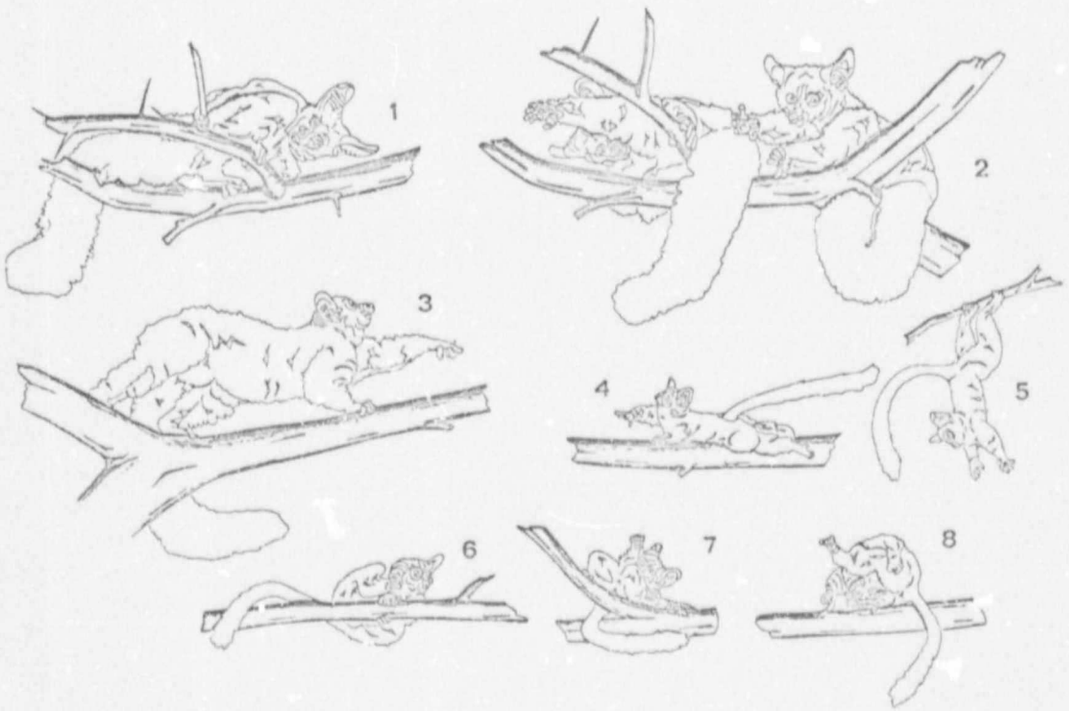

Figure 40. Drawings taken from photographs to show the similarities between the 'comfort' activities of G. crassicaudatus (1-3) and G. senegalensis (4-8).

groomed. A touch under the armpits causes the arm to be extended and held forwards. The latter action was also seen in autogrooming (figure 40). Both allogrooming and autogrooming were either leisurely or vigorous.

Grooming was recorded in terms of bouts consisting of more or less uninterrupted periods of either auto or allogrooming in one place. A total of 370 bouts recorded during the study period comprise 53% autogrooming and 47% allogrooming. Each bout varied in duration from one or two minutes up to twenty-five minutes at a time, but periods in which the animals groomed themselves and then one another intermittently were

common and sometimes lasted for up to forty minutes. Juveniles accounted for the 20% of the bouts of allogrooming which were accompanied by play.

Short bouts of autogrooming occurred during brief stops in the course of slow movement from place to place (15%). Longer bouts occurred during periods of rest after locomotor and feeding activity (47%). It has already been noted that particular trees and tree forks were often chosen where the animals would rest and groom regularly. Autogrooming occurred immediately after feeding (15%), after waking in the evening (12%) and before finally moving up to the sleeping site at dawn (11%).

Like autogrooming, allogrooming also occurred at the very beginning and end of each night but was most common during periods of rest, when the entire group might allogroom simultaneously, while mounting and holding one another in a huddle. Pinto (1972) records that the highest frequency of allogrooming in captive G. crassicaudatus occurs about two hours after nightfall, during a lull following other activities. In the wild the periods of rest were more scattered and the frequency of allogrooming varied accordingly.

Bouts of allogrooming were most often seen between the members of the maternal group (female/offspring - 38%; offspring/offspring - 28%). The adult male, however, allogroomed with members of the maternal group almost whenever he came into contact with them and this accounted for 34% of the total bouts (male/female - 7%; male/offspring - 17%). As far as could be ascertained, each individual, including the adult male, initiated allogrooming with roughly equal frequency. A number of calls were associated with allogrooming, and these are described elsewhere (see section 15.4.3).

Several authors have reviewed primate grooming, which seems to serve important social as well as biological functions. Grooming does not merely keep the skin and fur in good condition but can be related to the establishment and reinforcement of social bonds; the facilitation of bodily contact before copulation; a reduction of tension and restoration of integration within a group following a set of events which threatens the integration of the group; or a pacificatory function between individuals which are not familiar with one another (Andrew, 1964; Marler, 1955; Moynihan, 1967; Terry, 1970). Allogrooming provides a bond between

superior and inferior as well as between equals (Andrew, 1964). Its frequency and duration varies considerably between species and it can sometimes be related to dominance position and aggressiveness (Marler, 1965; Terry, 1970; Doyle, 1974).

G. crassicaudatus are able to autogroom almost all parts of the body, yet they frequently engage in allogrooming. Andrew (1964) and Jolly (1966b) point out that friendly behaviour in many adult primates can be traced back ontogenetically to the early contactual relationship between mother and infant. In G. crassicaudatus, where close association between the mother and her offspring is greater and persists for longer than in G. senegalensis (Bearder, 1969), social grooming is more frequent and the bouts last for longer in the wild. In captivity, however, where group members are artificially kept together, G. crassicaudatus and G. senegalensis allogroom with approximately equal frequency (Pinto, 1972). This suggests that allogrooming is largely a result of contact between familiar individuals which serves to strengthen the bonds between them (hence the grooming between adult males and other group members). In an evolutionary context the maintenance of close bonds is of obvious importance for the development of the offspring and it ensures that the male has easy access to the female at the time of mating. Yet despite some degree of enhanced association between adults, cohesive adult groups are not found in bushbabies. The maturing offspring eventually leave the mother and they then develop relationships with other individuals. Laboratory evidence in the case of G. senegalensis indicates that this is achieved through friendly contact between adult or sub-adult males and females, in which allogrooming plays a large part (Bearder and Doyle, 1974b).

16.2 Play

Play is considered to be another strong cohesive force in many primate groups (Washburn and Hamburg, 1965). It has been considered in detail by Dolhinow and Bishop (1970) who stress its importance for the development of physical and interpersonal or social skills in the young in preparation for adult life. Like allogrooming, play appears to be pleasurable to the participants and is sought after and initiated by them. Repetition leads to increasing competence in motor behaviour and social interactions that are important in the life of the individual

and hence of adaptive value to the species' (Dolhinow and Bishop, 1970). It is argued by Bishop (1962) that play may have encouraged some understanding of objects among the ancestors of monkeys and thus indirectly favoured evolution of the control of objects. Play may interact with intelligence to open up new possibilities to the animal.

Three types of play behaviour were distinguished in infant and juvenile G. crassicaudatus which were recorded in thirty-nine bouts during the study period. Firstly, object play (7%) in which the bushbaby pulled or tussled with a leaf, a climber or the end of a branch, almost as if it were another bushbaby. Secondly, locomotor-play (13%) where the animal made boisterous, exaggerated jumping movements, twisting back and forth between branches and climbers. Thirdly, social play (80%) which involved chasing and contact between two or more individuals (figure 41). Occasionally all three types of play were seen at one time.

