
- H:3.3 The fear response of individual deer is unaffected by the number of hinds in the group.

## MATERIALS AND METHODS

### The Study Area

The experimental procedures were carried out on Lundy. Here winds are mostly Westerly or South-Westerly leaving the East side of the island relatively sheltered. It is along this coastline that the Sika deer live. The terrain consists of a series of gullies which get larger towards the North end. The habitat of the East side is made up of grasses and small shrubs interspersed by areas of rhododendron which cover the ridges between the gullies. The rhododendrons grow to about seven or eight feet in height and provide ideal cover for the deer's lairs. In the summer, the slopes are covered in ferns which grow as high as six feet, making observation extremely difficult. North of Gannet's Combe, the terrain becomes rugged heathland and the gullies are marshy throughout all but the driest weeks of the year. The deer have no natural predators on the island.

### The Study Population

The population of Sika deer on the island was made up of an estimated five stags, thirteen hinds and two fawns. The population size is likely to have changed slightly during the study time with one known death of a hind and two reported deaths occurring during the ten day pilot study cited previously. All three reported deaths occurred as a result of the deer grazing too close to the cliff edge. The two fawns were labelled as such throughout the study period due to the absence of antlers and their markedly smaller size. It is thought they were both hinds. The ages of the deer were not determined, but the stags were aged approximately by the number of their antler points.

### The Study Period

The first experimental procedure was carried out between September 1st and September 22nd 1987 and the second between December 12th 1987 and January 4th 1988. Therefore a total of 42 days was spent on the island. During this time, an estimated 250 hours were spent tracking the deer, of which approximately 50 hours were spent observing the deer or taking data from them. Data collection was carried out during the first three to four hours after sunrise and the last two to three hours before sunset, with the greater periods of time being possibly only in the summer when the days were longer.

### The Study Materials

For the first experimental procedure, cardboard figures of a lifesize man from the waist up and a 'tombstone' of a similar height and width were used. Both were covered with black plastic sheeting. In addition, two supernormal 'eyes' measuring approximately 11cm were used. These were white with black pupils of diameter 4cm. Again, these were cardboard covered with plastic sheeting. The two figures were each supported by a wooden pole, long enough to provide a short handle at the bottom. For the second experimental procedure, a British army combat jacket, green waterproof trousers and a navy blue balaclava were worn for all data collection. In addition, a varnished 2ft x 3ft wooden silhouette of a Sika deer with detachable antlers and a green safety helmet, also with detachable antlers fitted, were used. The deer silhouette was equipped with a sturdy handle and a viewing 'peep-hole' and support stand for binoculars. The antlers were 1ft 9in long and had four points each. When used with the

helmet, the antlers were mounted on either side, slightly more than half way round from the front and at an angle of 45° to the vertical. During both study periods, data were recorded verbally on a hand-held Dictaphone and 8 x 30 field binoculars were used.

#### **Experimental Procedure No. 1**

In the first experimental design, the 'man' silhouette (hereafter referred to as 'Man') and the 'tombstone' silhouette (hereafter referred to as 'Shape') were used in a total of eight combinations. The three variable were 1) Man vs Shape; 2) Eyes present vs No eyes present and 3) Movement vs No movement. In the 'Eyes present' condition, the two supernormal eyes were stuck in an appropriate place on the figure. In the 'Movement' condition, the figure was moved slowly up and down and from side to side. These combinations can be more simply represented using a three bit binary code, the order of the digits being determined by the order given above. For example 111 signifies a moving Man with eyes; 001 represents a moving shape without eyes, and so on, giving a total of eight stimuli.

Once a deer or group of deer was located, a vantage point was selected downwind of the animals such that one of the eight stimuli could be presented as a silhouette on the horizon. Thus, the distance from the deer was determined by the nature of the terrain. Once the deer had seen the stimulus, its subsequent behaviour was recorded on the dictaphone. This behaviour was later classified under a 'fear rating' score ranging from one to fourteen (see Appendix). Care was always taken to prevent the deer from seeing the experimenter and trials were never carried out until he was satisfied that the deer were unaware of his presence. In addition the distance between the experimenter and the original position of the deer was recorded as was the size and membership of the group.

This procedure was repeated until seventeen trials had been successfully completed, with at least one data point having been collected from each of the eight possible stimuli.

