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Behavioural adaptations in South African Galagos

Harcourt, Caroline Susan

2011-08-18
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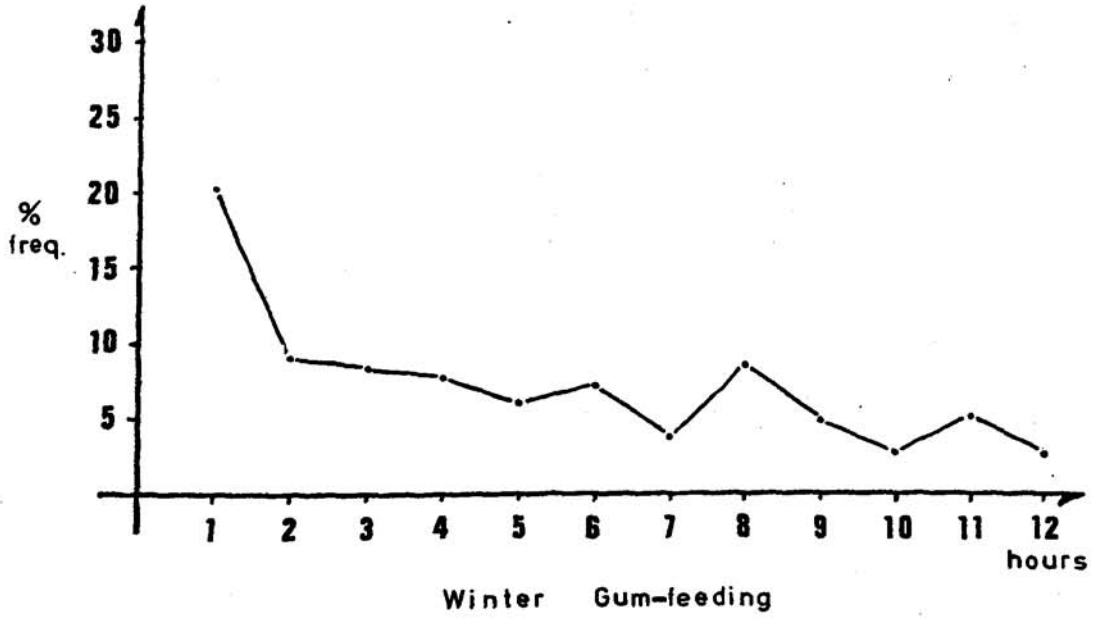
in the night, was found in both species (Bearder, 1969, 1975). In a later study (Bearder and Martin, 1979) it was found that, at least for adult males, ambient light affected the distance travelled by G. senegalensis during the night. They travelled further when the moon was full than at any other stage in the moon's cycle. Both sexes travelled furthest during twilight periods (Bearder and Martin, In prep).

The present study used two measures of activity to provide a picture of the patterning of behaviour under natural conditions: 1) percentage time allocated to each activity and 2) distance travelled. These should provide comparisons for the previous laboratory and field studies. Seasonal and species differences were also investigated. All statistical tables for this chapter are in Appendix 8.

4.2 Results

4.2.1 Percentage Time Allocated to Each Behaviour: One-way analyses of variance were used to test for differences in the percentage time allocated to each activity in each hour throughout the night. No significant differences were found for G. senegalensis in either season. In summer, for G. crassicaudatus, insect-foraging was the only behaviour where a significant difference was found ($F = 3,68$, $df = 5/9$, $p<0,05$). There was also a significant difference in gum-feeding in winter in this species ($F = 3,96$, $df = 5/11$, $p<0,05$).

Duncan's multiple-range tests were used to find which hours were different in the two analyses of variance where significance was obtained. Insect-foraging in summer was



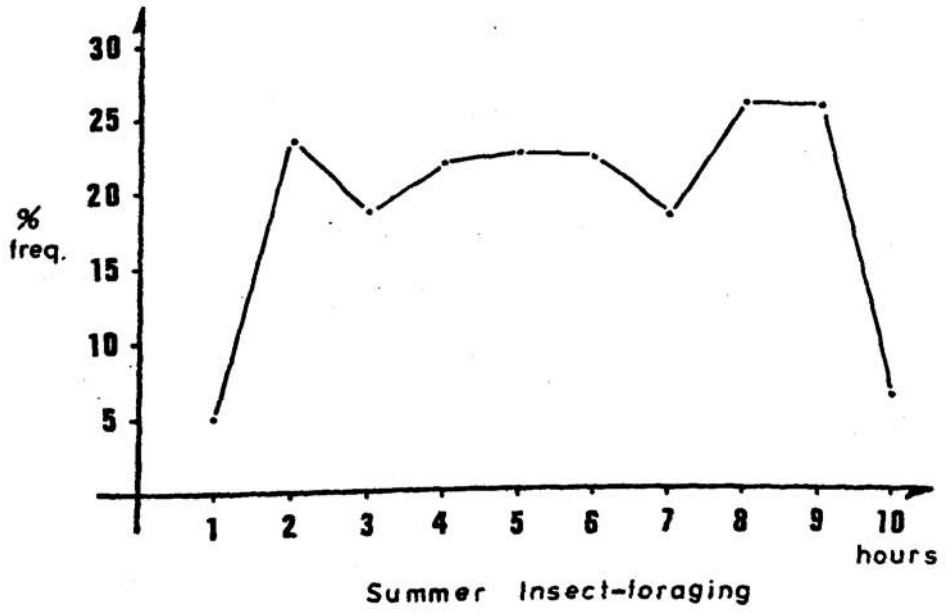


Figure 16. Time spent by G. crassicaudatus gum-feeding in winter and insect-foraging in summer in each hour through the night.

significantly lower in the first and last hours of the night (Fig. 16). Gum-feeding in winter was highest in the first hour of the night (Fig. 16).

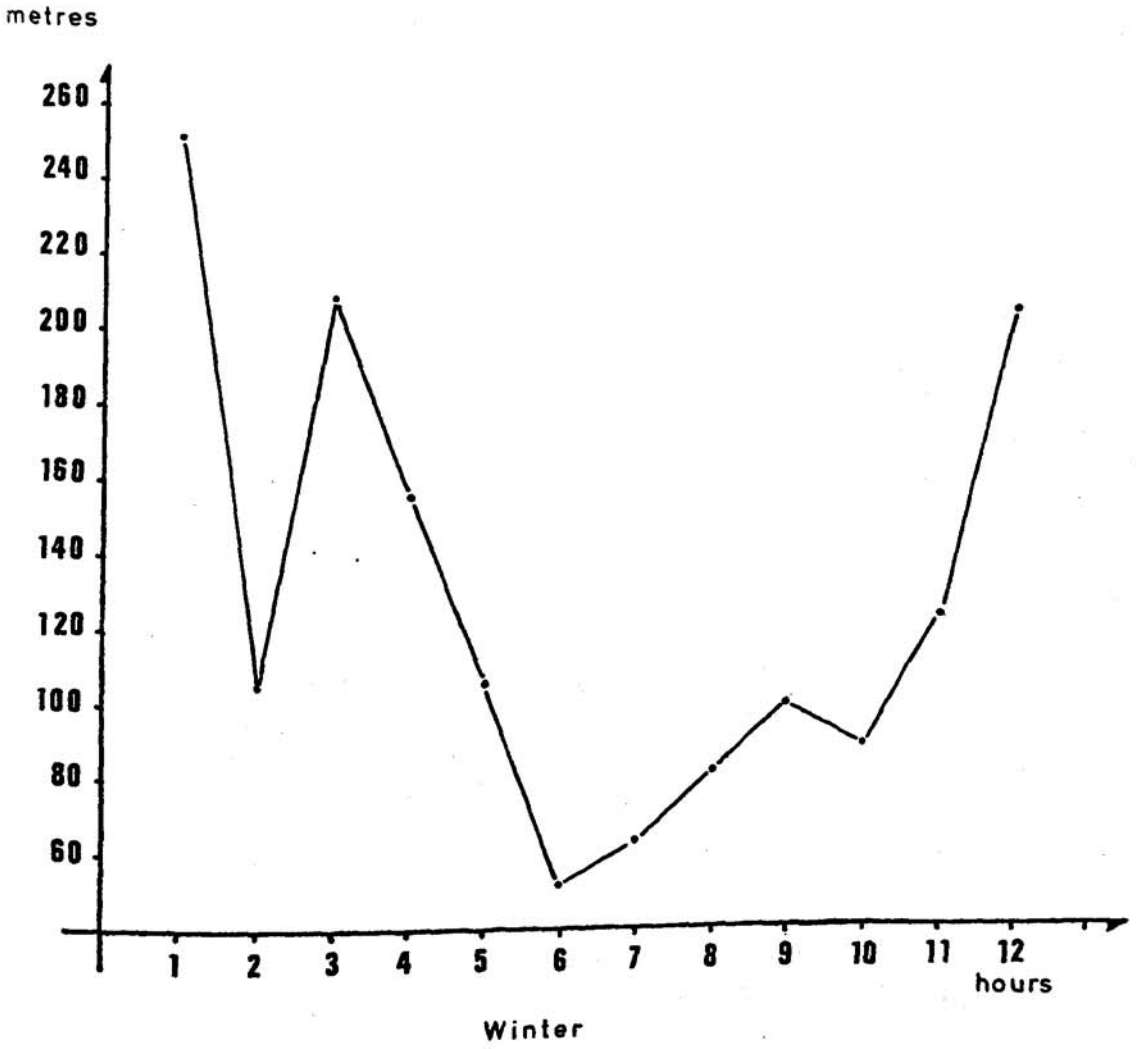
4.2.2 Distance Travelled: One-way analyses of variance, used to test for differences in distance travelled in each hour of the night, showed significance for both species in both seasons (Summer; G. crassicaudatus $F = 6,76$, $df = 9/50$, $p<0,01$; G. senegalensis $F = 3,03$, $df = 8/45$, $p<0,01$; Winter: G. crassicaudatus $F = 4,24$, $df = 11/60$, $p<0,01$; G. senegalensis $F = 3,34$, $df = 11/60$, $p<0,01$).

