Chemical communication in *Galago crassicaudatus*: investigation of the chest gland secretion

Z. Katsir and R.M. Crewe
Department of Zoology, University of the Witwatersrand, Johannesburg

The volatile properties of the three major components of the chest gland secretion of *Galago crassicaudatus* were studied. Artificial scents were prepared using these components and were tested under natural conditions at a field site in the Soutpansberg mountains of the Northern Transvaal. In order to establish a natural basis for analysing the communicatory function of the scent mark which results from chest rubbing behaviour, the social structure of the group of *G. crassicaudatus* at the study site was investigated. The chest gland secretion appears to function as a relatively short-lived cue which facilitates communication between individuals found near each other; and a relatively persistant cue which may be used for territorial marking.

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Die vlugtige eienskappe van die drie vernaamste bestanddele van die borsklierafskeiding van *Galago crassicaudatus* is bestudeer. Kunsmatige reuke is met behulp van hierdie bestanddele voorberei en onder natuurlike toestande op 'n eksperimentele terrein in die Soutpansberg in Noord-Transvaal, getoets. Om 'n natuurlike basis vas te stel vir analise van die kommunikeerfunksie van die reukmerk wat as gevolg van die borsskurende gedrag voorkom, is die sosiale struktuur van 'n groep *G. crassicaudatus* op die eksperimentele terrein ondersoek. Dit wil voorkom asof die borsklierafskeiding 'n relatief kortdurende aanwysing verskaf, wat kommunikasie tussen individue wat naby mekaar gevind is, vergemaklik; en 'n relatief langdurende aanwysing wat gebruik kan word vir gebiedsafbakening.

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Z. Katsir and R.M. Crewe*
Department of Zoology, University of the Witwatersrand, Johannesburg
*To whom all correspondence should be addressed

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Galago crassicaudatus is a favourable animal for studying chemical communication since, as a nocturnal animal, it is highly dependent on olfaction for communication and has the most prominent scent gland of all the African galagines (Clark 1975 & 1978a). Recent studies both in the laboratory and the field (Clark 1975 & 1978b; Tandy 1976) have indicated that it has a number of scent marking displays, which involve rubbing parts of the body against the substrate. One of the most important of these displays is the chest rubbing display in which material secreted by the chest gland is deposited. Evaluation of the communicatory function of these signals is complicated by the fact that they often involve what Charles-Dominique (1978) has called 'deferred social communication' *i.e.* there is a variable delay in time between the deposition of the scent (= signal) and the arrival of the receiver.

In order to discover the function of the chest gland scent, it is necessary to understand the sociobiology of the species. A recent study of its social structure and behaviour in the field (Bearder 1974), which concentrated on an isolated group composed of a male and a female with her offspring, has indicated that they have a restricted home range. The range of the maternal group was about seven hectares while the male's range was bigger and overlapped that of the maternal group. The adult male and female associated with each other for a number of years. Similarly, a study by Clark (1978b) indicated a social structure in accordance with that described by Bearder, although it included a number of groups of animals. The social structure of the groups of *G. crassicaudatus* described here extend and amplify the descriptions given above.

Studies of chemical communication in this species have concentrated on the chest gland secretion since it is present in sufficient quantities for chemical analysis. Wheeler, Blum and Clark (1977) identified a major component of the secretion, while Crewe, Burger, Roux and Katsir (1979) were able to confirm this identification and were able to demonstrate the presence of two additional major components. The three major volatile components identified in the secretion were benzyl cyanide, p-hydroxybenzyl cyanide and 2-(p-hydroxyphenyl) ethanol. In this paper we report on the volatile properties of these compounds which affect the kind of signal the prosimians will encounter. In addition, we report on the results of field experiments in which the reactions of *G.*

crassicaudatus to both natural (chest gland rubbings) and artificial (mixtures of synthetic compounds) scent marks were observed.