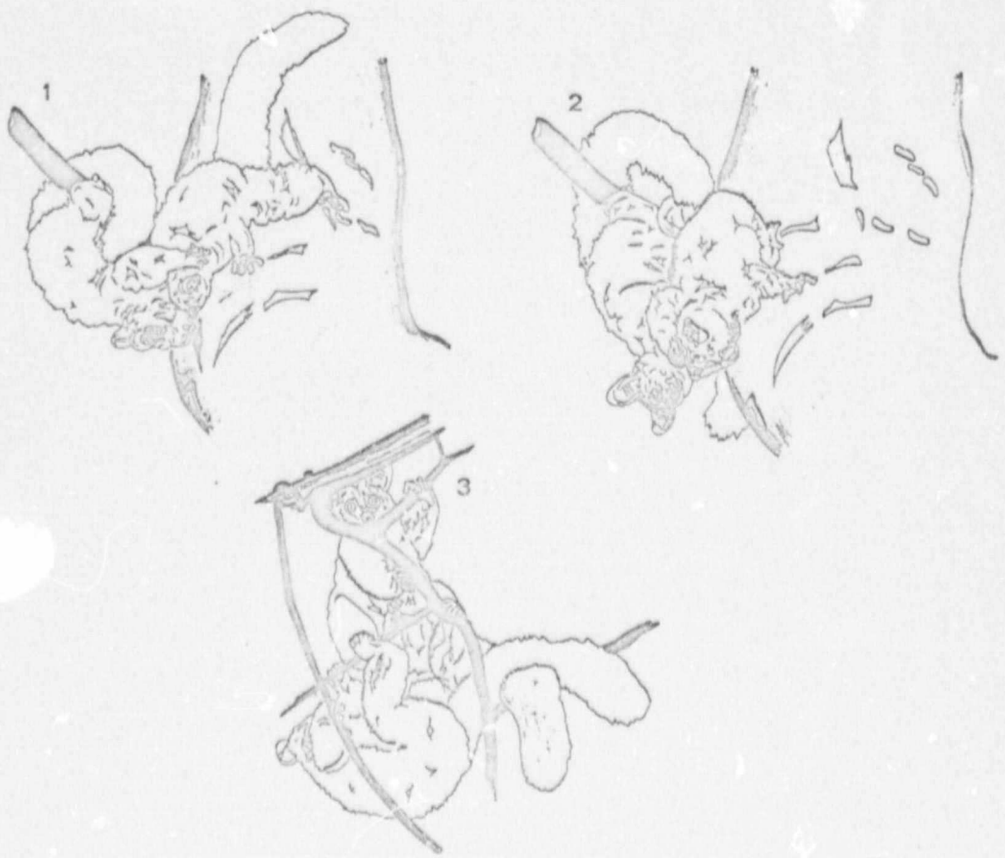

Figure 41. Drawings taken from photographs to illustrate mild agonistic contact between juvenile G. crassicaudatus at a gum lick (1-2) and social play (3).

Infant bushbabies began to play with one another and with the mother at a time when they were still being carried. Juveniles were generally more active than adults at all times and they frequently moved with a bouncing gait even during normal progression. Most play occurred between siblings but they would occasionally play with the mother or with the adult male. An adult male, female and two juveniles were observed playing together, but the adults did not play in the absence of the offspring.

Many adjectives may be used to describe the social play of G. crassicaudatus which has characteristics in common with that of G. senegalensis (Andersson, 1969) and Perodicticus potto (Bishop, 1964; Anderson, 1971). As much as 76% of all bouts of social play involved allogrooming. The young animals wrestled vigorously, boxed with open hands, hugged, nuzzled and pulled one another while their tails thrashed wildly. They often chased and jumped onto one another, grabbing at branches and hanging by an arm or a leg. Hanging-play, in which the participants grappled together suspended by the hind legs beneath a branch was common and, as with Lemur catta (Jolly, 1966b), one animal could support the weight of both. A variety of calls (spits, squeaks and moans) were made during social play, although it was usually completely silent.

Play preceded or followed periods of allogrooming and autogrooming, particularly before the bushbabies left the sleeping tree and before they returned to it in the morning. It was also seen in the middle of the night. The adult female (and the male if he was present) often rested while the juveniles played nearby. Two individuals of ten months old were seen playing together for a period of forty minutes before dawn, and in Rhodesia, juveniles regularly played on the roof of a house, chasing one another round and round in circles, which indicates that play sites may be chosen.

16.3 Marking and Rubbing Behaviour

Prosimians stand out among the primates for the wealth and variety of their olfactory communication (Jolly, 1966b). The importance of olfactory cues is evidenced by the moist rhinarium, relatively large olfactory lobes and the widespread occurrence of special scent glands (Montagna and Ellis, 1959, 1960; Montagna and Yun, 1962a and b; Montagna, 1962). Various marking and rubbing actions are performed for the deposition of odoriferous substances (glandular secretions, faeces and urine), and the animals frequently sniff one another and the substratum.

Scent marking is a common feature of many mammal species and it has been reviewed by Ralls (1971). Prosimian scent marking in particular is considered by Andrew (1964). A number of functions have been ascribed the various types of marking behaviour. They may be important in territoriality, courtship and mating, intra- and inter-group recognition during friendly or agonistic encounters involving social status. Scent deposition may deter rivals, or at least warn them of the presence of a particular individual, or it may be of significance in reassuring the marker within its own home range. It has been suggested that scent may also be used to mark out a trail or directly repel other species, while the often ritualized actions involved in marking might act as visual displays. In some species these actions have been retained even though the appropriate scent glands are lacking. Marking behaviour which occurs in the absence of specific eliciting stimuli may merely reflect a general state of excitement in the animal, without serving a communicative function, or it may be a displacement activity (Schilling, 1974).

The patterns of behaviour which are associated with scent marking in G. crassicaudatus in captivity have been described by Jolly (1966a), Andrew (1964), Pinto (1972) and Andrew and Klopman (1974). They are outlined in table 11 in comparison with those of G. senegalensis. The more conspicuous patterns which were observed in the field are illustrated in figure 42 and described below.

Table 11. Marking and rubbing behaviour of G. crassicaudatus in comparison with that of G. senegalensis (Andersson, 1969).

Behaviour	Species	Age class	Sex
Urine washing	G.c.	Ad. Juv. Inf.	Male & female
	G.s.	Ad. Juv. Inf.	Male & female
Rhythmic micturition	* G.c.	Ad.	Male & female
	* G.s.	Ad.	Male & female
Foot rubbing	G.c.	Ad. Juv.	Male & female
Chest rubbing (median bald patch)	G.c.	Ad.	Male & female
Body Rubbing	G.s.	Ad.	Male
Ano-genital rubbing	G.c.	Ad.	Male & female
	*-G.s.	Ad.	Male & female
Head and mouth rubbing	* G.c.	Ad.	Male & female
	* G.s.	Ad.	Male & female

* Not noticed under conditions of observation in the field, but observed in the laboratory (Andersson, 1969; Pinto, 1972; Jolly, 1966a; personal observation).

