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THE RESPONSE TO EYE-LIKE SHAPES BY BIRDS

II. THE IMPORTANCE OF STARING, PAIREDNESS AND SHAPE

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Abstract. Laboratory-reared 37-day-old white leghorn chicks were placed individually in an area with one of a range of eight three-dimensional stimuli. The chick's behaviour was recorded over a 3-min period. Each bird was exposed to a stimulus which varied in three ways, being either circular concentric (eye-like) or rectangular, single or paired and which appeared to either persistently look at (track) or look away from (avoid) the chick. All three manipulations produced significant effects on how close the bird approached. The most avoided combination was two, tracking, eyelike shapes. The results are discussed in the context of the problems involved in isolating the effective components of stares and the head forwards threat posture.

There is an increasing body of evidence to suggest that many species are particularly responsive to the frontal or en face aspects of conspecifics. This is expressed most clearly in the sensitivity to direct stares. Indeed, Chance (e.g. 1967) has proposed that some primate societies may be (spatially) organized according to an 'attention structure'. This system involves the dominant animal as the focus of attention, subordinates constantly monitoring his activities, maintaining themselves at a distance from him. Thus subordinates would show a high glance frequency. This would, however, be suppressed whenever the dominant looked at them, due to the threatening properties of the fixed stare. In such a situation the subordinate, would look away or 'cut-off' (Chance 1962) the aversive stimulus of the stare, an act which would at the same time reduce the subordinate's own (provocative) frontal aspect. Chance's proposal that attention is the basis of some social system may represent an extreme viewpoint but is still the most comprehensive statement about gaze signalling in animals. McBride, James & Shoffner's (1963) report of neighbour-influenced head orientations in a chicken flock also implies a constant monitoring of other individuals but this is the only other detailed example (besides those supplied by Chance and perhaps by Fox, 1970 for wolves) where an attention structure system might be affecting large numbers of animals.

The major problem with estimating the role of the eyes as a stimulus is that it is rarely possible to exclude interactions with, or effects of, other potential signals. For instance, Marler (1965) comments that (in primates) 'with visual signals the capacity for combining several elements is so widespread as to be virtually the rule rather than the exception'. Thus one can see from van Hooff's (1962) descriptions of higher primate facial expressions that fully opened eyes occur in the alert face, the attack face and the lip-smacking face, expressions which are connected with different sorts of social behaviour. This is less of a problem with birds, which lack extensive facial mobility, but even here they may be a sufficiently wide range of signals, emanating from head crest and bill positions, to prevent accurate analysis of the role of the eyes. The problem is further complicated by the fact that movement of the eyes is often brought about by changes in head position. Thus the frontal threat posture of many birds and its equivalent in primates may well be effective because of the particular aspect of the eyes in that situation but it must also (to an unknown degree) involve the altered perspective of the whole head.

Similar sorts of comments may be made about the role of the eyes in the identification of predators. The work of Curio (e.g. 1969, 19 on Darwin's finches ((Geospizinae) and the pied flycatcher (*Ficedula hypoleuca*) demonstrates that the effectiveness of the eye as a stimulus is very much influenced by other cues from the head and body, at least for the species he uses. Further, the response of birds to predators is often a variable one, as is witnessed by the variation in mobbing behaviour, and it would be unwise to assume that the perceptual processes involved are necessarily any simpler than those concerned with intraspecific behaviour.

This then is the problem: estimation of the potential signalling properties of a stimulus which almost certainly never acts except in concert with other signals. The difficulty is summarized by Cullen (1972, pp. 105–106): 'the real behaviour involves the perception by a companion of complex, subtle actions which crude dummies have no hope of simulating, yet without experimentally teasing apart the total matrix of the behaviour in some way one cannot see how the various components contribute to the whole'.