Materials and Methods

Volatile properties of synthetic compounds

p-Hydroxybenzyl cyanide and 2-(p-hydroxyphenyl) ethanol were purchased from Aldrich Chemical Company, Milwaukee, USA. Benzyl cyanide was obtained locally (98% pure by GLC). The volatile properties of these compounds were studied by dissolving 10 mg of each in 1 ml of diethyl ether (Protea, AR). A sample of 5 μl of each of these solutions was applied to filter paper discs (Whatman No. 1:5,5 mm diameter) and weighed after set time intervals on a Mettler ME 22 microbalance. Between weighings the paper discs were kept exposed in the laboratory. Discs with 5 μl of ether placed on them were used as controls and each experiment was repeated three times. The temperature during the experiments was between 24 – 26 °C and the relative humidity 50% – 70%.

Field Studies

The observations and experiments were carried out at a field site established by A B Clark in the Soutpansberg mountains of the Northern Transvaal. The study area consisted of a strip of riverine forest between cultivated and open fields (Fig. 1) which consisted predominantly of *Acacia* and *Combretum* species. Insects and gum from acacia trees comprise the bulk of the diet of this population (Clark 1978b). *G. crassicaudatus* present in the study area (Table 2) were captured using the method described by Bearder (1974) and marked on the tail for easy identification as well as on the ears for more permanent identification. Most observations were made while remaining at strategic sites which numbers of prosimians passed during the night (Fig. 1). *G. crassicaudatus* were observed by means of a red light headlamp and their behaviour was recorded by description on a tape recorder. The home ranges of the constantly present galagos were delimited (Fig. 2) by marking the places where particular galagos were seen during the study on a map.

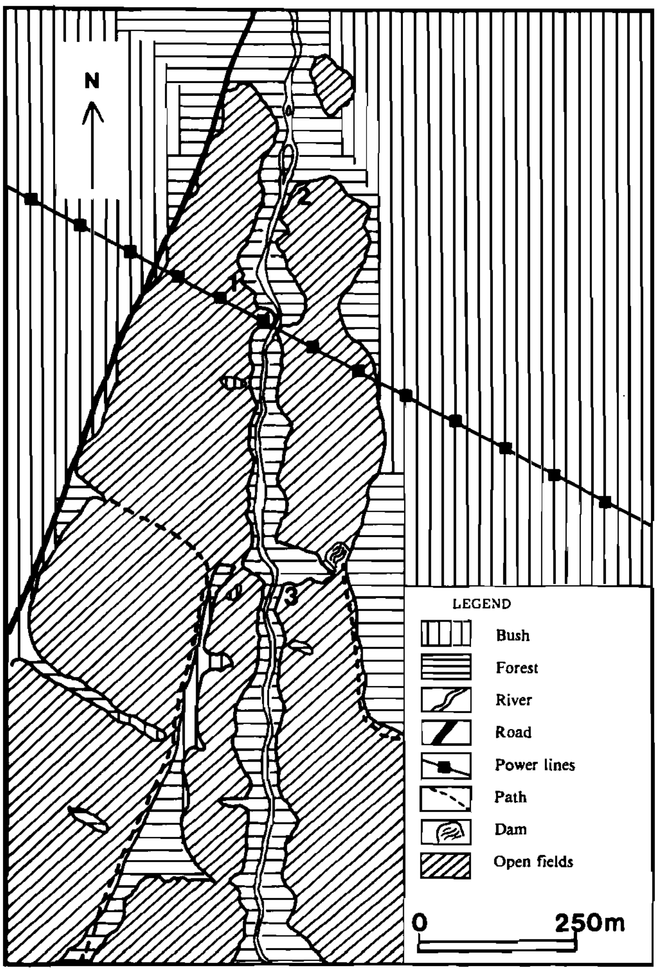

Fig. 1 A map of the study area showing the locations of observation sites 1, 2 and 3.