Duncan's multiple-range tests were used to find which hours were significantly different. In winter G. crassicaudatus travelled greater distances in the first, third and last hours of the night than during the other hours (Fig. 17). In summer this species travelled less in the penultimate hour compared to the first hour (Fig. 17). G. senegalensis showed increased travelling in the first hour of the night in winter and the first two hours of the night in summer (Fig. 18).

4.2.3 Species and Seasonal Differences in Behaviour: Two-way analyses of variance were used to compare the percentage time devoted to each activity by both species in both seasons.

There was a seasons main effect in both moving ($F = 122,11$, $df = 1/20$, $p<0,01$) and gum-foraging ($F = 42,79$, $df = 1/20$, $p<0,01$). In summer moving increased and gum-foraging decreased when compared with the winter data (Fig. 19).

A species by season interaction was found for resting ($F = 7,68$, $df = 1/20$, $p<0,05$), autogrooming ($F = 37,34$, $df = 1/20$, $p<0,01$), allogrooming ($F = 96,0$, $df = 1/20$, $p<0,01$),



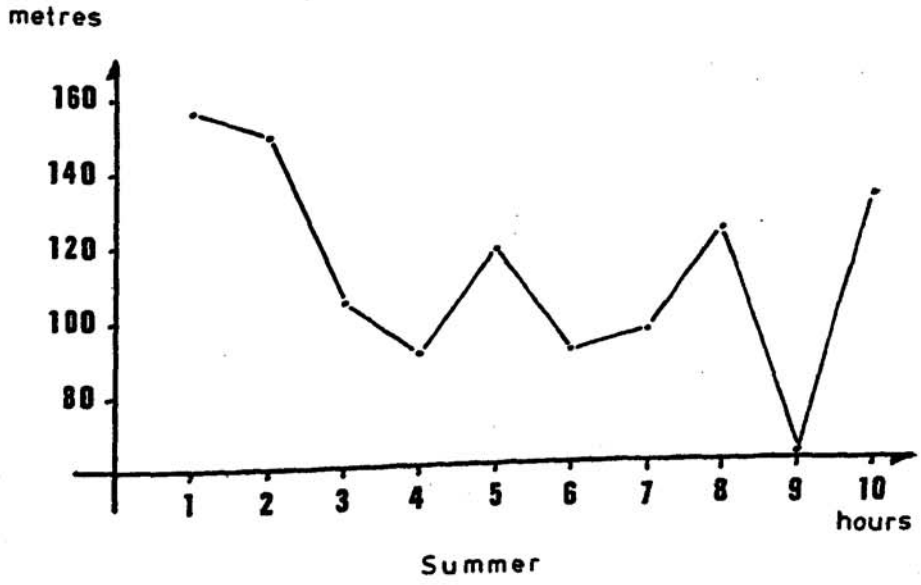


Figure 17. Mean distance travelled by G. crassicaudatus in each hour through the night in winter and summer.

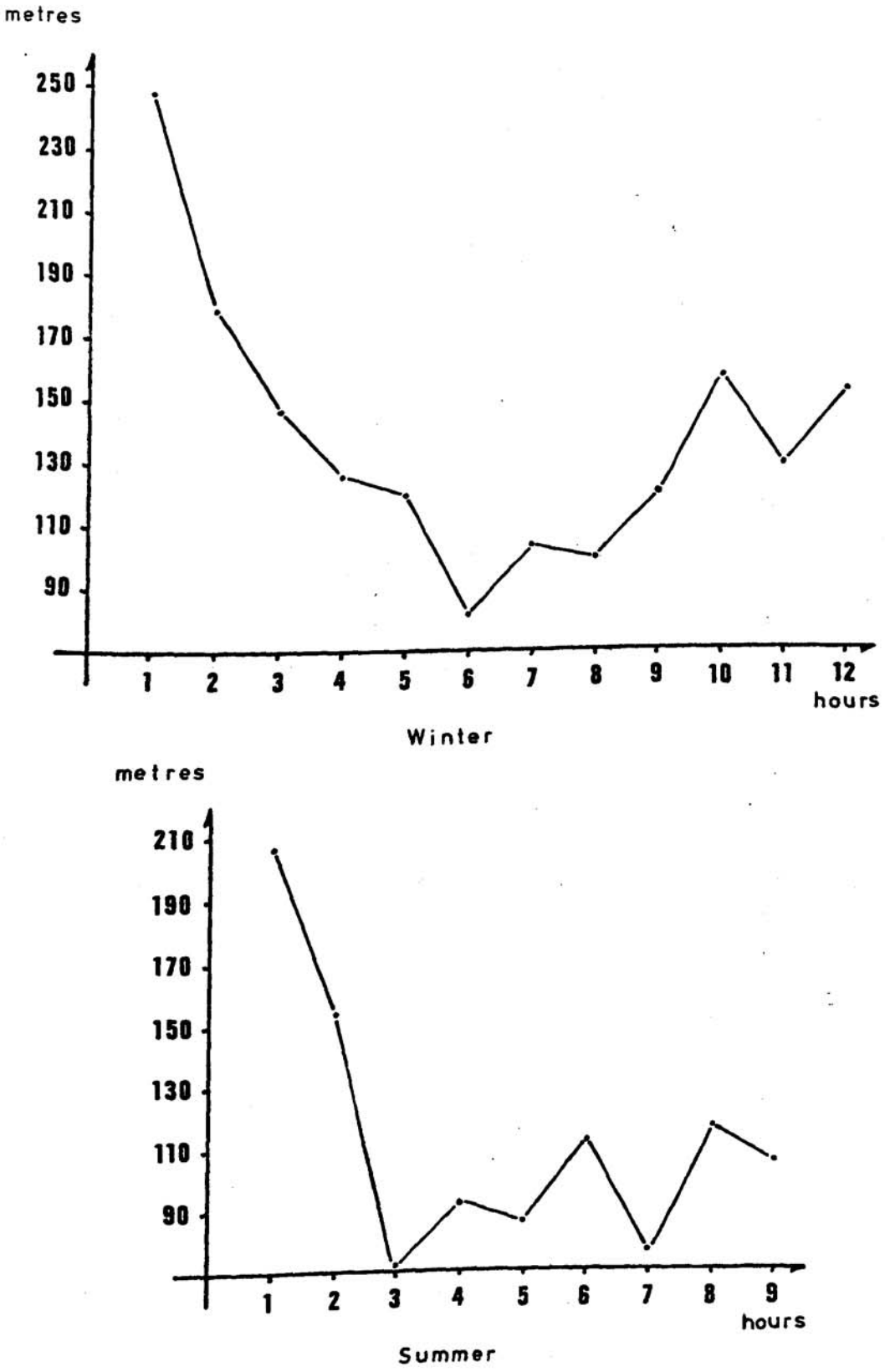


Figure 18. Mean distance travelled by G. senegalensis in each hour through the night in winter and summer.