To accept that there is something special about eyes, i.e. that they are not responded to simply as conspicuous objects, it is essential to show that the animal responds to changes in the appearance of the stimulus in a way that would not be expected if conspicuousness were the only important feature. The most obvious change that can be made to this end is to alter the apparent direction of gaze of the stimulus. A wide variety of animals are thought to be responsive to changes in the appearance of the eyes. Andrew (1963) believes that, for primates at least, such changes originate in protective responses. Thus the thick-tailed galago (*Galago crassicaudatus*) narrows the eyes as other animals turn to face and closes the eyes completely in grooming encounters. Similarly, Lill (1968) reports that chicks close the eyes in allopreening. Such changes could obviously be selected for as signals. Wolves avoid eye contact with a dominant conspecific, looking away with whining noises and body lowering if such contact is made (Fox 1970). That staring can be effective interspecifically is also seen in Exline's (1969) report that averted gaze elicits fewer threat gestures than direct stares in human–rhesus macaque interactions. Gallup, Cummings & Nash (1972) claim that chickens remain immobile (experimental induction) significantly longer when the experimenter stares than when he looks away. In another experiment Gallup (1972) reports that increased immobility is produced by allowing the bird to see either its reflection in a mirror or a dead bird with open eyes. He argues that this is due to the sight of staring eyes. In a 1971 paper Gallup, Nash & Ellison report that chickens immobilized by being turned on their backs beneath a pair of glass eyes stay down significantly longer than birds beneath the eyes covered with tape or beneath dowelling rods. This they interpret as due to the fear-inducing properties of predator eyes. There is also some physiological evidence to suggest sensitivity of animals to staring. Wada (1961) notes that changes in brain-stem activity can be produced in monkeys by the experimenter's stare and Nichols & Champness (1971) recorded significant changes in human galvanic skin response for eye contact versus averted gaze in the recipient. However, in the first case at least, novel objects are equally effective in eliciting the response. The most convincing evidence of acute sensitivity to eye contact comes from Gibson & Pick (1963). Using human subjects and a 'yes'–'no' response they demonstrate that the observed person can detect an angular displacement of the eyeball of less than 3 degrees at 2 m, corresponding to looking at the bridge of the nose rather than the edge of the face. Human infants of less than 4 months are also sensitive to gaze direction, using it as a cue for where to look themselves (Scaife & Bruner 1975).

Among the other cues suggested as possibly involved in eye recognition have been shape and number (Coss 1972). Coss believes that the property of being paired is more important than the patterning. His experimental procedure basically involves variations on a flat circular-pattern scheme. Using a variety of primates, normal and autistic children and normal human adults, he reports levels of visual fixation to the 'optimal' arrangement of two, horizontal, concentric-circular elements compared with other numbers, other orientations and, in one experiment other (less circular) shapes. In further tests he reports findings using pupil dilation or brow-movement techniques. In the majority of the experiments he proves his point by finding a persistent differential response in line with his hypotheses. However, there are problems in interpreting the data, for instance whether a difference in gaze fixation between two models implies aversion to one or attraction to the other model or both of these things. Further, Coss notes in his normal children experiments that only one subject reported, in response to questions, that the patterns were perceived as eyes. Coss regards this as evidence for subliminal responses but there seems no reason why it may not purely be a case of lack of similarity. However, whatever the underlying explanations, a difference between two and one was demonstrated.

This paper describes an experiment with chickens to estimate whether eye-like stimuli, effective in increasing avoidance when displayed on the head of a hawk or strange bird (non-conspecific) (Scaife 1976) are themselves avoided when presented in isolation. If the birds respond to the stimuli as eyes they should avoid 'staring' more than 'averted 'patterns. The generality of Coss's conclusions on number and the effects of pattern shape are also tested for.

Methods

Eighty male leghorn chicks purchased at 1-day-old from a commercial hatchery and comunally housed in a windowless room were maintained on a 14-hr on/10-hr off photoperiod at circa 20°C. All were healthy and habituated to the proximity of humans. They were tested at 36 or 37 days old.

Birds were tested in a windowless room away from the home environment. They were transported in their home cages to the test room, and left undisturbed overnight before the day of testing.

The testing area was a cubicle 24 × 12 × 27-m high. The floor was grey plastic and three walls were white. A hessian curtain was used to seal the open end. This acted as an efficient one-way screen. The floor was marked with chalk into eight zones, each 30 × 120 cm. Zones were arranged parallel to the hessian (observer end) wall. The stimulus to be tested was poked through a hole in the curtain (see Fig. 1).