#### **Experimental Procedure No. 2**

In the second experimental design, there were three broad conditions. In the first condition, a deer or group of deer was located and the experimenter situated himself downwind of them at a distance of approximately 120 metres. Having satisfied himself that the deer were undisturbed by his presence and that they were not looking in his direction, the experimenter then sat upright in such a way as to ensure that he was clearly visible from the waist up but not fully or partially silhouetted. This helped to control for figure shape and figure contrast variability. Typically, the deer saw the figure in the grass, showed a certain amount of interest and eventually became satisfied that it was harmless and carried on feeding. At this point, the experimenter carefully lowered himself and approached the deer by a few metres, freezing whenever the deer looked up and only continuing when he was satisfied that the deer were undisturbed by his presence. This procedure was repeated until the sight of the waist-up figure was perceived by the deer as being threatening enough to elicit a flight response. At this point, the Flight Distance (FD) of the deer was established by measuring out the distance between the experimenter and the position of the deer immediately prior to flight. Care was taken by the experimenter never to be seen to move whilst the deer were watching him. If the deer ran off at any time other than when the experimenter was sitting fully upright and motionless, the data were discarded. The deer group size and membership were recorded. This procedure was repeated until nine data points had been collected.

In the second condition, exactly the same procedure was followed using the wooden deer silhouette. The antlers were attached in all trials and the construction was large enough to allow the experimenter to crouch unseen behind it, observing the deer through the peep-hole. Six data points were successfully recorded in this condition.

The third condition again followed roughly the same procedure, this time with the experimenter wearing the helmet and antlers. However, in this condition circumstances sometimes meant that a FD was not established in the normal way but was defined as being the closest distance that the experimenter achieved between himself and the deer. In addition, the starting distance was sometimes considerably less than 120 metres. Once again, group size and membership were noted and full details of the deer's behaviour were recorded onto the dictaphone either as it happened or immediately after flight if circumstances did not permit this. Data in this condition were much fuller and somewhat anecdotal in nature.

## RESULTS

### Experimental Procedure No. 1

The raw data collected in experimental condition No. 1 are shown in full in Table 1.1 below and are summarized in Table 1.2. Multiple regression analysis was performed on the data. Movement had the most significant effect on the deer's fear response (FR) ( $p < 0.005$ ). In addition, the 'Man' stimulus elicited a significantly greater FR than the 'Shape' stimulus ( $p < 0.01$ ) and the presence of eyes on the stimulus also led to a significantly greater FR being elicited ( $p < 0.025$ ). Finally, the further away the stimulus was presented, the lesser was the FR that resulted ( $p < 0.025$ ). The number of hinds in the group and the number of stags in the group had no significant effect on the obtained fear ratings.

**Table 1.1:** Responses of Sika Deer to Silhouettes.

Raw data collected from experimental procedure No. 1. The nomenclature "Group (h) (s)" denotes "Number of (h)inds and (s)tags in the group". The length of vigilance before the given behaviour was elicited is shown.

Stimulus	No.	Group (h) (s)	Distance (m)	Fear Rating	Vigilance (s)	Behaviour	
111	1	1	65	13	126.0	Run home	
101	1	1	50	11	46.0	Gambol home	
	2		65	14	4.5	Run home	
110	1	2	80	3	522.0	Walk = >home	
	2	7	45	11	120.0	Gambol home	
	3	1	65	9	84.0	Run = >home	
100	1	3	65	1	15.0	Grazing	
	2	3	65	1	12.0	Grazing	
011	1	5	35	14	10.0	Run home	
	2	1	30	14	20.0	Run home	
001	1	2	60	11	36.0	Gambol home	
	2	3	80	3	88.0	Walk = >home	
010	1	1	50	1	4.0	Walking (as before)	
	2		3	80	2	161.0	Grazing
	3		3	80	1	12.0	Grazing
000	1	7	80	1	6.1	Grazing	
	2	7	45	1	3.0	Play behaviour	
	3	1	50	1	1.0	Walking (as before)	

**Table 1.2:** Summary of data from experimental procedure No. 1

Stimulus	N	Mean Fear Rating	St.Dev.	Mean Distance(m)	St.Dev.(m)
111	1	13.00	0.00	65.00	0.0
101	2	12.50	2.12	57.50	10.6
110	3	7.67	4.16	63.33	17.6
100	2	1.00	0.00	65.00	0.0
011	2	14.00	0.00	32.50	3.5
001	2	7.00	5.66	70.00	14.1
010	3	1.33	0.58	70.00	17.3
000	3	1.00	0.00	58.33	18.9