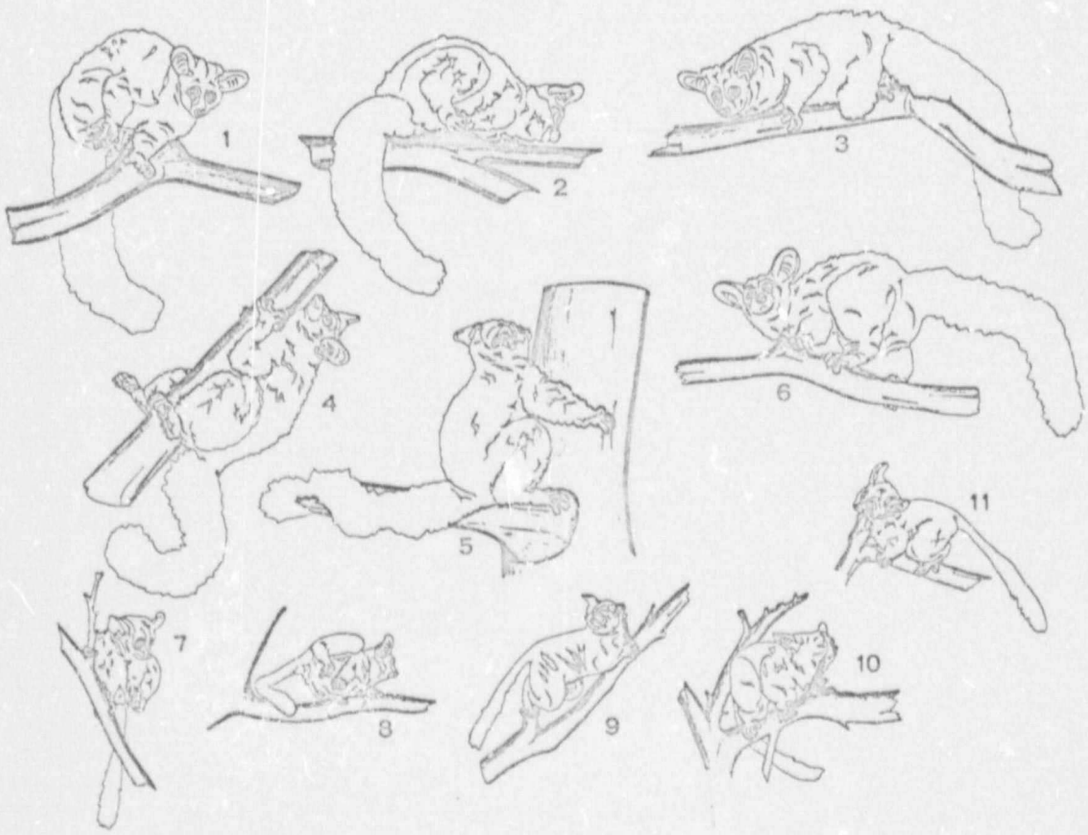

Figure 42. Drawings taken from photographs and field sketches to show the common marking and rubbing actions of G. crassicaudatus (1-6) and G. senegalensis (7-11). (1-2) Urine washing. (3) Chest/body rubbing. (4) Ano-genital rubbing. (5) Chest/body rubbing. (6) Foot rubbing, (7-8) Urine washing, (9) Biting, (10) Chest rubbing. (11) Chin rubbing.

Rubbing or marking actions were recorded on 146 occasions during the study (urine washing - 33%; leg rubbing - 31%; chest/body rubbing - 31%; ano-genital rubbing - 5%). This does not allow any definite conclusions to be drawn about the functions of scent marking in this species, assuming that scent is actually deposited, but field observations are likely to give clues which may be extremely important in clarifying laboratory observations and experiments. If the frequency of occurrence of the different behaviours can be taken as a guide, it would appear that, apart from ano-genital rubbing, they are each equally important in the life of the animal. Their significance may vary according to the situations in which they are performed.

16.3.1 Urine Washing

The highly ritualized movements involved in urine washing were almost identical to those described for G. senegalensis (Lowther, 1940; Sauer and Sauer, 1963; Andrew, 1964; Doyle et al., 1967; Andersson, 1969). The only difference was that they were somewhat slower and more deliberate. The hand and foot on one side of the body were raised simultaneously from the substratum. The hand was cupped beneath the uro-genital region and a few drops of urine discharged into it. The hand then rubbed or grasped the sole of the foot from one to several times and the animal regained its original position. This sequence was sometimes incomplete and it was usually, but not always, repeated on the opposite side. Most urination was accompanied by urine washing although copious streams of urine could be produced alone, particularly when the animals were disturbed.

Urine washing was performed by all age/sex classes and occurred several times at the beginning of the active period but thereafter only occasionally during the night. Pinto (1972) observed a similar distribution in captivity, where she found a surprisingly low overall frequency of urine washing in G. crassicaudatus in comparison with G. senegalensis and Microcebus murinus. In the field, urine washing did not occur at regular marking places within the home range, apart from the sleeping trees and trees adjacent to them, but it did show a relationship to toilet and comfort activities such as grooming and stretching. Urine washing by an individual in physical contact with other bushbabies which is reported for G. senegalensis (Andersson, 1969; Bearder, 1969), was not seen in G. crassicaudatus.

Andrew and Klopman (1974) have noted that urine washing in the Lorisoidea is evoked during mobbing, exploration of a strange area, defence and attack, social interactions and by stimuli associated with urine washing such as another animal performing the action. It may also occur as part of normal urination, which would explain the frequency with which it is performed when bushbabies awake each evening. Doyle et al.(1967) note that urine washing in G. senegalensis is most common in adult males and that it increases in frequency during courtship. Urine washing is not confined to the Lorisoidea but is also found in some ceboids and cheirogaleines. Andrew and Klopman (1974) examined the occurrence and causation of urine washing in comparison with other movements involved in scent application in a variety of species. They also considered the systematic

distribution of species which behave in this way, but they concluded that that the origin and evolution of urine washing remains mysterious.

The relative frequency of urine washing in a variety of situations leads to the supposition that it may serve a number of functions. In the event of scent deposition the question arises as to why such a complex ritualized action of wiping the hands and feet should be necessary when direct urination onto the support could be achieved more easily. The most obvious explanation is that it is an efficient method of laying down scent trails which the animals can follow in moving from place to place. This has been suggested for G. senegalensis (Sauer and Sauer, 1963), G. crassicaudatus (Eibl-Eibesfeldt, 1953) and for the lorises (Seitz, 1967). Field observations of the African galagines, however, indicate that this is not the case and the suggestion has been discounted for G. senegalensis (Bearder, 1969) and for the three galagos of Gabon (Charles-Dominique, 1971, 1972). Observations of the movements of G. crassicaudatus indicate that it is equally unlikely to be true of this species. The smell of urine on branches may familiarise the animals with particular places or carry information concerning the bushbaby that made the mark but there is no evidence to suggest definite trails along fixed routes.

Alternatively it may be argued that wiping the hands and feet with urine provided an effective means for one animal to transfer its scent onto its companions during social encounters and thus the action arose in a social or sexual context. Urine washing by adult male G. senegalensis when in contact with females has been reported by Doyle et al. (1967) but this appears to be an exception. Furthermore the frequency of urine washing by adult males in this species, particularly during courtship, is unusual. Andrew and Klopman (1974) found that only G. senegalensis urine washed in a social situation or in bodily contact with a fellow. In ten other species which they studied, scent cues from the female seemed to be unimportant and they did not find any association between urine washing and copulation.

Only one other hypothesis concerning the functions of urine washing accounts for such elaborate behaviour and that is the proposal of Sauer and Sauer (1963) that it may facilitate the grasping of branches during movement through the environment. The main objections to this idea are that urine washing occurs irregularly and it does not necessarily precede locomotor activity, but the suggestion warrants closer inspection.

When G. crassicaudatus and G. senegalensis are kept in activity their cage surfaces soon become coated with urine to which loose hairs will adhere, indicating that it is sticky. In addition when the animals are handled their hands and feet are found to be damp (personal observation). Thus the sporadic occurrence of urine washing has at least the potential of improving grip on dry and dusty supports. Pinto's (1972) evidence that urine washing was more frequent in the more active species which she studied lends tentative support to this hypothesis which might also explain why urine washing, unlike other forms of scent marking, is seen in all age groups including small infants.

It is generally assumed that the ancestral Eutherian mammals possessed claws which were replaced by nails with the advent of grasping arboreal progression (Napier, 1971). This was accompanied by special development of friction pads on the hands and feet as an aid to grip, but this alone does not explain the loss of claws, which are an asset rather than a hinderance for arboreal locomotion. Many mammals apart from primates are extremely agile in trees and use their claws to great advantage. Even certain primates (aye ayes, marmosets and tamarins) possess claws on most of their digits and Martin (1972b) presents evidence to suggest that these are in fact secondarily modified nails, derived as an adaptation for maintaining grip more effectively. Other species, Microcebus murinus, M. coquereli, Phaner furcifer and Euoticus elegantulus have pointed (or keeled) nails which are used to a greater or lesser extent as an aid to grip, particularly on broad or over-hanging surfaces (Martin, 1972b; Petter et al., 1971; Charles-Dominique, 1971). The disappearance of claws in the first place may have been more closely associated with development of the hands for precise manipulation of objects such as food items (Elliot-Smith, 1902, 1927; Bishop, 1962). This was most probably related to the extreme development of the grasping action of the foot as an adaptation for hind-limb dominated arboreal locomotion, which tended to free the hands to a greater extent for other purposes (Walker, 1967a; Napier and Walker, 1967).