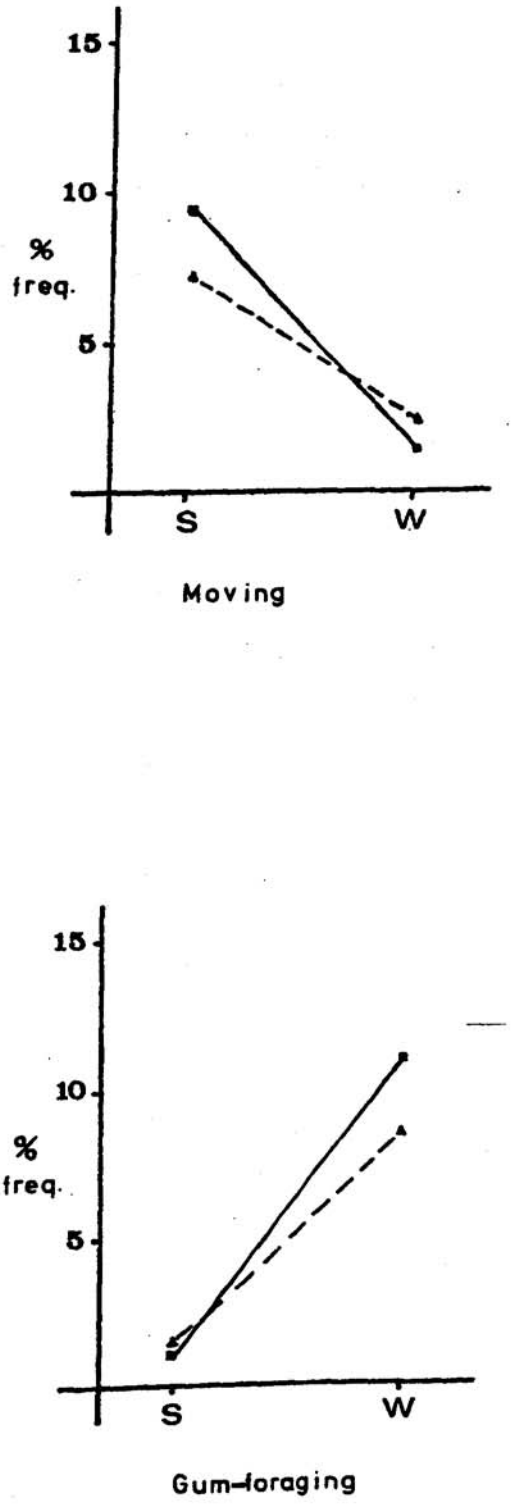


Figure 19. Time spent moving and gum-foraging by both species in each season.

insect foraging ($F = 16,9$, $df = 1/20$, $p<0,01$) and gum-feeding ($F = 9,63$, $df = 1/20$, $p<0,01$). Resting decreased in G. senegalensis from summer to winter and increased in G. crassicaudatus; G. crassicaudatus rested more than G. senegalensis in winter but less in summer. Autogrooming increased from summer to winter in G. crassicaudatus and decreased in G. senegalensis but was lower in G. crassicaudatus than in G. senegalensis in summer though higher in winter. Allogrooming showed a seasonal trend similar to autogrooming in both species but was higher in G. crassicaudatus in both seasons. Insect-foraging increased in summer in both species, it was higher in G. crassicaudatus in summer and lower in winter compared to G. senegalensis. Gum-feeding increased in winter in both species, it was higher in winter for G. senegalensis than for G. crassicaudatus but was very nearly the same for both species in summer. (Figure 20 shows the interactions between species and seasons in all these behaviours).

There were no significant differences in insect-feeding or in travelling between species or seasons.

4.3 Discussion

G. senegalensis did not show consistant temporal variation of any behaviour in either summer or winter, which suggests that the cost or benefit of the individual activities did not change consistently throughout the night. There were periods of an hour or more of complete inactivity during some nights but there was no pattern or obvious reason for these. There is no reason to expect that this small-bodied

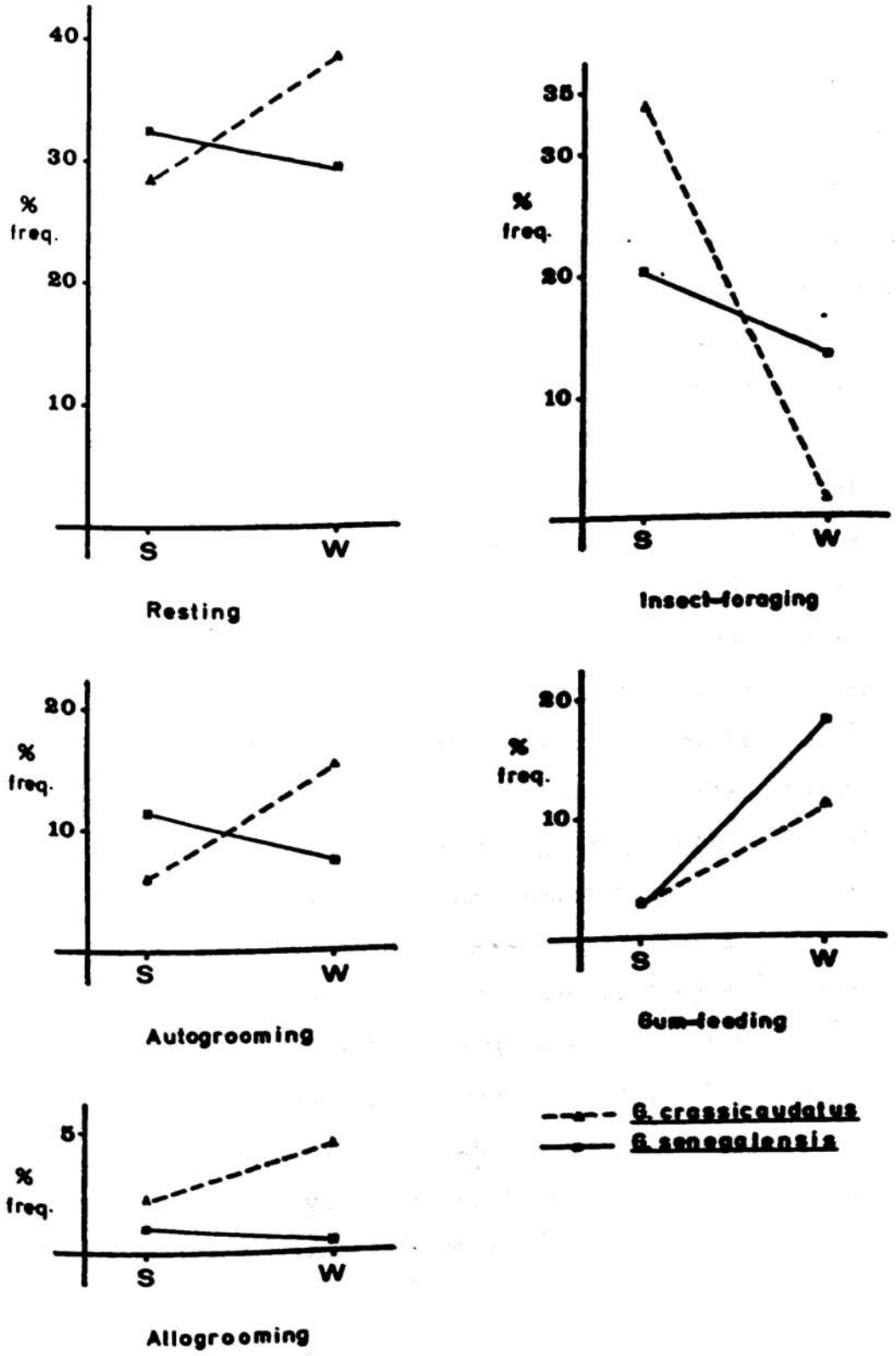


Figure 20. Time spent resting, autogrooming, allogrooming, insect-foraging and gum-feeding by both species in each season.

animal, with its consequent high metabolic rate, would need a long midnight rest for digestive purposes. It was ingesting comparatively small quantities of food throughout the night and these probably would not require long periods of digestion. There were also no consistent changes in light intensity or temperature during a night to which the bushbaby could have adapted the temporal pattern of its behaviour.