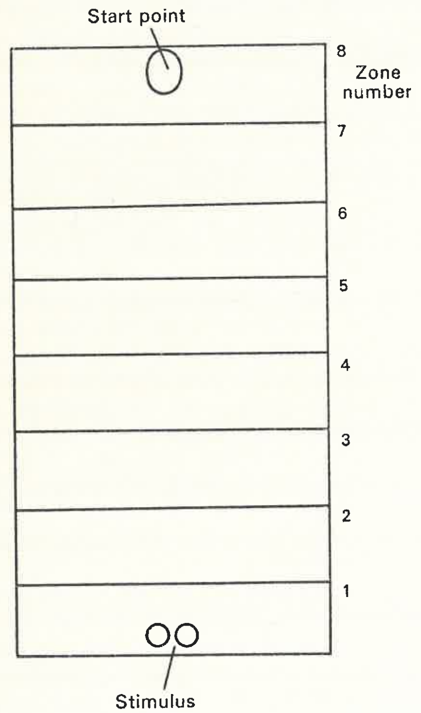

Fig. 1. Plan of test arena.

Tests were carried out in the following manner. A bird was taken from the holding pen and carried to a wooden confinement box which was upended over the bird placed at the mid-point of zone 8. The box was connected via a rope and pulley system to a point outside the arena from where it could be raised, freeing the bird. The stimuli (listed below) were supported by a camera tripod behind the curtain, and protruded through a hole in the hessian screen at about 10 cm above chicken eye level. The tripod ball and socket mounting allowed the stimuli to be moved in the horizontal and vertical planes.

After the birds were released from their confinement they usually remained immobile for a few seconds. Any bird not moving at the end of 60 s was discarded. During this period the stimuli were kept covered with a hessian flap and only on the first movement was the test initiated. At this point the flap was lowered with a deliberately jerky motion, which drew the bird's attention to the now exposed stimulus. The stimulus was left unmoved for 5 s and then manipulated in a predetermined manner as explained below. Birds were left in the arena for 3 min after initiation of the test, then removed, marked and returned to the pen.

Each stimulus condition could be classified in one of two ways on three separate counts.

(A) Shape. Alternatives were either eye-like (E), a glass hemisphere, 2·54 cm diameter with 1·27-cm black 'pupils' and surrounding yellow 'iris'; or strip (S), a Perspex rectangular block 5·08 cm × 2·54 cm × 1·25 cm with a central horizontal black rectangle 2·54 cm × 0·64 cm and yellow surround, Fig. 2. In both cases patterns were painted on the front surface.

(B) Number. There could be either one or a pair of the shapes.

(C) Behaviour. Stimuli either track (T) with the pattern moving and carefully aimed so that it constantly 'looks at' the bird's head wherever it moves, or avoid (A), the pattern moving in a similar way but 'looking' at a point just in front of the bird's feet. The pattern was still clearly visible but not apparently oriented towards the head. Differences between T and A correspond to differences in angle of between 8 and 26 degrees depending on where the bird was located within the arena.

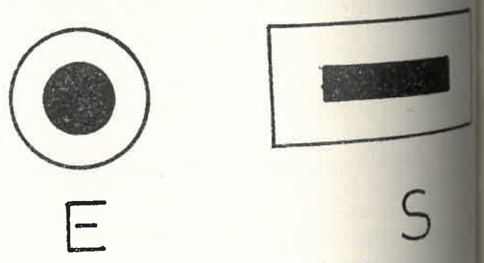

Fig. 2. Stimulus shapes.

All combinations were used. There were, therefore, eight test conditions each using ten birds. Each condition is referred to by its compound label. Thus 2ET indicates two eyes tracking, 1SA indicates one stripe avoiding and so on.

Each bird was used for only one test. Subjects were chosen randomly for a particular test and tests were performed in random sequence. The experiment was completed within a 2-day period.

The position of the bird was noted continuously over the test period. The measure adopted was termed 'average position'. This is simply the mean point of the distribution of time spent in the eight zones. A bird which spent all its time in zone 8 would receive a score of 8·5 since the zone is considered to run from 8 to 9. A score of, say 5·5 means that the subject spent equal amounts of time either side of the midpoint of zone 5. Zone entry was scored whenever both feet were over the zone boundary.

Results and Discussion

The data do not follow a normal distribution and are therefore subjected to a log transform. All analysis is on log scores although the data themselves are given as untransformed values.

The basic data for all subjects are given in Table I, grouped according to the stimulus presented. The table gives the group means at three levels of representation. Table I(a) shows means for groups of birds classified on one factor summed across the other two, Table I(b) means for groups classified on two factors, summed across the other one, and Table I(c) means for groups classified on three factors. Thus each row in (a) represents forty birds, in (b) twenty birds and in (c) ten birds.