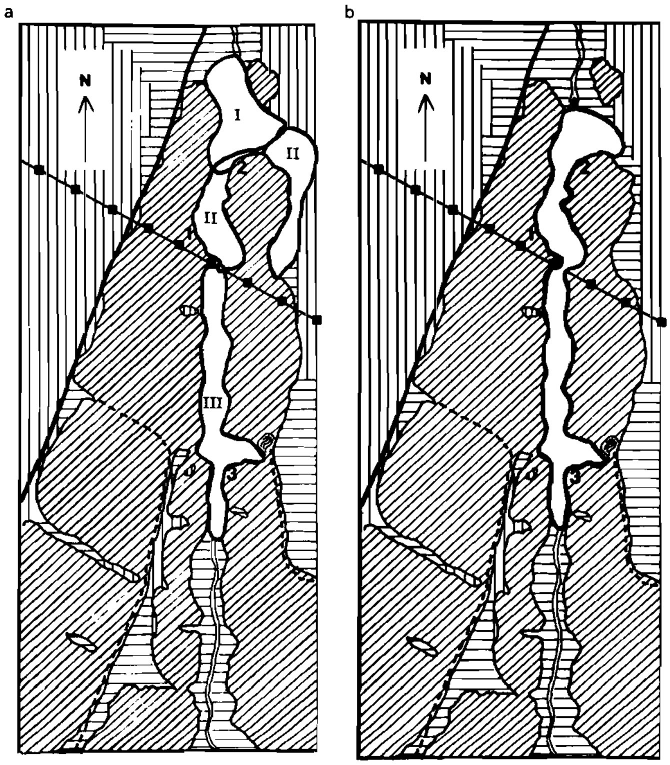

Fig. 2 Home ranges of adult *G. crassicaudatus* in the study area. The legend is the same as in Fig. 1. (a) Home ranges of: I female G, II females D and M and III females K and Je. (b) Home range of male B.

Field experiments with artificial scents

For the field experiments, standard solutions of each of the synthetic compounds were prepared. These contained 1 mg of the substance of interest in 1 ml of dichloromethane (Merck, pesticide residue grade). The various artificial scents that were used were prepared by mixing samples of the standard solutions as in Table 1. The mixtures were prepared according to the relative concentrations of the volatile components in male and female galago chest gland secretions (Crewe *et al* 1979). Ten μl of the artificial scent was applied at a time.

Experiment A

The responses of galagos to artificial scent marks consisting of benzyl cyanide (bc), 2-(p-hydroxyphenyl) ethanol (phpe) as well as to a mixture of these (M-1) were

Table 1 Composition of the artificial scents used in the field experiments. bc = benzyl cyanide, phpe = 2-(p-hydroxyphenyl) ethanol and phbc = p-hydroxy-benzyl cyanide

	Standards[a]		
Mixtures	bc (ml)	phpe (ml)	phbc (ml)
M-1	0,5	0,5	–
M-2	0,7	0,2	0,1
M-3	0,5	0,35	0,15

[a] 1 mg/ml dichloromethane

compared. The artificial scents were applied to polyethylene pipes which had been attached to trees at observation site 1 (Figs. 1 and 3). A clean pipe was used as a control. Pipes were cleaned by thorough washing in warm water with a detergent. Pipes which had been left in the cages of laboratory animals for a week were sealed individually in plastic bags, transported to the field and then used in these tests. The occurrence of sniffing behaviour at each artificial scent mark was recorded. The experiment was repeated for nine nights and each night the control pipe was cleaned, the artificial scents renewed and a new laboratory conditioned pipe (l.c.) put in place.

Fig. 3 Sniffing behaviour exhibited by female T at an artificially marked pipe placed in a tree at observation site 1.

Experiment B

The synthetic mixtures M-2 and M-3 (Table 1) were used to make artificial scent marks which were applied directly to the trees at observation site three. Dichloromethane was used as the control scent. The scent marks were applied to the branches which the animals used on their regular route past the observation site and to branches closer to the ground which were not on the regular route. Again the occurrence of sniffing behaviour at the marks was recorded. The experiment was repeated on three nights. In both experiments the scents were applied at sunset (18h15) and the animals arrived at the observation sites 10 – 15 min later.

