CHAPTER 4. ACTIVITY.

Introduction

The Grey Headed Flying Fox is predominantly nocturnal, expending the majority of energy on the crepuscular feeding flights (Thomas, 1975) and on feeding itself. During the daytime however, these animals are far from inactive and display a very considerable range of activities and behaviour, which will be discussed in this and a following chapter respectively.

Feeding, the predominant night time activity has been already discussed in an earlier chapter, while thermoregulatory, reproductive and social behaviour are discussed in later chapters. The major points of interest here are sleep or inactivity, a description of the 'mechanics' of thermoregulatory behaviour, a full discussion of maintenenace activities, locomotion, and reaction to disturbing influences. Each definable activity in these areas shall now be discussed.

Wrapped up asleep - the animal hangs by one or both legs, the wings are folded vertically around the body and the head is 'tucked up' inside the membranes, as seen in Plate 1a. Sleeping may occur at any time of the day but is far more predominant in the early morning and late afternoon. Total sleep per day,during daytime in winter,from figures 14 and 15, averaged 3hours 3 minutes. This figure was relatively constant between males and females and monogamous and polygamous males but females with young appeared to spend less time (2hours 15 minutes) sleeping than did single females (3 hours 22 minutes). The figures for these groups are speculative as the sample sizes are too small to allow positive statements.

Fig. 14. Male Activity 16/6/81 - 15/7/81 inclusive

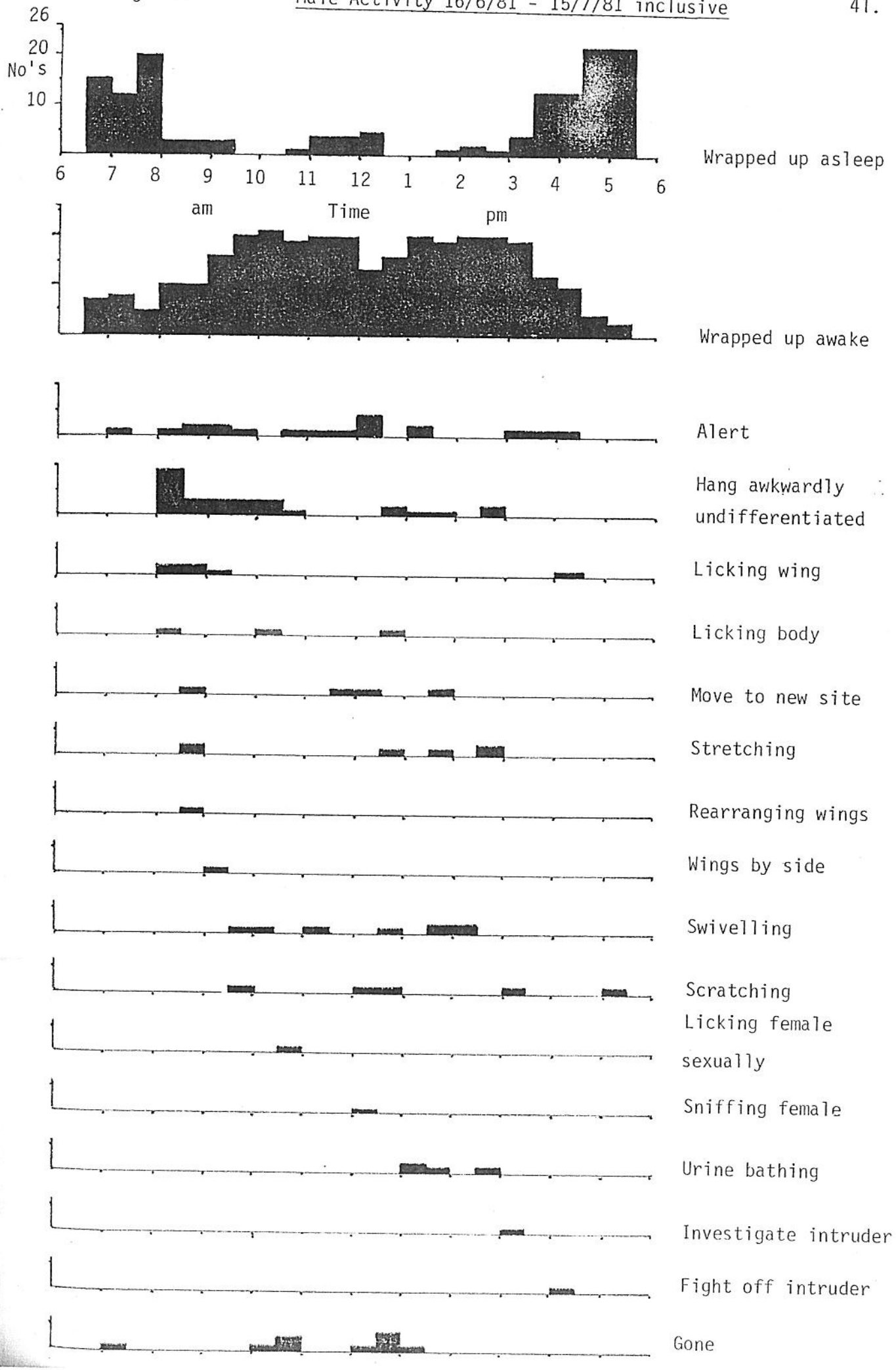
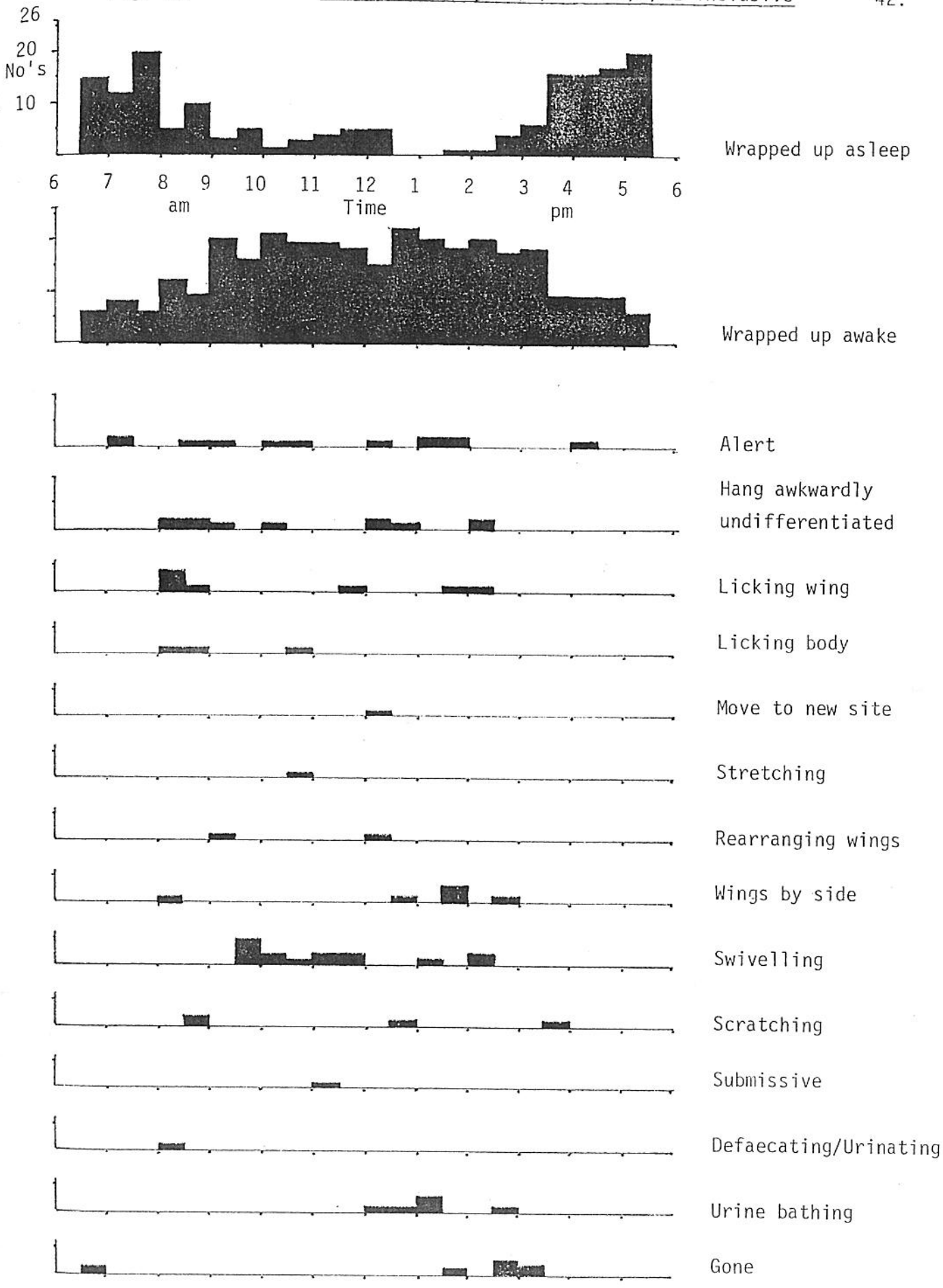