These data are analysed in Tables II, III and IV. Table II presents a 2 × 2 × 2 factorial analysis of variance on the effects of the three factors of shape, number and behaviour of the stimuli. Tables III and IV represent further analysis of the data using a Student–Newman–Keuls test (Sokal & Rohlf 1969) to separate the groups from Tables I(b) and I(c), i.e. those groups classified on two and three factors respectively. The purpose of this test is to compare differences between group means using the range as the basic statistic. The effect of altering single factors is also shown graphically in Fig. 3. These analyses will now be discussed with respect to specific questions.

Table I. Average Position Means Given for Groups Classified on (a) One Factor Summed Across the Other Two; (b) Two Factors Summed across the Third and (c) Three Factors

(a) One factor	E	6·78	1	5·99
	S	5·89	T	6·58
	2	6·68	A	6·09
(b) Two factors	2E	6·99	1T	6·28
	1E	6·57	1A	5·75
	2S	6·37	ET	7·08
	1S	5·46	EA	6·47
	2T	6·93	ST	6·13
	2A	6·43	SA	5·70
(c) Three factors:	2ET	7·22	2ST	6·65
	2EA	6·76	2SA	6·1
	1ET	6·85	1ST	5·61
	1EA	6·19	1SA	5·31

(a) The effect of shape. The data reveal, Table II, that stimuli of circular shape are approached significantly less than are the rectangular patterns.

(b) The effect of number. An increase in the number of stimuli presented from one to two caused a significant increase in avoidance, Table II.

The hypothesis of a real difference between eye-like and control stimuli in terms beyond contour and area is supported by the finding of a smaller effect of doubling the stimulus number for the circular as opposed to the non-circular, Fig. 3(b). A view of one eye would be the commonest sight of a conspecific in the chicken's social environment and one might expect it to attend to the 1E stimulus quite strongly if it pays attention to conspecific eyes in the 'wild'. A rise in response to two would be expected on grounds of increased stimulation (greater area, etc.) alone. The question of whether two is a 'biologically significant number' (my phrase)

Table II. Analysis of Variance on Average position Data (Log Scores)

Source	SS	*df*	MS	*F*	Variance Component (%)
E–S	0·1851	1	0·1851	11·2865**	40·6
1–2	0·1285	1	0·1285	7·8353**	27
T–A	0·0854	1	0·0854	5·2073*	16·6
E–S/1–2	0·0108	1	0·0108		
E–S/T–A	0·0122	1	0·0122]		
1–2/T–A	0·0009	1	0·0009]		
E–S/1–2/T–A	0·0046	1	0·0046		
Residual	1·1826	72	0·0164		15·8
Total	1·6101	79			

Key to table: E = eyelike; S = stripe, T = track. A = avoid.
$^{**}P < 0{\cdot}01$, $^{*}P < 0{\cdot}05$.

Table III. Student–Newman–Keuls Comparison Between Means Classified on Two Factors Summed Across the Third for Average Position

(i)	2E	1E	2S	1S
(ii)	2T	2A	1T	1A
(iii)	ET	EA	ST	SA

Means arranged from furthest to closest away from stimulus.
Underscored means not significant different at $\alpha = 0{\cdot}05$.

as Coss (1972) claims, is arguable. Coss's evidence is derived from findings of decreased responsiveness, on what he describes as a gaze fixation measure, to two versus one or three-concentric-circular patterns. He equates avoidance with lack of fixation. The comparison of two with three was not made in the present experiment. It was expected that if two was a 'significant' quantity of eye-like shapes then it should have been possible to show that differences in response to 2E (two eyes) versus 1E are greater than for 2S (two stripes) versus 1S.

In other words two effects are postulated. One is the increased stimulation due purely to the physical increase in total stimulation due purely to the physical increase in total stimulus

Table IV. Student–Newman–Keuls Comparison Between Group Means Classified on Three Factors for Average Position

2ET	1ET	2EA	2ST	2EA	2SA	1ST	1SA

Means arranged as in Table III.

area. This should be the same for the transition from 1E to 2E as for the transition from 1S to 2S. The second factor is that of 'completing the gestalt' for the 1E to 2E transition, i.e. giving the closest impression of real eyes. This should not hold for the 1S to 2S transition since these patterns lack the basic attribute of circularity and number change alone cannot, therefore, complete a 'gestalt' in this case. However, the non-significant interaction effect E-S/1-S, Table II, shows that there is no difference between the two transitions, 1E to 2E and 1S to 2S. This makes sense, as argued above for chickens. It is not a contradiction of Coss's claims for primates. However, he does not restrict the scope of his remarks to that group alone. The results of this experiment would indicate that this may be unwise.