In G. crassicaudatus feeding and foraging were the only behaviours that showed temporal variation. In both seasons it was the time spent looking for or feeding on the main food resource for that season that consistently varied across the night. The pattern found in insect-foraging almost certainly did reflect that of insect-feeding (see later). There are two possible explanations for the decreased insect-foraging in the first and last hours of the night. It is possible that G. crassicaudatus, which is a large, relatively clumsy animal in comparison with G. senegalensis, find it easier to catch insects once the temperature has dropped slightly and made the insects more torpid, but before it is so cold that they remain still and are difficult to find. Temperature falls steadily through the night, however (Weather Bureau, 1965) so the decrease in the last hour cannot be explained by a rise in temperature making the insects too active again. Alternatively the thick-tailed bushbaby may be foraging for nocturnal insects which may not begin their activity until some time after sunset and cease before sunrise. (Park and Keller, 1932). The peak of gum-feeding in the first hour of the night in winter was probably due to this being the warmest hour of the night. The

strategy of this species was to conserve energy by becoming inactive at low temperatures (resting increased in winter, see above). In the expectation of having to cease any activity later in the night, the bushbaby took in as much energy as possible in the first hour of darkness. This peak will be further increased if the animal had to rest for long periods of the previous night as it will be particularly hungry after the daylight inactive period, having settled with little food in its stomach.

On very cold nights, with temperatures below freezing, both species do show a tendency to go to their sleeping sites two hours or more before dawn (S.K. Bearder, pers. comm.; pers. obs.). At very low temperatures invertebrates are probably totally inactive and difficult to find. Therefore, even for G. senegalensis, the optimal strategy is to conserve energy by inactivity and by huddling together with other animals. It is also possible that the gum becomes extremely solid at low temperatures and no longer worth licking.

The differences in distance travelled between the hours are not easy to explain in either species. As the effect of ambient light has been shown to be fairly considerable (Bearder and Martin, 1979, in prep.) this should have been taken into account when collecting and analysing the data. However, a considerably larger sample size would be needed than was used in the present study and light intensity would have had to be measured throughout each night. On a night when there was a full moon distances travelled in each hour through the night would be expected to be greater than on any other night. When there was no moon fairly high peaks of travelling during twilight would be expected. In both species there was

a tendency to travel further in at least the first hour of darkness (twilight) which does suggest that the bushbabies were affected by light levels.

The species and seasonal differences in behaviour found in this study can mostly be explained in terms of animals of a different body size having different behavioural adaptations to their external environment and these changing as external conditions changed.

The time spent resting was similar in both species in summer. This was the time of the year when food was most plentiful. The species were using similar resources and there were no adverse external conditions that could have been expected to produce major differences in the time they spent resting each night. In winter G. senegalensis showed a slight decrease in the time spent resting whereas G. crassicaudatus increased its resting time fairly substantially. The small-bodied animal would loose heat more rapidly than the larger one and this loss would be increased if it was inactive in the low temperatures of a winter night. Its optimal strategy was to remain active and keep its energy intake up in winter. For G. crassicaudatus, a relatively large animal, the best strategy was to conserve energy by becoming inactive at low temperatures.

Allogrooming increased in winter in G. crassicaudatus and decreased in winter in G. senegalensis. The female lesser bushbaby had very few interactions with any other galagos in winter (see chapter 6), whereas in summer she was still meeting her November infant fairly frequently and most of the allogrooming recorded was with this infant. In winter it

appeared that G. senegalensis had little time for social interactions, which suggests that the benefit received from these interactions was minimal. G. crassicaudatus, in contrast, is a more social animal. It interacted with more galagos in both seasons than did G. senegalensis (see chapter 6). The infants of this species remained in frequent contact with their mother until they were nearly a year old. Even when new infants were born the offspring from the year before continued to meet their mother on occasions. These interactions frequently included a period of allogrooming. The increase in allogrooming by G. crassicaudatus in winter was mainly due to the female grooming her six month old offspring more often than she did when they were two months old in summer (see chapter 6 for a fuller consideration of this).

Autogrooming also increased in winter in G. crassicaudatus and decreased in G. senegalensis. The most likely reason for the seasonal change is that autogrooming usually occurred during bouts of resting and as resting increased in winter in G. crassicaudatus so did the time spent autogrooming; as it decreased in winter in G. senegalensis so did the time spent autogrooming. The differences between the species are not easily explained. The higher incidence of autogrooming in summer in G. senegalensis than in G. crassicaudatus may be compensating for the slightly lower incidence of allogrooming in the former species. A difference in the number of parasites in the two habitats may also account for some of the variation.

Time spent insect-foraging was reduced in both species in winter, but more so in G. crassicaudatus than in G. senegalensis. The reduction was due to the decrease in inverte-

brates available in both study sites. The greater reduction in G. crassicaudatus was the result of this species being able to survive fairly well on a basic diet of gum in winter thus being able to decrease the number of insects in its diet when they were difficult to find. This strategy was not used by G. senegalensis in the present study (see chapter 3). Insect-feeding did not show any change between species or seasons but this was almost certainly due to the difficulty of seeing when an insect was taken. If an animal was foraging high in a tree or in thick vegetation the chances of recording every insect that it caught were small. There were differences between seasons in the number of insects recovered from faecal samples (see chapter 3) so there is a strong probability that the time spent eating them varied also.

Gum-feeding decreased in summer in both species as insects were readily available and these were taken in preference to gum. However, a small quantity of gum was taken even in summer and it is probable that this resource contained essential minerals not found in insects. G. senegalensis spent longer feeding on gum in winter than did G. crassicaudatus but this, as pointed out in chapter 3, does not necessarily mean that it was eating more gum than the thick-tailed bushbaby. As would be expected, time spent gum-foraging showed a trend between seasons similar to that found in gum-feeding.

Moving decreased in winter in both species. It is possible that short, inessential movements were reduced in the cold weather to conserve energy. The amount of time spent travelling did not vary between species or seasons. This, though, is not a measure of distance travelled as speed of

travel will be important in this respect (see Chapter 5 for further consideration).

In the laboratory different patterns of behaviour can be obtained by altering the quantity of food available or the time of its presentation (Charles-Dominique, 1977). Therefore some of the variation in pattern in the laboratory studies on G. crassicaudatus and G. senegalensis (Ehrlich, 1968; Haddow and Ellice, 1964; Pinto, 1972; Pinto et al, 1974; Randolph, 1971; Sanderson, 1957; Sauer and Sauer, 1963) was probably the result of differences in feeding schedules. In addition the predictable and impoverished laboratory environment will have contributed to the stereotyped pattern of activity found in some of these studies. In the much more unpredictable and varied natural habitat the animal changes its behaviour as external and internal conditions change and, as a result, there was no consistant temporal variation found in any behaviour in either species of bushbaby.

Wilson's 'principle of stringency' may hold true when environments are poor in terms of energy availability. An animal has certain expectations about its environment. When energy levels are fluctuating at a low level, as in winter, the animal must assume that the worst conditions will occur and behave in such a way as to maximise energy intake under those conditions (see explanation for peak of gum feeding in winter). When energy levels are consistently high, as in summer, there is no need to operate in such a way as to maximise for the worst conditions, as sufficient energy can be obtained even at the lowest trough of the fluctuations that will be found in the energy rich environment. It is probably

the limits within which an animal can adapt its time-energy budget to the prevailing conditions, rather than the budgets themselves, that are subject to natural selection. From this study it would appear that G. crassicaudatus is slightly more adaptable than G. senegalensis in this respect. Consistent temporal patterning of activity within a species should be the result of fairly consistent external conditions. This would explain the frequent occurrence of bimodal patterning in diurnal species in places where a peak of temperature is found around midday and would also help explain the lack of a consistent temporal pattern in the behaviour of the bushbabies.

The availability and distribution of resources in an environment and the energy requirement of the animals will affect the amount of time spent on a particular behaviour, hence the seasonal and species differences in time use found in this study.

5. Use of Space

5.1 Introduction

Most mammals, as adults, spend their lives in a restricted area known as their home range (Burt, 1943). The advantage to an individual of staying within a particular area is presumably that it becomes familiar with its surroundings so knows the position of such resources as food, water, sleeping sites and safe resting places. This knowledge allows it to make best use of its habitat and, as with optimal time use, will enable it to maximize its chances of survival and its reproductive fitness.