From this it may be argued that urine washing developed at an early stage in primate evolution as an aid to grip in small agile forms which lacked claws (apart from the [illegible]laws) but otherwise had relatively unspecialized hands [illegible]ch a hypothesis does not exclude the fact that urine washing m[illegible]erve other functions, since these

could have developed subsequently. A strong selection pressure for good grip would have been that the animals were better able to reach certain sources of food and they would have been vulnerable to predation if they fell to the ground. In this case it is to be expected that urine washing should show a decline in significance or be lost in slow-moving species or those with large or otherwise highly specialized extremities, and this appears to be true in many cases.

It has already been noted that urine washing behaviour occurs frequently in G. senegalensis and Microcebus murinus and the same is true of G. demidovii (Andrew and Klopman, 1974). Doyle (1974) indicates that it is more common in galagines than in lorisines and it appears to be completely absent in Perodicticus potto and Arctocebus calabarensis. Both these species move slowly and deliberately and have associated morphological specializations. Urine washing is reported for Loris tardigradus (Ilse, 1955) and Nycticebus coucang (Hill, 1938; Ehrlich, 1970), which are likewise slow moving. The significance of this difference between African and Asiatic lorises remains unclear, but it has been suggested for Perodicticus potto that the shortness of its legs may prove to be connected with the loss of the pattern (Andrew and Klopman, 1974). The fact that a number of lemurs are extremely agile and yet do not urine wash seems to provide contradictory evidence to this hypothesis, yet specializations of the hands and/or feet have been reported for many of these species (pointed nails, large size, highly modified friction pads or extreme opposability of the digits). This is true of Lepilemur mustelinus (Charles-Dominique and Hladik, 1971); Phaner furcifer and Microcebus coquereli (Petter et al., 1971); Lemur (Bishop, 1962); Indri, Avahi and Propithecus (Petter, 1964b). This suggestion concerning the derivation of urine washing can be further investigated when information becomes available on the relative frequency of urine washing by the various species under natural conditions.

16.3.2 Foot Rubbing

This behaviour is a characteristic of G. crassicaudatus which is apparently not found in other prosimians. Andrew (1964) and Andrew and Klopman (1974) indicate that a bushbaby may wipe its feet in urine and then rub them alternately against the substratum. Jolly (1966a); Eaton, et al. (1973) and Pinto (personal communication), however, do not find that foot rubbing has any temporal relationship with urination and this is confirmed by observations in the field.

Foot rubbing involved a rapid scraping of the tarsus and sole of the foot against a branch or trunk. The leg was moved vigorously and noisily back and forward several times, sometimes with the foot clasped lightly round the branch. The action would usually be repeated with the other leg in a way which is reminiscent of urine washing. The sound of scraping gave the impression that the animal was attempting to clean the sole of the foot but the ritualized nature of the movement and its frequency indicated that this was not the case.

Foot rubbing was performed by juveniles as well as adults but it was most common in adult males in accord with the observations of Jolly (1966a). It was seen during social encounters and when the subject was confronted by the observer or a potential predator, indicating some degree of social excitement or anxiety. In adults it often preceded or followed chest rubbing at spots which were marked regularly. An adult male was observed to chest rub beneath a branch and give a vigorous double foot rub at the same time. The noise of scraping could often be heard at a distance and recognized by the observer and it is possible that this alone may serve a communicatory function.

16.3.3 Chest and Body Rubbing

It has been noted previously that adult males and females have a longitudinal bald patch in the midline of the chest which is larger and more conspicuous in the males and is most probably a cutaneous marking region. Martin (1968) describes marking with the gular marking gland in Tupaia belangeri and cites the widespread occurrence of secretory glands located on the ventral midline, for example, in the rabbit and hare and in several primates (Tarsius, Ateles, Papio, Theropithicus, Pongo and Hylobates). He suggests that it is either a primitive mammalian feature or merely a convenient position for a gland.

In G. crassicaudatus the chest and often the whole underside of the body was held close against a branch with the arms wrapped around it, while the animal crawled forward with a sliding movement. Rubbing was carried out in a variety of postures depending on the size and position of the support being rubbed. It was executed on top of horizontal or oblique supports (50%), particularly where there were small upright projections or stumps on the branches of large trees. Alternatively it was performed beneath a branch (30%) or against a vertical branch or trunk (20%).

Chest and body rubbing was confined to the adults and was given particularly by the adult males. It was quite common during social encounters when several spots within a small area would be rubbed one after the other. At other times 'marking posts' within the home range were rubbed on repeated occasions. Chest and body rubbing were frequently accompanied by sniffing, foot rubbing, ano-genital rubbing and biting of the branch and they appear to be one aspect of territorial behaviour in the species.

16.3.4 Ano-Genital Rubbing

Jolly (1966a) notes that G. crassicaudatus may lower their hindquarters and press or rub the vagina, or bare patch of the scrotum against a branch. This movement was observed during the present study but it usually followed chest and body rubbing and was rarely seen alone. When performed beneath a sloping branch, the legs and feet were held apart and the ano-genital region pressed and rubbed by the pull of the arms alone (figure 42.4). Crouching and micturition while moving slowly forwards has been observed in G. crassicaudatus in the laboratory ('rhythmic micturition'), but this differs from the behaviour described here in that the deliberate rubbing movements are not involved. As with chest and body rubbing the possible significance of this action as an aid to contact and spacing is underlined by the fact that it was only performed by adults. The application of the genital area suggests that this form of marking may carry information regarding the sex of the marker.

16.4 Vocalizations

The significance of calls which occur under laboratory or semi-natural conditions is often obscure and their frequency of occurrence may be unnatural. Andrew (1963a), for example, found that adult primates in captivity often retained essentially infantile or juvenile repertoires for unusual lengths of time. A natural classification of calls is less difficult in the wild where the number of stimulus situations in which the calls may be given and the responses which they evoke are often more varied (Altmann, 1967; Jolly, 1966a). On the other hand the conditions for hearing faint or subtle calls are often better in the laboratory where detailed records may allow the observer to name calls which would otherwise be missed.

The description and interpretation of primate vocalizations is a somewhat subjective process which leads to a considerable amount of disagreement between authors. The account which follows is based on guidelines set out by Hockett (1960), Marler (1961; 1968), Andrew (1962; 1963 a and b; 1964) and Altmann (1967). Particular reference has been made to the work of Struhsaker (1967a) on vervet monkeys (Cercopithecus aethiops), Andersson (1969) on G. senegalensis and Jolly (1966a) on C. crassicaudatus.

The vocalizations of G. crassicaudatus may conveniently be divided into three broad functional categories as follows: calls associated with social cohesion; calls associated with 'anxiety' or 'alarm' situations and calls associated with agonistic contact. Because agonistic contact situations also invoke anxiety the last category includes only those calls which are directed towards another animal during physical contact or when such contact is imminent.

16.4.1 Calls associated with Social Cohesion

G. crassicaudatus have five calls which appear to maintain intragroup contact and inter-group spacing. These may be directed towards conspecifics or undirected proclamations of the whereabouts of the caller.

Call No 1, Cry (figure 43): The cry is described by Jolly (1966a) as a territorial call which she likens to a 'crow-caw'. It consists of a series of loud cries in succession, the last of which fades away. Jolly notes that the frequency of these calls varied during the year with a peak occurring when her captive females were in oestrus. When calling the bushbaby usually stopped and raised its head and the cry was occasionally followed by chest rubbing or foot rubbing. Only if there were other cries from nearby would the call be repeated. Bushbabies derive their name from this call which sounds not unlike an angry child.

An analysis of 794 cries from the three study areas shows that they consisted of between three and seventeen units at a time, with six to nine units being most common (figure 44). Each cry had the potential of conveying the identity of the caller and after a while particular individuals could be recognized by the tone and quality of their calls. An incipient, shortened, form of the cry was also heard on rare occasions.

Cries were the most common of all loud calls in the field. They were usually made by adult males, but also by maturing males and adult females.