(c) The effect of behaviour of the stimuli. Alteration of the movement pattern of the stimuli from avoid (A) to track (T) produced a significant difference in the closeness of approach, Table II. These effects were the most interesting results obtained. In the introduction it was argued that to accept that there was something 'special' about eye-like objects, it was essential to show that an animal would respond to changes which did not seem to affect the conspicuousness of the stimulus but did alter its appearance in a biologically relevant manner. The demonstration of significantly enhanced avoidance to 'staring' stimuli would seem to partially fulfil this role. The T stimulus did not differ from its A counterpart in terms of simple parameters like contour, area, amount of colour (s). The difference was one altered perspective in the sense of a shift of the central area ('pupil') relative to the boundary of the stimulus. It might, of course, be argued that the loss of regularity involved is, per se, directly responsible for the decrease in aversive properties when the stimulus 'avoids'. However, this change seems such a small one for such a large effect that it is hard to accept this as the sole explanation. This is supported to some extent by the fact that the change ST to SA caused one of the smallest differences in response levels of any single factor alteration (Fig. 3(c)). Here a similar deformation of regularity is involved but the effect is less than for the change ET to EA.

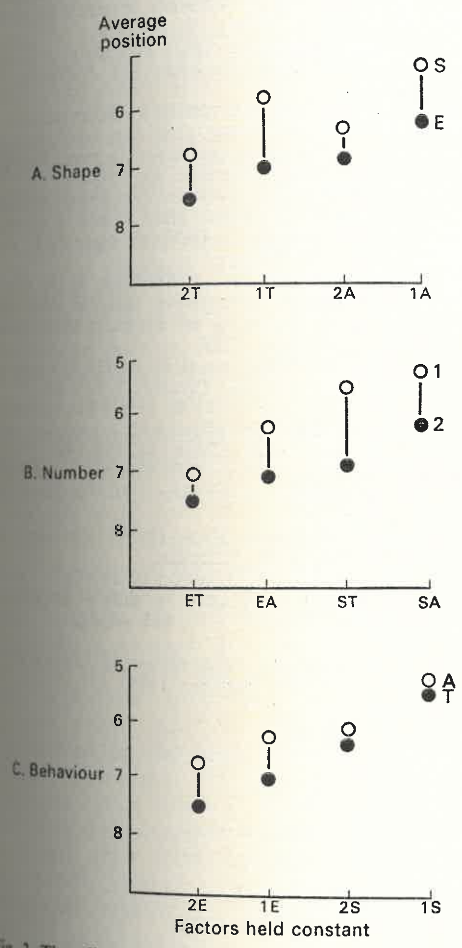

Fig. 3. The effect of changing one factor, the other two held constant, on average position.

(d) The relative importance of individual factors. The data show that manipulation of all three factors produce significant changes in behaviour. On the basis of their relative contributions to the total variance, Table II, the factors might be ordered (greatest to smallest) as shape, number and behaviour. The most effective stimulus would be labelled as ET2. It is in any case difficult to compare the effects of qualitatively different cues, but certainly the Coss (1972) hypothesis of number being a more important cue than shape in the response to eye-like stimuli is not supported, Nor, as already mentioned, was the primacy of two eyes over one clearly seen. In fact separation of the individual groups, Tables III and IV, was not great. Only the ET stimulus combinations were significantly different from all the comparison groups when two factor groups are considered, Table III. Separation is also poor for three factor groupings, Table IV, with ET2 differing significantly only from the 1ST and 1SQ stimuli in its effectiveness.

It is not, unfortunately, possible to state whether the responses observed here are founded in experience with conspecifics or perhaps represent the results of activation of a predator recognition mechanism. Gallup et al. (1971) interpret their data on immobilization periods under the stare of a pair of glass eyes on the latter basis. However, the qualitative and quantitative dissimilarities in the responses observed in another experiment (Scaife 1975) to isolated eyes and to a hawk, coupled with the fact that birds in the present experiment did make use of their option to approach, suggests that this may not necessarily be a correct interpretation. I would prefer, especially in view of the efficacy of one eye, (cf. extreme diminution of the pied flycatcher's mobbing response to owl with one eye removed, Curio (1975)) to regard the response as being based on conspecific experience. Gallup (1972) reports significant enhancement of immobility in the presence of a dead conspecific with open eyes. Such an opinion might seem to go against the obvious but usually neglected caution not to regard different eyes as being necessarily perceived as essentially similar : the large, yellow-iris stimulus used here and the small, brown-iris chicken eye. However, the caution is intended not as a statement of absolute disbelief in such stimulus generalization but as a note of warning that the proof for this is not available.