A home range has to be big enough to meet the energy requirements of the animal that occupies it and, as would be expected, a relationship between the body weight and home range size has been shown to exist in a number of species (Armstrong, 1965; McNab, 1963; Schoener, 1968). In more recent papers it has been demonstrated that both the body weight and the diet of primate species affect the size of their home range (Milton and May, 1976; Clutton-Brock and Harvey, 1977). Energy supply, though, is not the only determinant of home range size; other resources such as suitable sleeping sites or access to females may also be important (S. A. Altmann, 1974; Jewell, 1966). Home range size in most of the nocturnal prosimians shows marked intra-

specific differences according to the sex and (among males) the social status of the individual (Bearder and Martin, 1979; Charles-Dominique, 1977). However, in this study with the two species using the same food resources and the focal animal in each species being female, it was expected that the larger species would have the bigger home range. As with home range size, many differences in day range length are related to variations in food density. Day range length and home range size tend to increase when food availability is reduced (Clutton-Brock and Harvey, 1977).

All parts of an animal's home range are not necessarily used equally. In many studies the home range was found to be divisible into heavily used 'core areas' (Kaufmann, 1962) and other less frequently used areas. While the core area concept is still used (e.g. Oates, 1977) most recent studies of primates have tended to focus on the differential use of space in terms of time spent in different quadrats within the range (Goodall, 1977; Rudran, 1978; Waser, 1977). In these studies more than one area of heavy use is commonly found. Studies on the South African galagos have not considered in any detail how home ranges are used, although G. crassicaudatus was found to have a core area which was related to the distribution of sleeping trees (Bearder, 1975).

The differential use of the home range has been related to resource distribution (Charles-Dominique, 1977; Clutton-Brock, 1975; Oates, 1977). These observations suggest that range use is decided by food resources and that time spent in any part of the home range can be expected to depend on the food supplies found in that area. An extension of this, which

is rarely considered, is the factor which determines where an animal's non-feeding behaviour occurs. From a semi-Markov chain model (Ross-Ashby, 1956) it would be expected that the longer an animal spent feeding in one patch, the more likely it is to exhibit other, non-feeding behaviour in the same patch. Dawkins (1976) suggested that a hierarchical model of decision making may be used by animals in which one decision leads to progressively narrower subdecisions ending up with an observed act. It should be possible to relate Dawkin's model to the distribution of behaviour in space. If the environment is heterogeneous and consists of a number of discrete patches of different resource types then each patch type may be associated with a different optimal time-energy budget. The decision to enter and use a particular type of patch would involve a change in the animal's time-energy budget and this can be represented as a simple decision tree with the different budgets as the lowest level. By examining the correlation of different behaviours in space it should be possible to identify discrete groups of covarying behaviours which can then be related to different patch types.

So far, the use of horizontal space only has been considered. Aboreal primates have a vertical dimension to their home range and the use of this must also be investigated. Vertical zonation appears to play a part in the ecological segregation of sympatric, forest-dwelling primates including prosimians (Charles-Dominique, 1977; MacKinnon and MacKinnon, 1978). The heights at which each species is located depends on the food resources it is using. Bearder (1975) found that the amount of activity at different heights in the trees by

both G. senegalensis and G. crassicaudatus depended on the spacing of the trees and the availability of food in each habitat. In the present study, with the species being studied allopatrically, height differences may be the result of habitat differences. However, seasonal changes within a species in the amount of activity at different heights would almost certainly be a response to changing food resources. It is likely then that a difference in the way resources are used between species will also affect the heights at which they are foraging and feeding.

The present study looked in detail at the use of both horizontal and vertical space in the two species of galago.

5.2 Results

5.2.1 Home Range: When all observations, including trapping data and sleeping site positions, were taken into consideration the home range size of the two species was very different. G. senegalensis used an annual range of 2,7 hectares while G. crassicaudatus used 7,7 hectares. However, G. crassicaudatus spent 92,3% of the total observation time within the riverine strip of vegetation which was only 35% of its total range (2,7 hectares). There was not a similar heavily used area in the home range of G. senegalensis. In both species there was a reduction in the number of quadrats used in winter in spite of more hours of observation in that season. G. senegalensis used 204 quadrats in summer and 177 in winter; G. crassicaudatus used 186 quadrats in the riverine strip in summer and 167 in winter. The latter species was

out of the main study area for 6,4% of its time in summer and for only 1,3% of the observation time in winter. Sleeping sites were outside the riverine strip for 27% of the time in summer and for 6% of the time in winter. The percentage time spent out of the riverine strip is probably slightly more than that recorded in that if the animal was found sleeping outside the strip then observations were not begun until later in the night and if it headed off out of the strip in the early morning then observations ceased. Usually though, when the galago slept in the east field it headed back towards the river when it woke and was in the strip within ten minutes.

Distances travelled each night varied considerably but, for both species, they were usually in the range of 1000 metres to 1500 metres. G. senegalensis travelled approximately 120 metres per hour in both seasons with a maximum in an hour of 320 metres in summer and 354 metres in winter. In both seasons there were some hours in which the galago remained in the same tree for more than an hour. G. crassicaudatus travelled a mean of 115 metres per hour in summer with a minimum of five and a maximum of 288 metres in an hour. In winter it travelled a mean of 130 metres per hour with no travelling in some hours and up to 355 metres in others. There were no significant differences in mean distance travelled per hour between seasons within a species (G. senegalensis $t = 1,07$, $df = 10$,; G. crassicaudatus $t = 1,70$, $df = 10$), though there was in the distance travelled per night as a winter night was twelve hours long while a summer one was only ten hours long.

5. 2. 2 Range use: The number of times that each of the ten behaviours (foraging and feeding on gum and insects, travelling, resting, moving, allogrooming, autogrooming and urine-washing) occurred in each ten-metre quadrat was recorded. The distribution of these activities in space was examined using quadrat analyses (Greig-Smith, 1964). All behaviours of both species were found to be clumped in both seasons except insect-feeding by G. crassicaudatus in winter. The non-random clumped distribution showed that each behaviour tended to occur in relatively discrete patches (Figs. 21-26). The value provided by $s^2/\bar{x}$ reflects the extent to which the individual activities occurred in patches (Tables 2a and 2b and Appendix 9). The higher the value the more clumped the occurrence of the behaviour. The $s^2/\bar{x}$ values for all the behaviours except insect-foraging and insect-feeding were higher in winter than in summer for G. crassicaudatus. Resource use in G. senegalensis was clumped in both seasons but more so in winter than in summer. Travelling, autogrooming and urine-washing showed a similar pattern but resting, moving and allogrooming were less nucleated in winter than in summer.

Correlations of the frequency of the behaviours in each quadrat were carried out and matrices of the results for each species in each season were drawn (Tables 3a and 3b). Clusters of spatially co-varying activities were isolated using a significance level of $r_s = 0,3$. This comparatively high level was chosen as the sample size was large and the proabability of a type one error (rejecting the null hypothesis when it is true) increases with increasing sample size

Table 2a. Quadrat Analyses for G. crassicaudatus.

Activity	Summer $s^2/\bar{x}$	Winter $s^2/\bar{x}$
Travel	3,73	8,73
Rest	8,38	69,87
Move	3,06	4,34
Autogroom	6,90	25,28
Allogroom	4,78	8,61
Insect-forage	50,50	4,87
Insect-feed	2,28	0,99
Gum-forage	3,44	13,37
Gum-feed	6,77	38,47
Urine-wash	1,49	4,8

Table 2b. Quadrat Analyses for G. senegalensis.

Activity	Summer $s^2/\bar{x}$	Winter $s^2/\bar{x}$
Travel	4,54	60,22
Rest	18,43	7,4
Move	6,77	2,57
Autogroom	17,30	20,04
Allogroom	6,65	2,94
Insect-forage	13,97	126,40
Insect-feed	2,33	6,14
Gum-forage	8,45	20,36
Gum-feed	12,46	24,49
Urine-wash	2,34	2,15

Table 3a. Matrix Table showing correlations of behaviours in space for *G. crassicaudatus*.