### Experimental procedure No. 2

The raw data collected from experimental procedure No. 2 are listed in full in Table 2.1 and are summarized below in Table 2.2. Multiple regression onto FD showed that FDs were significantly smaller in the 'Man-Deer' condition than in either of the 'Man' or the 'Deer' condition ( $p < 0.005$ ). This finding was backed up by Kruskal-Wallis tests ( $p < 0.005$ ) which also showed that the latter two conditions could not be statistically discriminated by the FD (flight distance) measurements obtained. The number of hinds and stags in the group had no significant effect on FD. Further Kruskal-Wallis tests showed that group size had no significant effect on FD in any of the conditions and a Jonckheere trend test similarly showed that there was no significant trend for FD to decrease with increasing group size.

**Table 2.1:** Raw data for experimental procedure No. 2: Distances at which figures elicit flight.

Figure	No.	Flight Distance (m)	Group Membership	
			(h)	(s)
Man	1	70	2	
Man	2	75	2	
Man	3	75	2	
Man	4	85	1	1
Man	5	60	5	
Man	6	55	5	
Man	7	75	1	3
Man	8	75	1	3
Man	9	85	1	1
Deer	1	80	1	1
Deer	2	80	1	1
Deer	3	75	2	2
Deer	4	75	2	2
Deer	5	80	2	2
Deer	6	80	2	2
Man-Deer	1	20		2
Man-Deer	2	20		2
Man-Deer	3	25		1
Man-Deer	4	30	1	
Man-Deer	5	40	3	1
Man-Deer	6	45	3	1
Man-Deer	7	45	3	1

**Table 2.2:** Summary of raw data obtained from experimental procedure No. 2.

Condition	N	Mean FD (m)	St.Dev. (m)	Min. Value (m)	Max. Value (m)
Man	9	72.78	10.03	55.0	85.0
Deer	6	78.33	2.58	75.0	80.0
Man-Deer	7	32.14	11.13	20.0	45.0

Typically, in the 'Man' and 'Deer' conditions, the deer would pay virtually no attention to the figure until it came within about 95 metres. As the figure then came progressively close, the deer would then exhibit the following kinds of reaction.

90-95m : Sharp increase in vigilance time before returning to feeding.

85-90m : Ears brought forwards when vigilant to maximise auditory perception.

80-85m : Deer moves step or two closer to figure, bringing whole body to directly face figure, thereby minimising its own 'target area'.

75-80m : Swaying of the head and neck to gain a perspective view of the figure.

70-75m : Deer comes a few steps closer before finally taking to flight.

These behaviours are brought in cumulatively as the figure approaches, vigilance time continuing to increase as distance from the figure decreases. Also, from about 85m, the deer would lower its neck and head to continue grazing, then stop and bring it up again in a continuous movement. This may be repeated several times before the deer continues feeding.

The behavioural responses in the 'Man-Deer' condition were somewhat different from those described for the other two conditions and varied more significantly from one occasion to another. Therefore, three such occasions will be described in detail in order to draw out the most interesting observations.

i. 4.15pm on Tuesday 22nd December 1987.

Two young stags were located in the gully of Frenchman's Landing. The experimenter approached carefully to a distance of around 80m before presenting himself under 'Man-Deer' conditions. After a couple of minutes, the larger of the two stags saw the experimenter and remained vigilant for some minutes. He then walked slowly along the path he was on until directly below the experimenter, who was some 50m uphill from the deer. The stag stopped several times whilst doing this and remained constantly vigilant. The stag then started walking uphill at an angle of about 45° to the experimenter, advancing by lifting two diagonally opposite legs and then holding his position before bringing them down quickly and changing to the other two legs. After proceeding for some steps in such a manner, the stag would stop with his body broadside to the experimenter, and stare at him as if waiting for some response, before turning and repeating the walk with the opposite side of his body inclined at about 45° to the experimenter. The stag continued to 'zig-zag' his way up the hill, closely followed by his companion, until he was within 20m of the experimenter. At this point, the stag faced the experimenter head on and lowered his antlers once or twice. For his part, the experimenter lost his nerve and lowered his binoculars from his eyes, thus frightening the deer, who ran to the brow of Queen Mab's grotto.

ii. 8.30am on Wednesday 23rd December 1987.