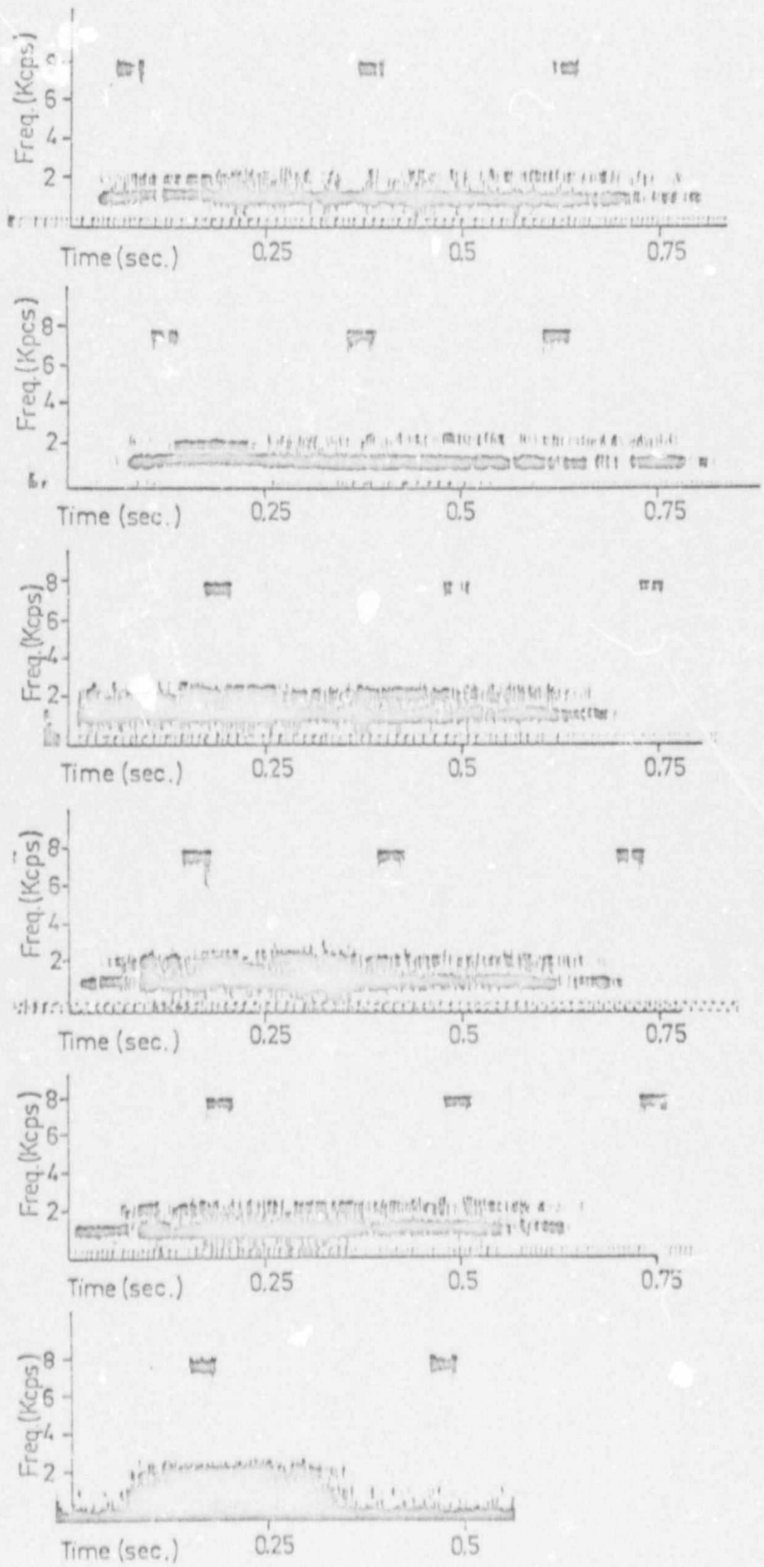

Figure 43. Spectrogram of a six unit cry (G. crassicaudatus) with each unit in sequence from top to bottom. The call builds up to a crescendo and subsides on the last unit. The black squares represent time signals.

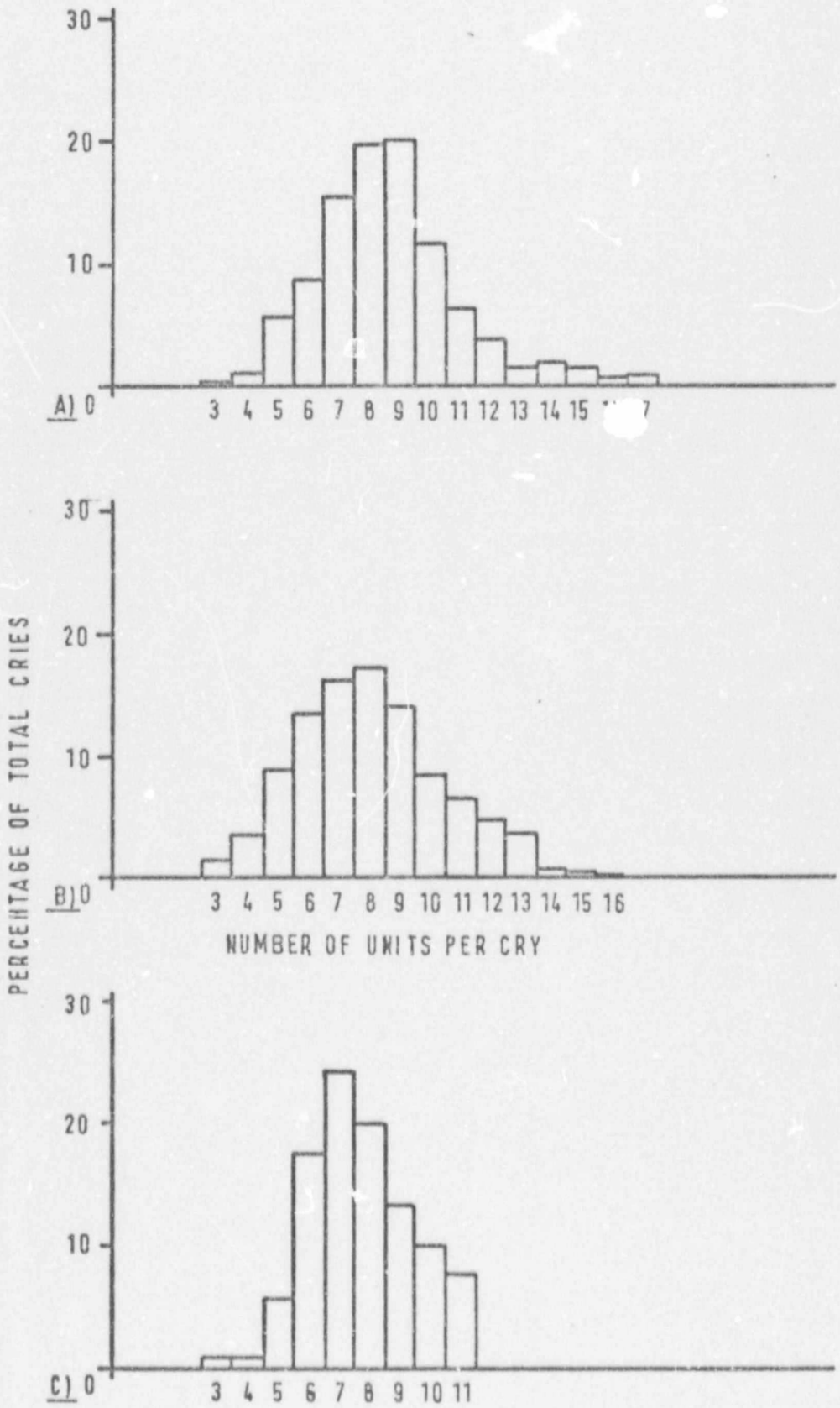

Figure 44. Histogram to show the frequency distribution of cries (G. crassicaudatus) with different numbers of units. (a) N.E. Transvaal (N = 300). (b) Zululand (N = 374). (c) E. Rhodesia (N = 120).

A cry would often evoke answering cries with as many as five bushbabies calling almost simultaneously. Answering was most frequent in the forest habitats of Zululand, less so in the open woodland of Rhodesia and quite rare in the North Eastern Transvaal, where the population density of bushbabies was low (figure 45). The adult male of a single isolated group rarely called more than six times in one night and sometimes not at all. In addition the cries showed seasonal changes in their frequency of occurrence, being most common during a period of intense social activity corresponding to the mating season in Zululand (figure 45 and table 12). During this period cries or incipient cries were given in response to a tape recording or imitation, whereas at other times they were difficult to induce. Cries were only rarely heard from the captive group in accordance with the observation of Jolly (1966a).