SUMMER

	T	M	R	Gs	Go	Si	Fi	Sg	Fg	u/w
T		0,39	0,49	0,45	0,36	0,10	0,07	0,20	0,12	0,22
M	0,17		0,48	0,34	0,21	0,02	-0,11	0,03	0,05	0,08
R	0,59	0,42		0,60	0,30	0,44	0,30	0,09	0,14	0,19
Gs	0,54	0,01	0,68		0,38	0,40	-0,01	-0,08	0,06	0,29
Go	0,48	0,45	0,73	0,63		-0,11	-0,30	-0,22	-0,04	-0,07
Si	0,19	-0,06	0,17	0,05	0,01		0,67	-0,09	-0,05	0,02
Fi	0,07	-0,09	0,03	0,06	-0,16	-0,13		-0,27	-0,19	-0,39
Sg	0,48	-0,01	0,39	0,42	0,25	-0,22	-0,01		0,62	-0,52
Fg	0,36	-0,04	0,19	0,12	0,10	-0,12	0,16	0,66		-0,31
u/w	0,41	-0,24	0,34	0,30	-0,09	-0,44	-0,64	0,32	0,35	

WINTER

T = Travel
M = More
R = Rest
Gs = Autogroom
Go = Allogroom
Si = Insect-forage
Fi = insect feed
Sg = gum-forage
Fg = gum-feed
u/w = urine-wash

Table 3b. Matrix table showing correlations of behaviours in space for *G. senegalensis*.

SUMMER

	T	M	R	Gs	Go	Si	Fi	Sg	Fg	u/w
T		0,53	0,50	0,28	-0,02	0,40	0,33	0,31	0,41	0,19
M	0,15		0,81	0,57	0,17	0,59	0,03	0,01	0,08	0,18
R	0,47	0,47		0,73	0,15	0,67	0,21	0,13	0,18	0,26
Gs	0,44	0,24	0,59		0,19	0,40	-0,04	-0,09	-0,03	-0,06
Go	0,26	-0,02	0,28	0,74		-0,03	-0,38	-0,22	-0,22	-0,46
Si	0,17	0,18	0,56	0,45	0,14		0,45	0,09	0,23	0,009
Fi	0,19	0,43	0,54	0,48	0,14	0,94		0,05	0,47	-0,27
Sg	0,41	-0,17	0,15	0,52	0,50	-0,10	-0,04		0,71	0,04
Fg	0,36	-0,14	0,17	0,35	-0,30	-0,09	-0,03	0,66		0,07
u/w	0,17	-0,48	0,01	0,06	-0,34	-0,13	-0,27	0,35	0,45	

WINTER

T = Travel
M = More
R = Rest
Gs = Autogroom
Go = Allogroom
Si = Insect-forage
Fi = insect-feed
Sg = gum-forage
Fg = gum-feed
u/w = urine-wash

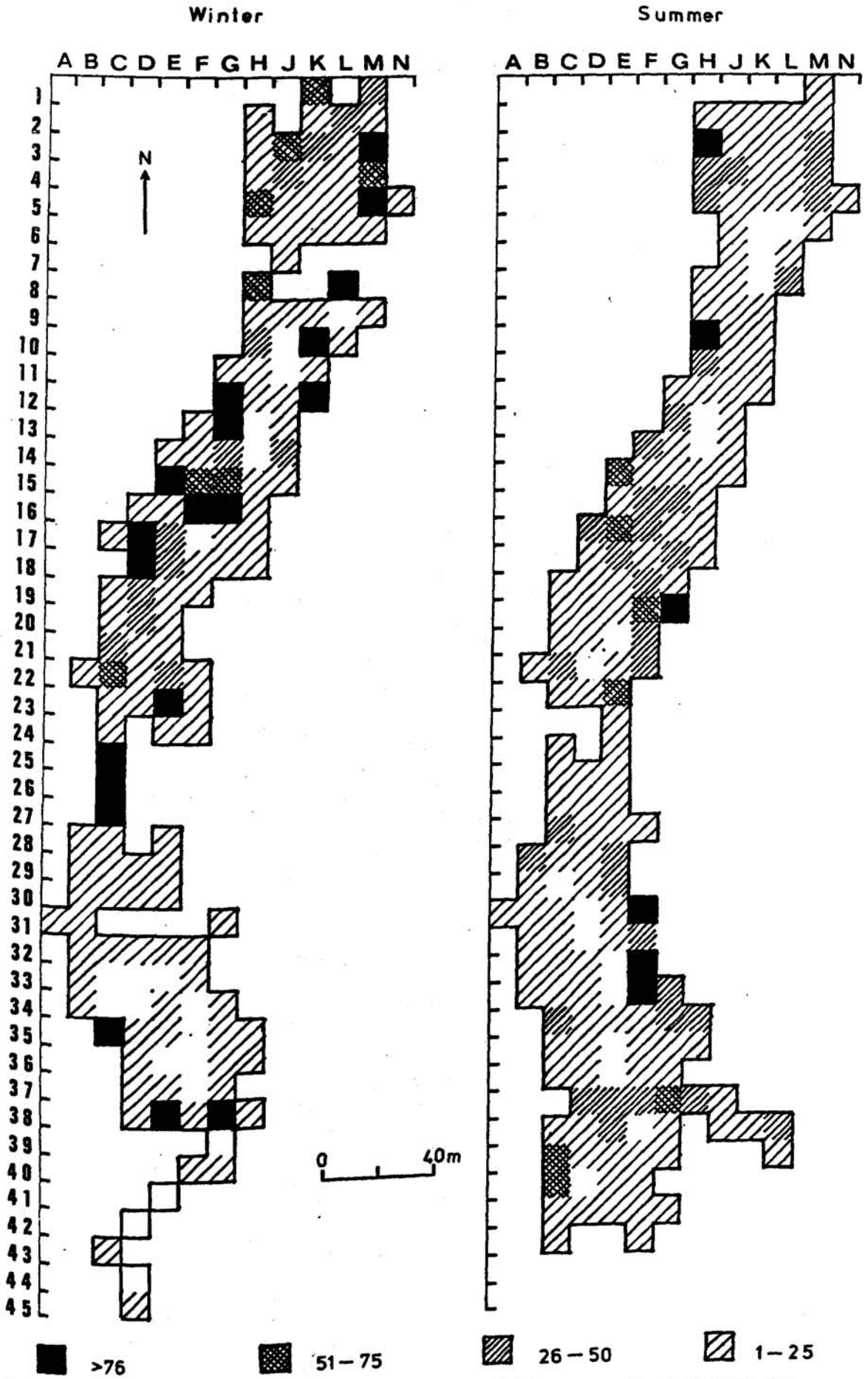


Figure 21. Number of observations of G. crassicaudatus in each ten-metre quadrat in its home range in summer and winter.