The experimenter was in the process of approaching a hind, north of Ladies Beach, when a stag emerged from the rhododendron bushes a little under 25m away. The stag turned and saw the experimenter, who was already in position under 'Man-Deer' conditions. The stag remained motionless for a few seconds and then swayed his head and neck around in order to gain a better perspective on the experimenter. The stag then started the haunched walk described previously but away from the experimenter. The stag continued this until disappearing into some rhododendron bushes about 60m from the experimenter.

iii. 9.00am on Wednesday 23rd December 1987.

A stag was located on the south side of the Sugar Loaf about 80m from the experimenter, who was just below the brow of the facing hill slope. The experimenter presented himself to the stag under 'Man-Deer' conditions. The stag responded by stamping the ground several times with his left leg before presenting himself broadside to the experimenter and then exhibiting the 'retreating haunched walk' until disappearing over the brow of the Sugar Loaf.

The results obtained from employing the 'Man-Deer' condition with the hinds were different again. In general, much smaller FDs were obtained, but in two instances, possible sexually-related behaviours were elicited. In one case, a hind at a distance of 50m, urinated with her back to the experimenter, whilst keeping her head turned to keep him in her field of view. In the other case, the 'flehmen' response was elicited in a hind at 40m. This behaviour was later observed by the experimenter being exhibited by a hind as part of a courtship ritual, confirming its use by Sika deer hinds in a sexual context.

## DISCUSSION

The results obtained in experimental procedure No.1 allow us to reject hypotheses H:1.1, H:1.2 and H:1.3 and confirm in a more scientific manner, Darling's field observations that figures incorporating movement, the presence of eyes or the shape of a man all elicit greater fear responses than do figures without these attributes which are otherwise similar. The data do not allow us to reject any of the H:3 hypotheses concerning the effects of group size and group membership on the level of fear response.

When features were taken from two stimuli to form a novel stimulus in experimental procedure No.2, the resulting behaviours that were elicited were both qualitatively and quantitatively different: quantitatively different, because the obtained FDs were significantly smaller than in the cases of the two contributing figures; qualitatively different since the rutting response was elicited from the stags and possible sexually-related behaviours were elicited from the hinds. Thus, both H:2.1 and H:2.2 can be rejected. Once again, none of the H:3 hypotheses can be rejected and the overwhelming evidence is that group size and group membership do not play a significant role in the mediation of fear levels in Sika deer.

The rejection of H:2.1 and H:2.2 throw serious doubts onto Curio's two-channel hypothesis but there are some qualifying points which need to be discussed before Curio's hypothesis can be usefully criticised. Firstly, the two contributory figures in procedure No. 2 were not, strictly speaking, predator figures. The 'Deer' figure did not elicit the responses that one might expect to a real stag, probably due to the two-dimensionality of the stimulus and the lack of convincing sign-stimuli (e.g. hair, eyes, legs etc). Although this might seem to undermine the attack on Curio's theory, it still challenges the basic idea of a combination of stimuli from two figures eliciting an equal or lesser response of a similar nature to one or other of the contributory figures. More importantly, even an actual stag would not be expected to elicit the 'retreating haunched walk' found in experimental procedure No. 2. This behaviour would seem to suggest that fear and aggression lie on a continuum rather than being independent drives. In addition, the fact that a novel response is obtained in the 'Man-Deer' condition, which is both qualitatively and quantitatively different from the responses obtained in the 'Man' and 'Deer' conditions, suggest that a hypothesis incorporating independent perceptual decoding mechanisms is inappropriate. Finally, the finding that distance is a mediator of the fear response is indicative of the fact that several factors may be involved in an arousal-based 'response multiplier' system. It is proposed that such a system would connect with the afferent pathways of the decoding mechanisms thus intensifying the response under certain conditions (e.g. when the figure was in close spatial proximity, when eyes were present or when the figure was moving).

Combining these proposals, an alternative model to that of Curio's is suggested here (see Fig 3) which would be mediated by the attribution of arousal to either fear or aggression depending on the output from feature extraction mechanisms (see Schacter & Singer (1962) for an account of how the attribution of arousal can affect behaviour). These mechanisms would be hierarchically arranged to decode features into predator or deer stimuli. The output from these mechanisms would be appropriately weighted and would carry a positive or negative bias — a positive bias indicating a fear-related output and a negative bias indicating an aggression-related output. The outputs would combine at this point and the summation of the coded outputs from the feature extraction mechanisms would then pass through the arousal-based 'multiplier'. The output from the multiplier would then be converted into a point along a fear:aggression continuum and a resultant behaviour would be elicited. This model is shown diagrammatically in Figs. 3.1 and 3.2. Figure 3.1 gives a detailed representation of the model described above and Figure 3.2 is a more generalised version. This, of course, is a highly simplified model and deals only with the case of a predator/stag distinction being made by another stag. However, the general principles remain the same when hinds are considered and when a greater variety of behavioural responses are brought in.