Table 12. The mean number of cries per hour which were heard in the three study areas

AREA	MEAN NUMBER OF CRIES PER HOUR	HOURS OF RECORDING	POPULATION DENSITY
N.E. Transvaal	0,50	742	Low
Rhodesia	2,20	80	Medium
Zululand	5,40	37	High
Zululand (mating season)	24,50	19	High

The frequency of cries heard at different hours of the night is shown in figure 46. Cries were given throughout the night but they reached a peak three quarters of an hour after the bushbabies left their sleeping places and again approximately one hour before they returned in the morning. Their occurrence showed no obvious correlation with the state of the moon (figure 45), unlike similar calls in Lepilemur mustelinus (Charles-Dominique and Hladik, 1971) and they could not be related to the prevailing weather conditions. External factors are thus insufficient to explain the pattern of calling which has been observed.

The cry of G. crassicaudatus has several characteristics in common with the bark of G. senegalensis (Andersson, 1969) and with the loud calls of several other primates. The howler monkey (Alouatta palliata)

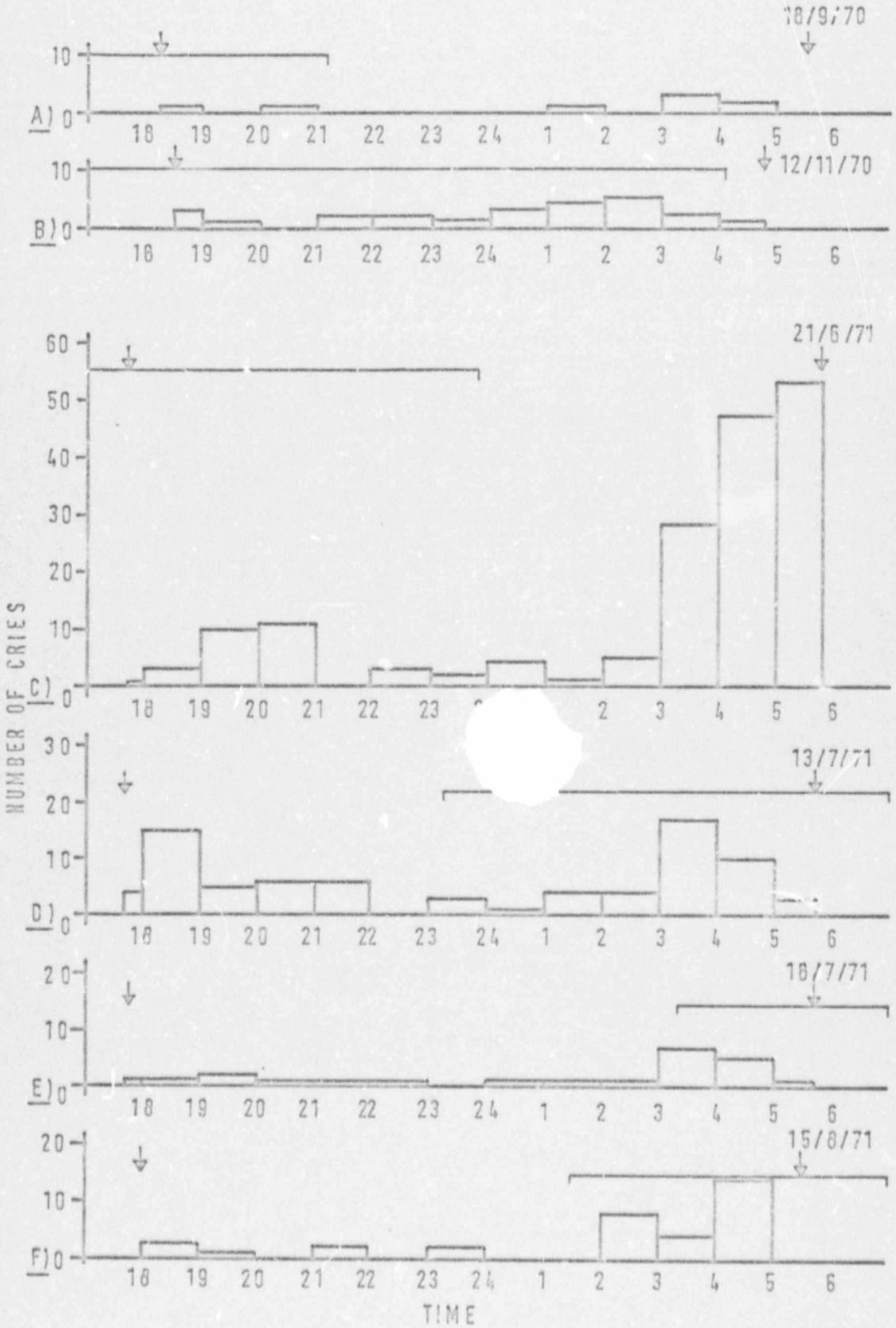

Figure 45. Histograms to show the frequency of cries (G. crassicaudatus) during the night in different localities. (a) N. E. Transvaal (isolated group). (b) N.E. Transvaal (several groups). (c) Zululand, dune forest (mating season). (d) Zululand, temperate forest. (e) Zululand, dune forest (outside mating season). (f) E. Rhodesia. The continuous lines represent periods of moonlight. Arrows indicate the times of sunset and sunrise.