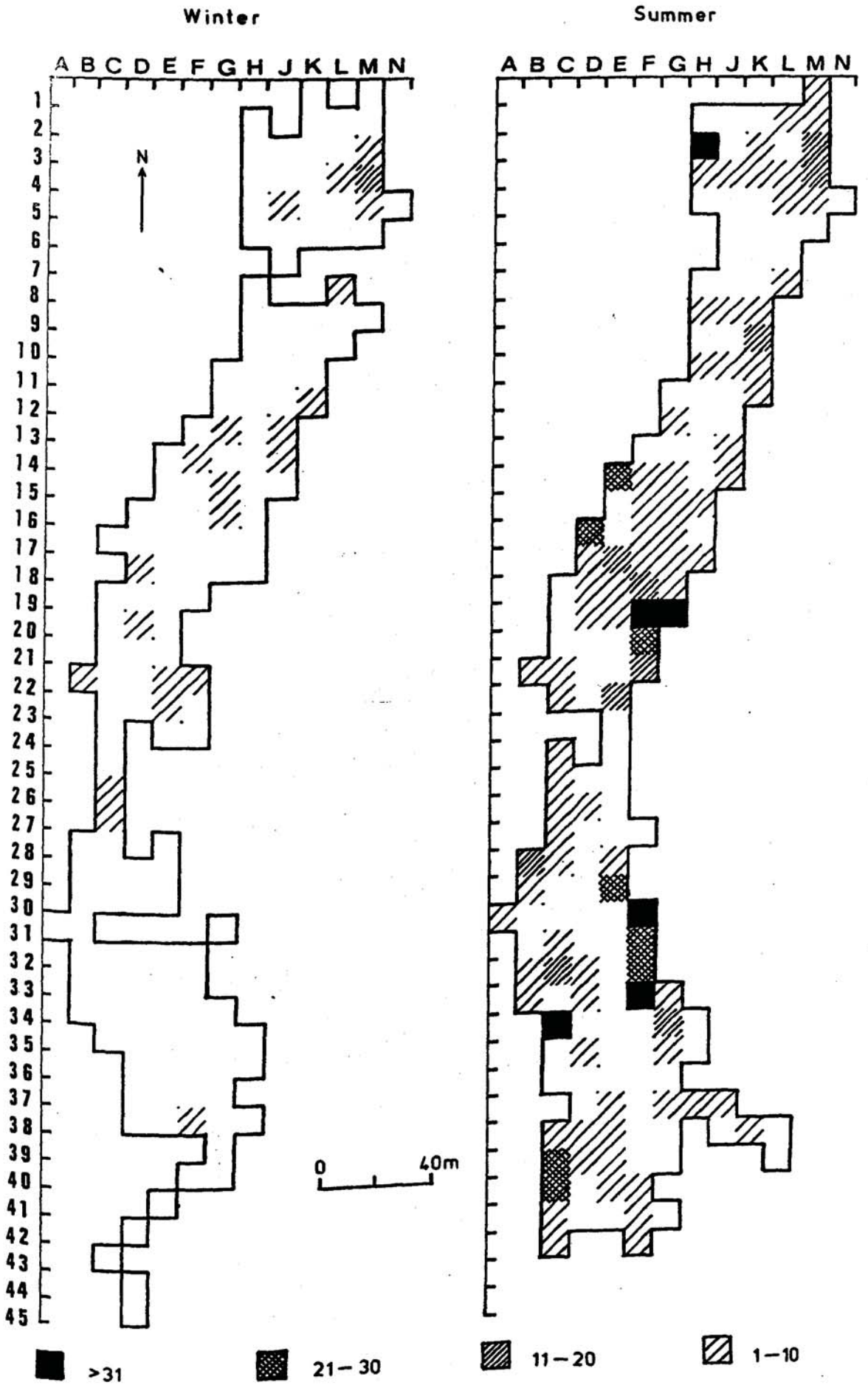


Figure 22. Number of observations of G. crassicaudatus feeding and foraging on insects in each ten-metre quadrat in its home range in summer and winter.

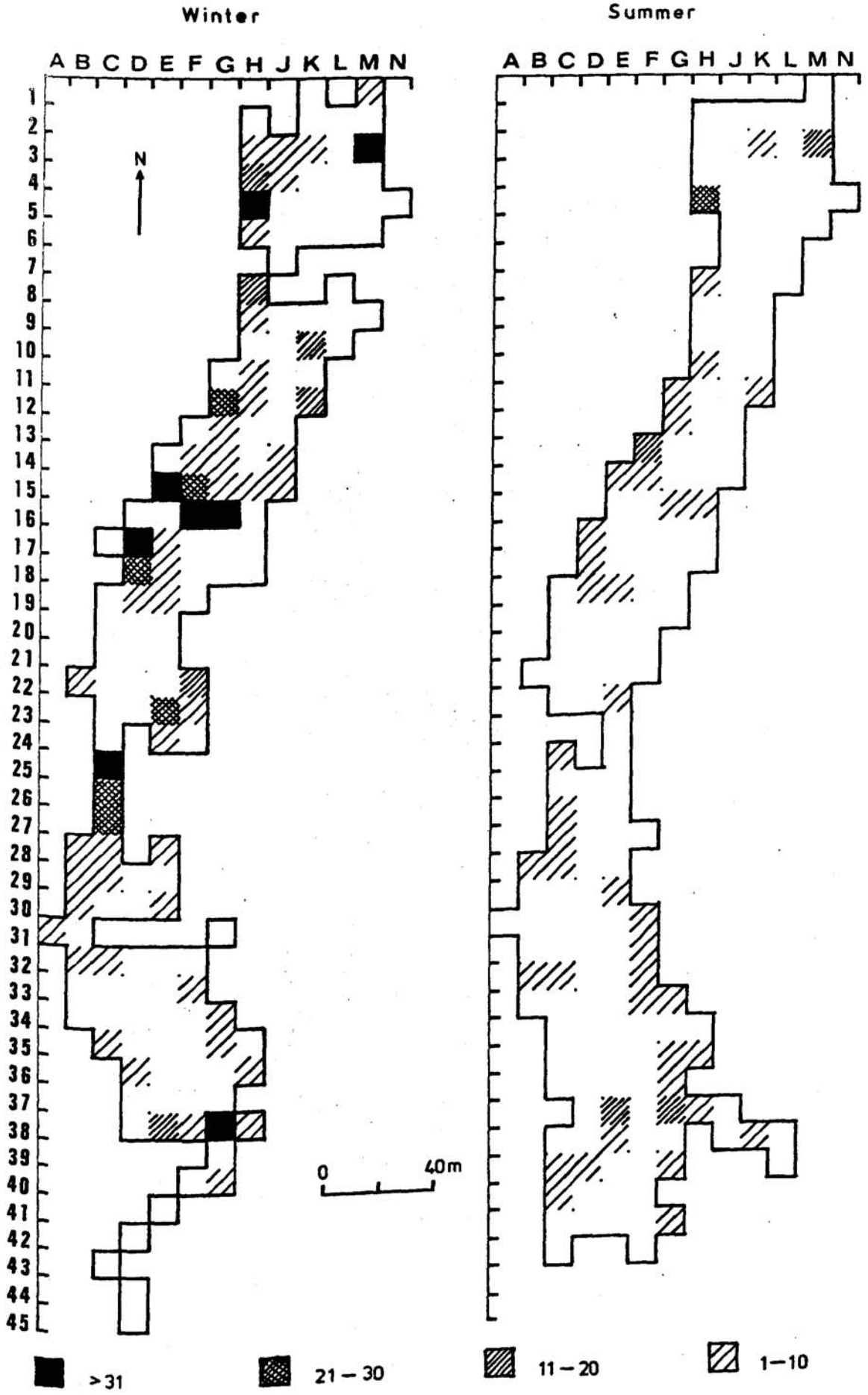


Figure 23. Number of observations of G. crassicaudatus feeding and foraging on gum in each ten-metre quadrat in its home range in summer and winter.