Results

Volatile properties of artificial scent components

The results of the experiment to determine the volatile properties of the three test compounds are shown in Fig. 4. From the figure it is clear that the rate of evaporation of the major component of the secretion, benzyl cyanide, is rapid and that it would be an olfactory significant part of the scent mark for an hour. The concentrations of the other two major components decay relatively slowly and they would be present in the scent mark for a number of days.

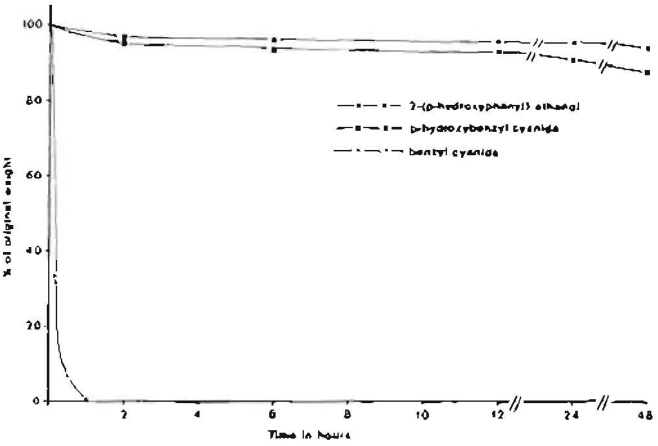

Fig. 4 The relative mass of each standard compound which had evaporated after set time intervals. The 95% confidence limits for all three curves = ±3%.

Field studies

Observations of the social organisation and population dynamics of this population of *G. crassicaudatus* were conducted on the animals listed in Table 2. The adult galagos were constantly present in the study area while the younger individuals left the area or died.

The four adult females and female Je lived in three distinct home ranges (Fig. 2a). Females from different home ranges defended their areas against each other by fighting and scent marking on the border zones. Occasionally they were found grooming each other in the overlapped zones. Females which shared a home range probably had different core areas and when foraging with their infants utilized areas rich in gum on a differential time basis *i.e.* female adults M and D were seen at observation site 1 simultaneously only once (on 26.3, Table 3) and their groups often used the area on different nights (22.3 and 23.3; 30.3 and 31.3, Table 3).

The home range of male B was large and overlapped those of the five females (Figs. 2a and 2b). He was the oldest male in the study area and dominated all the other males that were foraging in the area. As he was in different parts of this range at different seasons (29.3 to 5.4 at observation site 1, Table 3), the area should be called 'male B controlled area' and B the resident male. The younger adult males appeared in the study area only occasionally and were assumed to have much larger home ranges (males Ti, Gr, C and J, Table 3). The younger

Table 2 Marked animals observed in the study area. Data before August 1977 obtained from Clark (pers. comm.). Animals still in the study area at the end of September 1978 do not have a date in the last column

No	Name	Born	Mother	Date last seen
1	♂ B	Adult		
2	♀ D	Adult		July 1978[a]
3	♀ M	Adult		
4	♀ G	Adult		
5	♀ K	Adult		
6	♂ J	Nov. 1974?		
7	♂ C	Nov. 1974?		July 1978
8	♂ P	Nov. 1975?		June 1978
9	♀ Jc	Nov. 1975	K	
10	♂ Po	Nov. 1975	D	Nov. 1977
11	♀ V	Nov. 1975	D	Aug. 1977
12	♀ Ma	Nov. 1975	D	March 1978
13	♂ Ax	Nov. 1975	M	Feb. 1977
14	♂ Pb	Nov. 1975	M	March 1977
15	♂ Al	Nov. 1976	D	Nov. 1977
16	♂ N	Nov. 1976	D	June 1978
17	♂ Ke	Nov. 1976	M	Nov. 1977
18	♂ Ti	Nov. 1976	M	May 1978
19	♂ Gr	Nov. 1976?		May 1978
20	♂ Br	Nov. 1976		Aug. 1977
21	? U	Nov. 1976?		
22	♂ A	Nov. 1977	D	
23	♀ T	Nov. 1977	D	
24	♂ To	Nov. 1977	M	July 1978
25	♂ Je	Nov. 1977	M	
26	♂ Mo	Nov. 1977		
27	♂ L	Nov. 1977		
28	♂ R	Nov. 1977	Ma?	
29	♀ Q	Nov. 1977	Ma?	March 1978

[a] Presumed to have died from a diasease caused by a Rickettsia-like organism found in a blood smear.