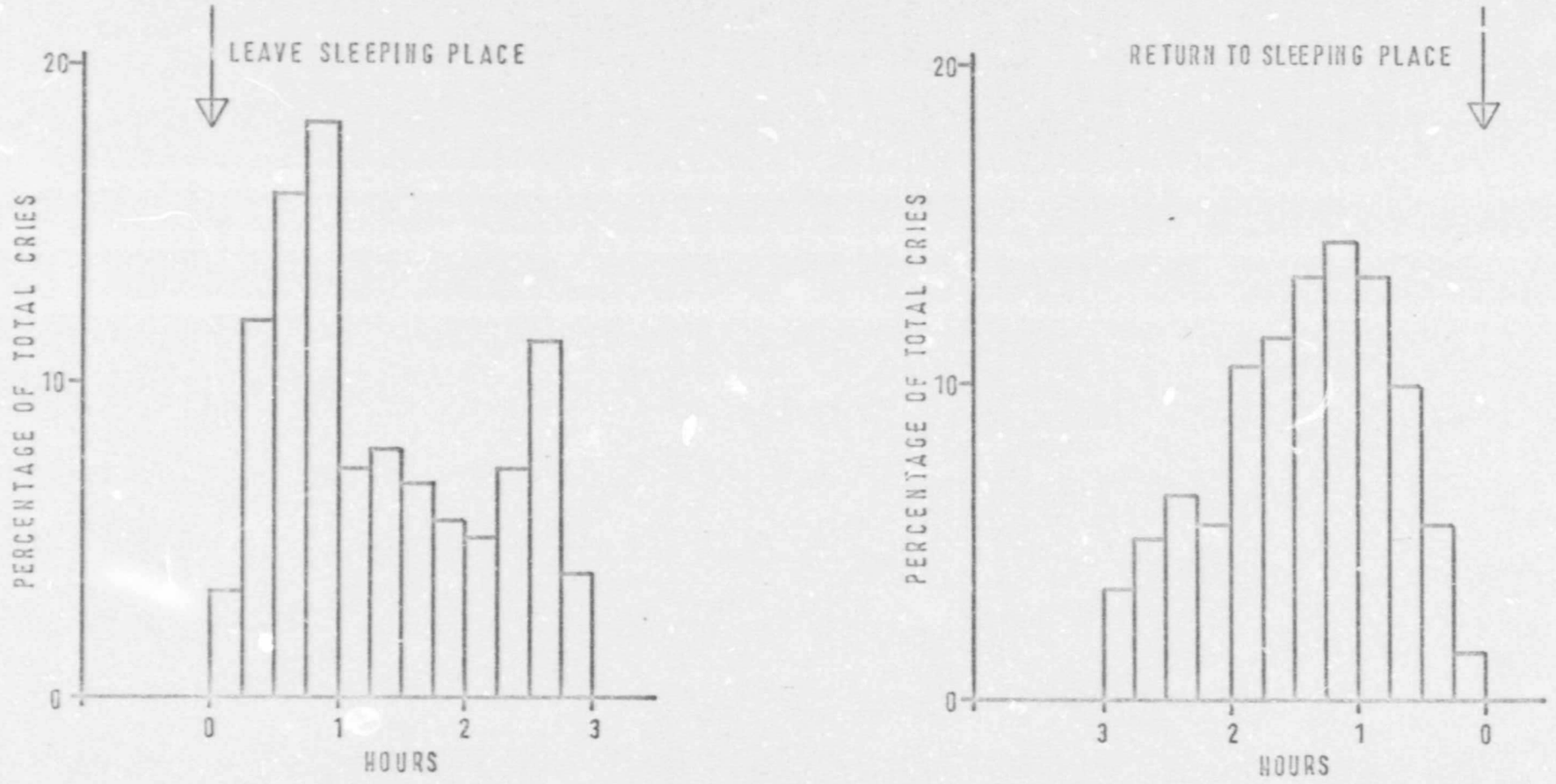

Figure 46. Histograms to show the frequency of cries (G. crassicaudatus) during fifteen minute intervals. (a) After the animals had left their sleeping places on forty nights (N = 176); (b) Before they returned to their sleeping places on seventy nights (N = 629).

is well known for the loud calls of the adult males (Carpenter, 1934). Mason (1966) describes calls for Callecebus moloch which pass rapidly through the forest. Jay (1965) records a loud 'whoop' for adult male langurs when a group is about to move suddenly or for a long distance. Adult male black-and-white colobus monkeys (Colobus polykomos) give a loud call which is especially common after dawn and in the evening and it is contageous between groups (Ullrich, 1961). Similar calls are reported for lemurs, Phaner furcifer and Indri indri (Petter et al., 1971; Petter, 1974). Each of these calls have characteristics which are generally considered to aid long-range spacial regulation (Bates, 1970; Marler, 1968). They are relatively low frequency, loud, repetitive sounds which can be located at a distance even above background noise. They occur particularly at the beginning and end of the active period, frequently being answered by neighbouring individuals or groups, and they differ from many other communication signals in that they often appear to be given spontaneously without any particular eliciting circumstances.

The present observations suggest that the cry of G. crassicaudatus not only maintains a distance between rivals but also attracts familiar individuals towards one another. In one instance a female and two juveniles responded to the cry of a male at dawn by immediately reversing their direction of travel and moving rapidly towards him. Thereafter the four animals settled to sleep in the same tree. On another occasion a juvenile heard the movements of G. senegalensis and followed in that direction. On hearing a cry from near its usual sleeping place, however, the juvenile stopped abruptly and looked up before changing direction and moving towards the caller.

It would appear that the cry of G. crassicaudatus acts as a vocal advertisement, informing members of a social group, or rivals, of the whereabouts of a particular individual. The frequency of cries during the night and at different times of the year appears to be related to social cohesion and spacing (movement towards the sleeping place at dawn, mating, separation of rivals). It is possible that the cries are merely expressions of arousal or excitement at these times but they may also be elicited by subtle cues which are difficult to observe (odours or faint sounds). Cries were sometimes given from the same spots on different nights.

Call No 2, Buzz: The buzz is a short nasal sound which is repeated rapidly and occurs in bouts which get louder or softer. Buzzes were some-

times directly preceded by cries, or interspersed with clicks. The call was common throughout the year, being given by juveniles and rarely by adults when group members had become separated. Buzzing was accompanied by searching movements which could be frantic. The caller moved back and forth rapidly, stopping now and then to stare or to sniff at a branch. It responded to the sounds of moving branches or to calls from its fellows by immediately going towards them. Answering buzzes were rare but in general individuals which had been left behind soon rejoined their group and the calling ceased.

The buzz appears to be important in ensuring that juveniles do not become lost when following the mother. The repetitive nature of the call makes it suitable for auditory localization (Marler, 1965). No equivalent call exists in G. senegalensis which is presumably a reflection of the more solitary habits of this species.

Call No 3, Cluck: Females with young infants often made a short, sharp and faint knocking sound which consisted of single notes with a varying time interval between them. This cluck came from the back of the throat and was occasionally associated with a rattle. Clucks were only given when the mothers were close to their offspring and it is possible that they ensured recognition of the mother by the infants while maintaining contact between them. When the youngsters attempted to follow the mother she would occasionally return to them, calling quietly. A similar call in G. senegalensis, the coo, is given in the same situation (Andersson, 1969).

Call No 4, Click and Call No 5, Squeak: The young G. crassicaudatus made a number of squeaking, clicking and crackling notes. Squeaks were given by struggling infants of a few days old when being carried by the mother. Clicks were the most common calls given by infants and they were occasionally heard from juveniles up to the age of seven months, often in association with buzzes. While clicking the mouth was held open and the lips drawn back in a snarl.

Clicks and squeaks were made in 'distress' situations, particularly following loss of physical contact with the mother. As soon as the infants were capable of following the mother there was a sharp increase in the amount of clicking. Older infants and juveniles moved around actively while calling, showing signs of agitation. These calls evidently act as contact signals between a mother and her infants as a

counterpart to the maternal cluck. They also occurred in situations which would evoke alarm calls from older animals. The clicking of juveniles may represent the retention of an infantile call as suggested by Andrew (1962). He found that clicks accompanied by withdrawal of the mouth corners may extend even into adulthood in captive G. crassicaudatus. In the wild, clicks were largely replaced by buzzes in juveniles and were no longer heard by the time the animals were sub-adult. Similar calls are made by infant G. senegalensis (Andersson, 1969) and Microcebus murinus (Martin, 1972a).

16.4.2 Calls associated with 'Anxiety' or 'Alarm' Situations

A number of calls seem to reflect the motivational state of the caller following arousal by an outside stimulus. They are either undirected expressions or directed towards the evoking stimulus. Jolly (1966a) describes a 'mobbing' call which may occur at several intensities. The faintest, which is almost inaudible, focuses the attention of a group on a potentially dangerous object. The call may then increase in loudness, pitch and intensity. Jolly notes that, like the mobbing response of lemurs, the call entrains the rest of the group so that several animals may call in synchrony while orientated towards the danger, but a false alarm may be ignored. The mobbing call has been divided into seven parts which may be heard alone but which also grade into one another, almost imperceptibly, via a series of intermediates. The parts of this series can be arranged along a continuum of increasing intensity which not only reflects a change in the sound but also a general change in the type of stimulus necessary to elicit the call, the behaviour of the caller, and the nature of the responses shown by other bushbabies (table 13 and appendix 6). The two remaining calls in this category were often heard in association with the mobbing sequence but appear to be discrete calls, differing markedly from the repetitive notes of the continuous series.

Call No 6a, Sniff: A very faint non-tonal sound which is repeated at regular intervals for short periods, sometimes in association with moans. The sniff was heard only occasionally, being given by bushbabies which were inquisitive. The caller approached hesitantly staring and pointing its nose at the object of interest. Its call merely caused other members of the group to stare briefly.

Table 13. A comparison of related calls in the continuous 'mobbing' sequence of G. crassicaudatus showing increasing intensity from left to right. The total numbers of each call heard during the study are indicated in brackets.

Parameter	Sniff	Knock	Creak	Squawk	Whistled-yap	Whistle	Chirp
Loudness	Faint	Faint to intermediate	Intermediate	Intermediate to loud	Loud	Loud	Loud
Pitch	Low	Low	High	Intermediate	High	High	High
Quality	Low	Breathy to gutteral	Squeaky	Harsh	Shrill	Shrill to squeaky	Shrill to squeaky
Units/ minute	±60	42 - 108	78 - 108	24 - 54	54 - 114	78 - 114	?
Maximum duration	2 min	40 min	5 min	20 min	1 hr 30 min	25 min	1 hr
Frequency of occurrence	Rare (4)	Frequent (88)	Occasional (19)	Frequent (61)	Frequent (58)	Occasional (9)	Rare (1)

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Maximum duration	2 min	40 min	5 min	20 min	1 hr 30 min	25 min	1 hr
Frequency of occurrence	Rare (4)	Frequent (88)	Occasional (19)	Frequent (61)	Frequent (58)	Occasional (9)	Rare (1)

Call No 6b, Knock (figure 47a): A repetitive knocking sound which may be faint and breathy or louder and guttural and which varies considerably in speed and duration. It was often interspersed with moans (50% of the records) or it became high-pitched, grading into a creak. Alternatively it became louder and harsher, passing imperceptibly into a squawk. Knocks were made in a variety of situations, particularly towards the observer; by bushbabies observed for the first time in remote areas; during the time of mating and by females with infants. Such females were abnormally agitated by the presence of the observer and they continued to call long after the youngsters had lost interest.