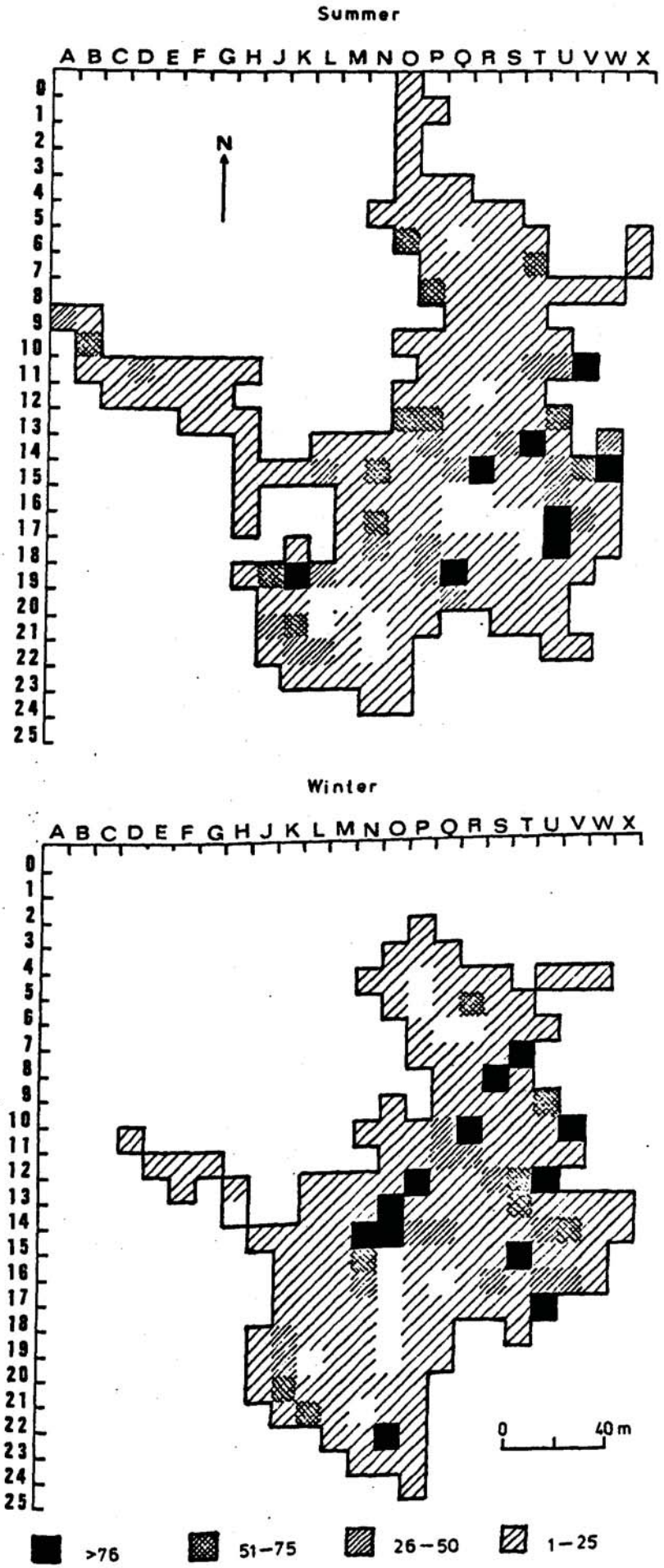


Figure 24. Number of observations of G. senegalensis in each ten-metre quadrat in its home range in summer and winter.

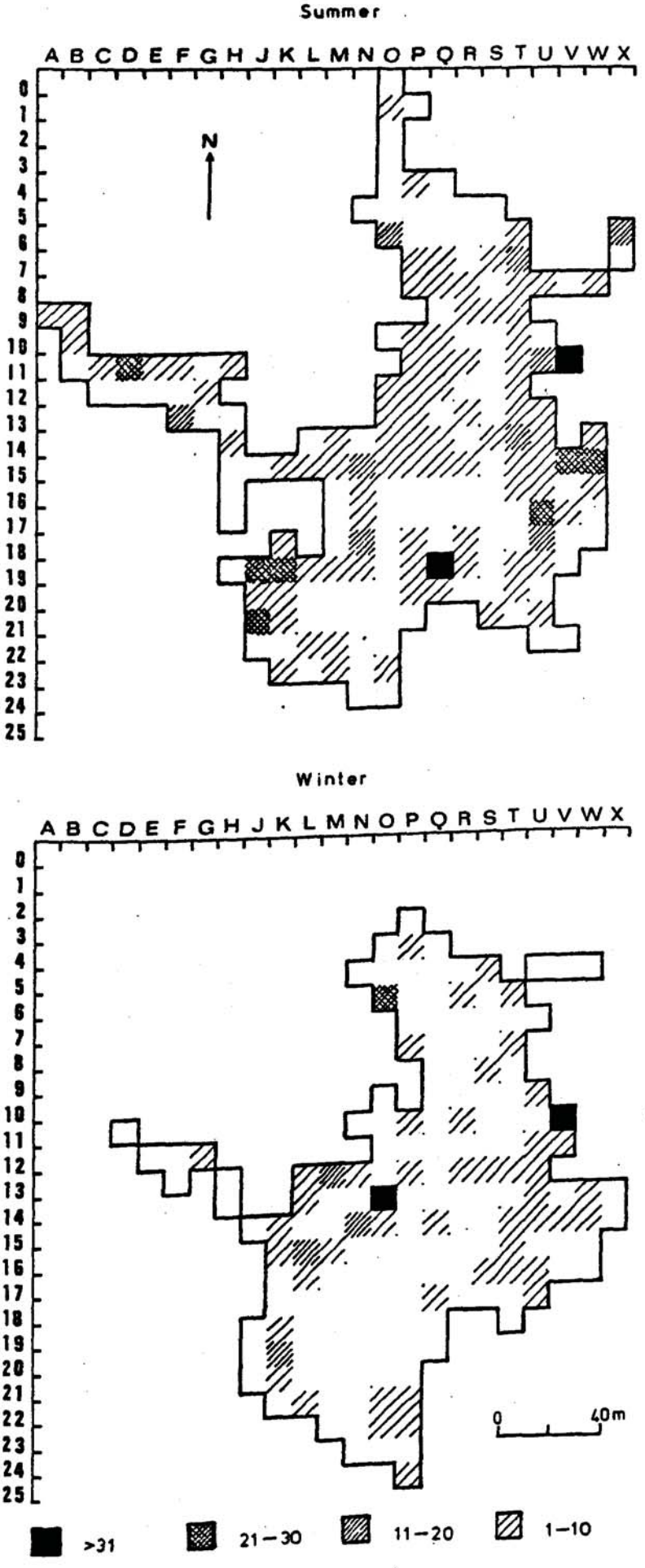


Figure 25. Number of observations of G. senegalensis feeding and foraging on insects in each ten-metre quadrat in its home range in summer and winter.

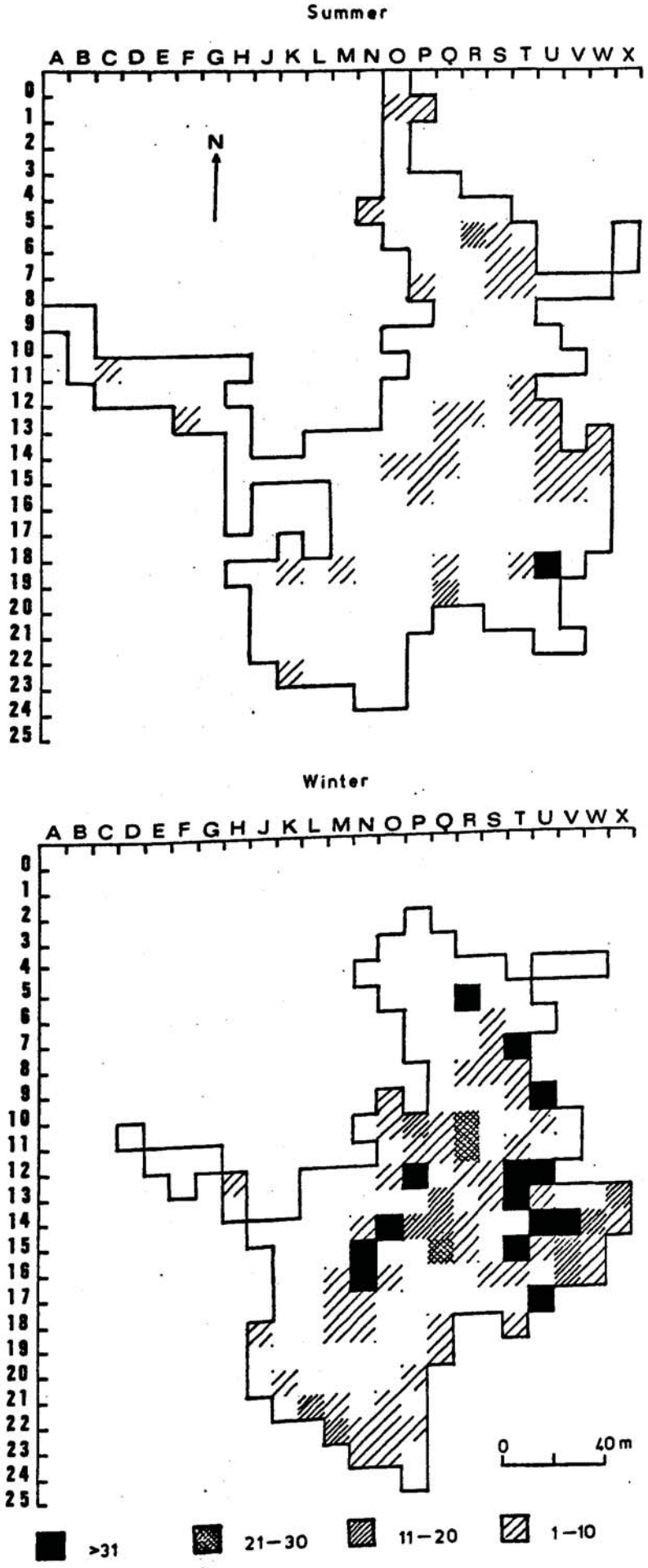


Figure 26. Number of observations of G. senegalensis feeding and foraging on gum in each ten-metre quadrat in its home range in summer and winter.