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Fig. 3.1: Proposed 'Feature Extraction and Arousal Attribution' (FEAA) model.

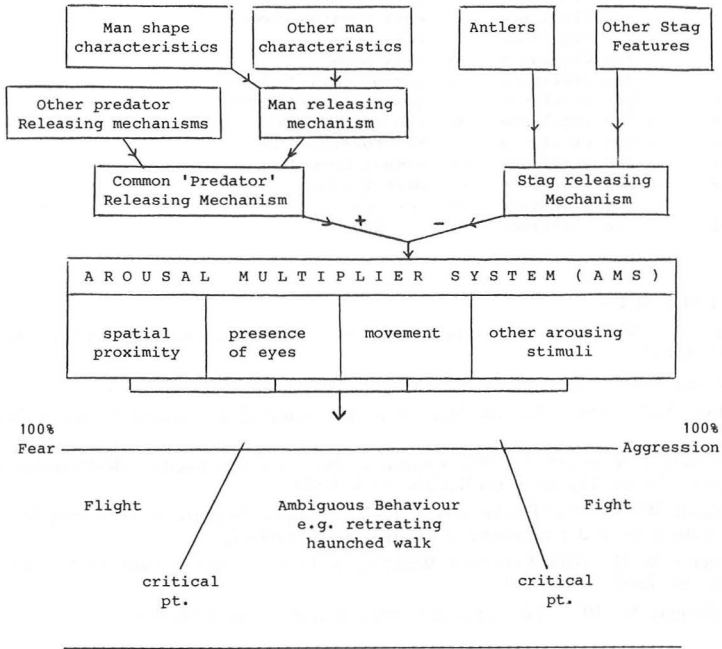
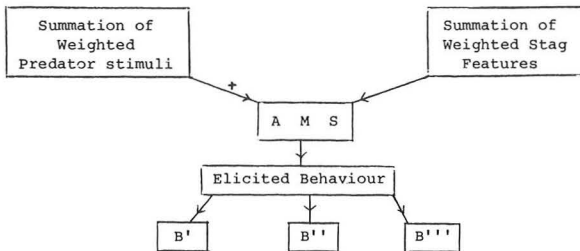


Fig. 3.2: Simplified version of FEAA model. B', B'' and B''' are possible elicited behaviours depending on output of AMS.





## APPENDIX: Fear Ratings used in Experimental Procedure No. 1.

<u>Score</u>	<u>Associated Behaviour</u>
1	< 20s vigilance followed by ( => ) return to previous activity
2	> 20s vigilance => return to previous activity
3	> 20s vigilance => walk towards home
4	< 20s vigilance => walk towards home
5	> 20s vigilance => walk home
6	< 20s vigilance => walk home
7	> 20s vigilance => gambol towards home
8	< 20s vigilance => gambol towards home
9	> 20s vigilance => run towards home
10	< 20s vigilance => run towards home
11	> 20s vigilance => gambol home
12	< 20s vigilance => gambol home
13	> 20s vigilance => run home
14	< 20s vigilance => run home

### REFERENCES

- Curio, E. (1975) Anti-predator behaviour in the Pied Flycatcher. *Animal Behaviour*. 23(1) 1-113
- Darling, F.F. (1937) A herd of Red deer. Oxford. Oxford University Press.
- Eaton, A.D. (1987) The Sika Deer of Lundy island. Unpublished. Available from author.
- Schacter, S. & Singer, J. (1962) Cognitive, social and physiological determinants of emotional state. *Psychological Review*. 69 379-399
- Schleidt, W.M. (1962) Die historische Entwicklung der Begriffe 'Angeborener Anlose mechanismus' in der Ethologie. *Z. Tierpsychol.* 19 697-722.
- Schleidt, W.M. (1964) Verhalten. Wirkungen Ausserer Faktoren auf das Verhalten. *Fortschr. Zool.* 16 469-499
- Tinbergen, N. (1951) The study of instinct. Oxford. Clarendon Press.

**Note 1.** Eaton, A.D. (1987) The social behaviour of deer. Unpublished review available from author at Psychology Dept. of Exeter University at time of writing.