The importance of the present experiment is that it demonstrates sensitivity to an eye-like shape out of context, suggesting that birds, or at least chickens, are responsive to such cues even if they may not always make use of them. Secondly, it shows that there is a strong sensitivity to orientation, the birds tended to avoid staring stimuli. Taken together these results are strong support for the idea that sensitivity to changes in eye appearance may be directly involved in response to the (usually) threatening head forward posture and that it is not merely changes in beak direction or the like that are responsible. The origins of the responses observed, however, await detailed investigation.

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DISCRIMINATION BETWEEN INDIVIDUALS BY SCENT IN *LEMUR FULVUS*

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Abstract. When a captive *Lemur fulvus* is habituated to the scent of another *L. fulvus* by repeatedly presenting it with that individual's scent, and is then presented with the scent of a second individual, the amount of sniffing of the scents increases, indicating that it discriminated between the scents of the two individuals. The two individuals' scents were significantly discriminated in eight of eleven different combinations of scent receiver and pair of scent donors. The two scent donors were always of the same sex and subspecies, and they could be discriminated by members of their own or of another sex or subspecies.

It seems likely that many mammals are able to discriminate between other individuals of their species by scent, because scent is an important means of communication for most mammals, and because recognition of individuals within a social group is probably basic to the organization of many mammalian societies. Experimental evidence for the ability of an adult animal to distinguish other conspecific adults solely by their scent has been obtained for mice (Bowers & Alexander 1967; Kalkowski 1967), flying phalangers (Schultze-Westrum 1965), rats (Krames 1970), dogs (Schmid 1935), black-tailed deer (Müller-Schwarze 1971), mongooses (Rasa 1973) and gerbils (Halpin 1974). Dogs are also able to discriminate between the scents of individual horses (Schmid 1935) and men (Kalmus 1955), including identical twin men.

The following experiments were designed to find out if the prosimian primate *Lemur fulvus* could discriminate between the scents of other individuals of its species. Like other prosimians, *L. fulvus* has well-developed scent glands and elaborate scent-marking behaviour. Histological studies of the skin of other members of the genus, including the closely related and perhaps conspecific *L. macaco*, have shown that almost the whole surface of the body is covered with very large and numerous sebaceous and apocrine sweat glands, which are especially concentrated on the head and the ano-genital regions (Montagna, Yasuda & Ellis 1961; Montagna 1962). Adult *L. fulvus* of both sexes mark with their ano-genital regions. Males also mark with their foreheads and the palms of their hands. Mutual sniffing of the head and ano-genital regions is very frequent. Field observations (Harrington 1971 1974, 1975) of *L. fulvus* over 5 months at one locality in Madagascar indicated that most scent-marking and sniffing occurs during sexual behaviour, alarm to a man on the ground, territorial encounters between conspecific groups, or undisturbed moving around in the trees. In the forests of Madagascar *L. fulvus* lives in persistent social groups of about a dozen animals including adults and young of both sexes. (Petter 1962; Harrington 1971; Sussman 1972). Therefore, *L. fulvus* combines a high degree of sociality with highly developed olfactory communication.

Methods

Information on the sex, subspecies, provenance, age and genetic relationships of the nine animals used in the experiments is given in Table I. All of the animals belonged to the subspecies *Lemur fulvus fulvus* or *L. f. rufus*. The taxonomy of the *L. fulvus* group is in an uncertain condition and will probably need to be revised as more information on the morphology, distribution, behaviour, cytogenetics, and biochemistry of these forms becomes available. The geographical distribution of the approximately seven subspecies is not well known, but one subspecies or another seems to be found in nearly every part of Madagascar except the deforested central highlands and the subdesert South (Hill 1953). The subspecies are distinguished from each other mainly by differences in the pelage. Morphology and, as far as it is known, behaviour are very similar in all of them (Nute & Buettner-Janusch 1969). There are cytogenetic differences between populations of *L. fulvus* that are not consistent with the present classification based on pelage (Chu & Bender 1962).

The subjects were part of a collection including both wild and captive-born animals that had

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