Table 3 Movements of bushbabies past observation site 1 during March and April, 1978. + = identified in the area of the observation site, ________ = animals foraging together

Date	Animals											
	M ♀	Je ♂	To ♂	T ♀	A ♂	D ♀	N ♂	Ti ♂	Gr ♂	C ♂	J ♂	B ♂
21.3				+	+	+	+	+	+	+		
22.3				+	+	+	+				+	
23.3	+	+	+									
24.3							+					
25.3				+	+	+	+					
26.3	+	+	+	+	+	+	+	+	+	+		
27.3							+		+		+	
28.3	+	+	+									
29.3	+	+	+				+					+
30.3				+	+	+			+	+		
31.3	+	+	+	+			+	+				+
1.4			+	+	+	+						
2.4				+	+	+						
3.4			+	+	+	+		+				+
4.4							+	+		+		+
5.4	+	+	+	+	+	+	+				+	+

males usually foraged solitarily, although some occasionally foraged together (26.3 males N, Ti and Gr; 30.3 males Gr and C, Table 3). Young females did not return to the study area intermittently as the young males did, and having once disappeared from the area did not return.

Social interactions between the males showed seasonal variations. During the summer (November to April) they were often seen in mutual grooming, and aggressive interactions were rare, while during the winter (especially in the mating season, June to July) they were more aggressive towards each other. The resident male was clearly dominant.

For the interpretation of the responses to chemical signals, the following observations are important:

- The natural scent marks are placed at certain points on the routes that galagos regularly use in moving about their home ranges. These are deposited by rubbing the chest gland on the substrate in a characteristic way. The reaction of the galagos to a natural scent mark involves prolonged sniffing and a peculiar display in which the galagos survey the surroundings, followed by sniffing of the mark again. The age of the mark largely determines subsequent behaviour.
- A fresh chest mark of the resident male elicited sniffing behaviour from another male and often caused him to retreat back along the route which he had used to arrive at the observation site. There was no observation of retreating when the mark was more than an hour old.
- When following a female in oestrus, the dominant male used chest rubbing as a threat display towards other males.

Field experiments with artificial scents

Experiment A

This yielded the results which are given in Table 4. It is clear that the galagos did not sniff pipes treated with a single artificial scent component with a greater frequency than they sniffed the untreated control. The mixture of the two components elicited almost the same frequency of sniffing as pipes marked with the scent of a laboratory animal. Both laboratory marked and M-1 marked pipes received a much higher level of attention than the control pipes. For eight of the nine nights the responses of the

Table 4 Total number of occurrences of sniffing behaviour in response to pipes treated with artificial scents over a period of nine nights. Control = a clean pipe, l.c. = laboratory conditioned pipe, bc = 10 μl of standard solution of benzyl cyanide, phpe = 10 μl of standard solution of 2-(p-hydroxyphenyl)ethanol and M-1 = 0,5 ml bc + 0,5 ml phpe

Control	bc	phpe	M-1	l.c.
6	4	5	20	23

animals to l.c. and M-1 were more numerous than to the controls ($p < 0,026$; Sign test). An example of the behaviour is shown in Fig. 3.

Experiment B

The experiment was conducted at observation site 3 and produced the results given in Table 5. Both mixtures elicited significant sniffing responses. It was not possible to test whether the responses given to the scents left on the regular route taken by the galagos were significantly different from those placed on the lower branches, since the test was conducted for too few nights. However, the observations indicate that when the galagos descended to the lower branches they often ignored the artificial scent mark there while the response given to the mark on the regular route was conspicuous and involved prolonged sniffing.