Knocking was a clear indication that a bushbaby was mildly aroused or agitated in a potentially dangerous situation. It would stare intently, move hesitantly, urinate and approach or move away from the evoking stimulus. The knocking sound became louder and more rapid when the danger was close-by but trailed off or stopped as the distance increased. Two or three bushbabies were heard to call simultaneously and they were occasionally seen to groom while calling.

Call No 6c, Creak: A rapid squeaking sound similar to a damp chamois-leather being rubbed up and down on glass. The call followed knocks or whistles without a break and was often accompanied by moans. It occurred during social interactions and followed a disturbance such as that caused by the presence of the observer. Creaks indicated that danger from the eliciting stimulus was not imminent or that the stimulus had ceased to attract the full attention of the caller. Calling stopped as the animal moved away and it rarely lasted for more than a few minutes at a time. This relatively faint call was heard infrequently and it occupies an anomalous position in the mobbing sequence, offering a short-cut from whistles to knocks, without grading into squawks. It may be considered as an incipient whistle or whistled-yap.

Call No 6d, Squawk (figure 47b & c): A raucous series of single or two-tone barking notes often starting slowly, becoming faster and more whistled and changing gradually to units of whistled-yap or whistle. Squawks either started suddenly or built up from, and subsided to, knocks. The squawk component of an alarm series did not last longer than twenty minutes. On rare occasions squawks were interspersed with units of chatter or associated with screams.

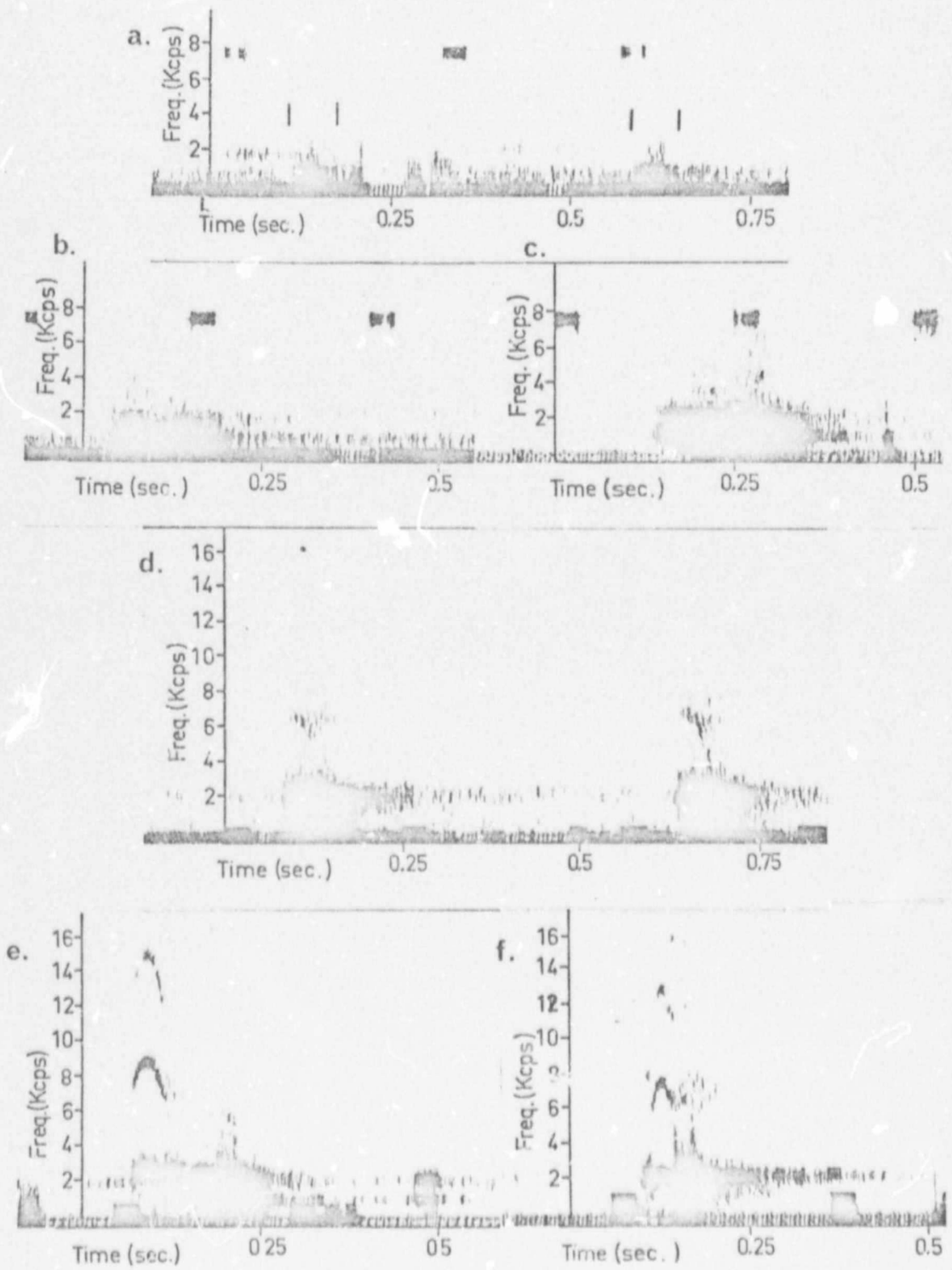

Figure 47. Spectrograms showing a sequence of calls in the 'anxiety/ alarm' series of G. crassicaudatus. (a) Knock, (b) Low squawk, (c) Harsh squawk, (d) Whistled-yap, (e) Whistled-yap variation, (f) Whistle.

Squawks were made when a bushbaby was startled or threatened by a strange animal or object. The caller often moved to a vantage point where it remained still and stared. Alternatively it moved right away from the evoking stimulus, particularly where this was a rival bushbaby. The call would cease briefly if the bushbaby was further disturbed but then continue more rapidly. Other bushbabies in the vicinity remained still and stared, joined in with a squawk or whistle-yap, or continued their activity after a brief pause.

Call No 6e, Whistled-yap (figure 47d & e): and Call No 6f, Whistle (figure 47f): A series of high-pitched, bird-like, notes which are repeated rapidly for periods of up to one and a half hours at a time. The whistled-yap often developed from a squawk, varying considerably in tone, pitch and speed, becoming a whistle or subsiding to a creak. Whistled-yaps and whistles occurred with approximately equal frequency to the squawk and were often interspersed with short bouts of rapid chatter.

These two calls were heard in similar situations to the squawk but, by contrast, they usually persisted for long after the evoking stimulus had disappeared. The caller gave the impression of considerable agitation. He moved back and forth haphazardly, staring fixedly or looking in all directions while the call subsided or increased in speed, or stopped, intermittantly. Duetting and choruses were heard during which the bushbabies often began or ended the call almost simultaneously.

Call No 6g, Chirp: A loud, high-pitched, rasping call which is repeated rapidly and reaches a screaming pitch. The call was heard only once, when given by an adult male bushbaby, during an encounter with a large snake. It was associated with knocks and moans as the bushbaby kept the snake in view, approaching it to within one metre and following it when it moved. The calling increased in intensity as the bushbaby advanced. The interaction lasted for over an hour, causing the bushbaby to return to its sleeping place twenty-five minutes later than usual.

The calls of the mobbing series were heard throughout the year and showed no seasonal peaks in their frequency. Whistled-yaps, whistles and squawks were somtimes as loud as the cry, enabling the caller to be located at a distance, but they were less frequent. The series was given by juveniles as well as adults of both sexes with the exception of the