Table 5 Total number of occurrences of sniffing behaviour observed over three nights in response to scents placed at observation site 3. o.r. = on regular arboreal route, l.b. = on branch off regular arboreal route and composition of M-2 and M-3 given in Table 1

Control	M-2		M-3	
	o.r.	l.b.	o.r.	l.b.
2	16	5	11	4

Discussion

The differing rates of evaporation of the three major components of the chest gland secretion (Fig. 4) indicate that the odour that a recipient galago would perceive would depend on the amount of time which had elapsed between the deposition of the scent mark and the arrival of the recipient. Those arriving soon after the deposition of the scent mark (within an hour, with a scent loading of 10 μg/component) would receive a scent signal composed of a mixture of the three components, with the relative proportion of the most volatile component (benzyl cyanide) diminishing relatively rapidly during that time. After an hour, the synthetic scent mark would be releasing a signal which consisted of the two less volatile components. Thus two messages may be made available by these volatile components of the secretion, firstly a short term message based on a mixture of the three major compounds in which there is a rapid decay in the contribution of benzyl cyanide, and secondly a longer term message based on a mixture of the two less volatile compounds.

The field studies revealed a social structure in which females live in distinct home ranges and defend their area against other females. However, more than one female may share a territory, apparently on a differential time basis. Males did not show territorial behaviour but established a dominance status in which an adult male dominated all other males in the area under study and his home range extended over that of five females and their offspring. The subordinate males were present in the area only intermittently and their position in the social structure remains to be determined. Young galagos eventually left the home range of their mother, in the case of most of the females permanently (Table 2). These findings are in accordance with those of Bearder (1974) and Clark (1978b), except that in the present study, agonistic interactions between males have been observed and seem to be related to competition for receptive females. As Clark (1978b) has noted, the galagos used regular 'arboreal routes' in moving about their ranges. Hence, marking the routes appeared to supply the information needed to maintain both spatial and temporal separation of the maternal groups, as well as for communication between the males. The dominance of the resident male at least outside of the mating season is partially maintained through the deposition of the chest gland marks.

In attempting to evaluate the kind of information galagos may receive from a scent mark, Clark (1975) measured the preference of individual animals for particular scent marks by noting the time spent sniffing the mark. Using a similar measure, which is independent of subsequent behaviour, we recorded the occurrences of sniffing behaviour at our artificial scent marks. In experiment A, this kind of analysis suggested that when individual scent components were presented to the animals in the field, they did not elicit the sniffing responses. Mixtures of the components did elicit responses from the galagos and suggested that, as in the case of many invertebrate olfactory signals (Roelofs 1979), it is the mixture rather than the individual components of the mixture which constitute the signal. Indeed, this is an experimental demonstration that a mixture of components functions as a signal in mammals, whereas the individual components of the mixture are inactive. The fact that in experiment A all three components were not used, was a result of the unavailability of the p-hydroxy benzyl cyanide at the time when these experiments were undertaken.

Experiment B, in which an attempt was made to place the artificial scent marks in a more natural situation, indicated again that the mixtures were effective in eliciting sniffing. However, the signal appears to operate over a very short range and to be active should be on a regular route the galago will take. This is suggested by the fact that the galagos were not attracted to marks which were placed in positions off the regular arboreal routes.

These experiments indicate that the major volatile components of the chest gland secretion are effective in eliciting sniffing behaviour and may supply time cues to the recipient galagos. Indeed, the release of the pronounced sniffing behaviour by these components may be important in ensuring that the galago pays sufficient attention to the mark to obtain additional information which may be present, such as the identity of the individual which made the mark. Artificial scent marks consisting of chest gland secretions collected from animals in the group under study, fortified with mixtures of the synthetic compounds, need to be investigated in order to distinguish between the effects of the volatile components which are common to all secretions and of the less volatile material that may have an idiosyncratic composition.

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