Fig. 15. Female Activity 16/6/81 - 15/7/81 inclusive



The thermoregulatory significance of this activity is discussed in a later chapter, but very briefly the wings provide considerable insulation. With its head tucked inside the wings the animal must continually rebreath warmed air and thus conserves heat. This activity is more common on overcast days and at reduced temperatures as seen with reference to Figures 22, 23, 24, 25. Mothers enclose the young within their wings and form a single thermoregulatory unit necessary to the young's survival. (Bartholemew, et.al., 1964, Noll, 1979b) - see central animal in plate 1d.

Wrapped up awake - distinguished from the previous activity only by open eyes, mobile pinnae and minor movements, this 'activity' is, at least during winter, the most common of all activities - see Plate 1b. From figures 14 and 15 the average time spent in this state per day was 6 hours 3 minutes. This figure would be drastically reduced at the higher temperatures of summer, when heat shedding activities are engaged.

In relation to thermoregulation there is one point that needs clarification. The activity 'swivelling' is quite similar to 'wrapped up awake' except that the body is rotated at intervals. Because of the point-in-time method of sampling, animals which are engaged in swivelling, a very common activity at moderate temperatures, will most often be classed as 'wrapped up awake'. This results in this activity being given more importance (and swivelling less) than it actually has.

Referring to Figure 16 we can see that a female and an elderly (7-8 months) young only hang seperately almost exclusively in the afternoon. This coincides with the warmer temperatures found in the early afternoon in winter. At this age the young is capable of maintaining its own body temperatue at adult standard (Noll, 1979b), but by wrapping up with

Fig. 16. Female with baby 2/6/81 - 8/7/81

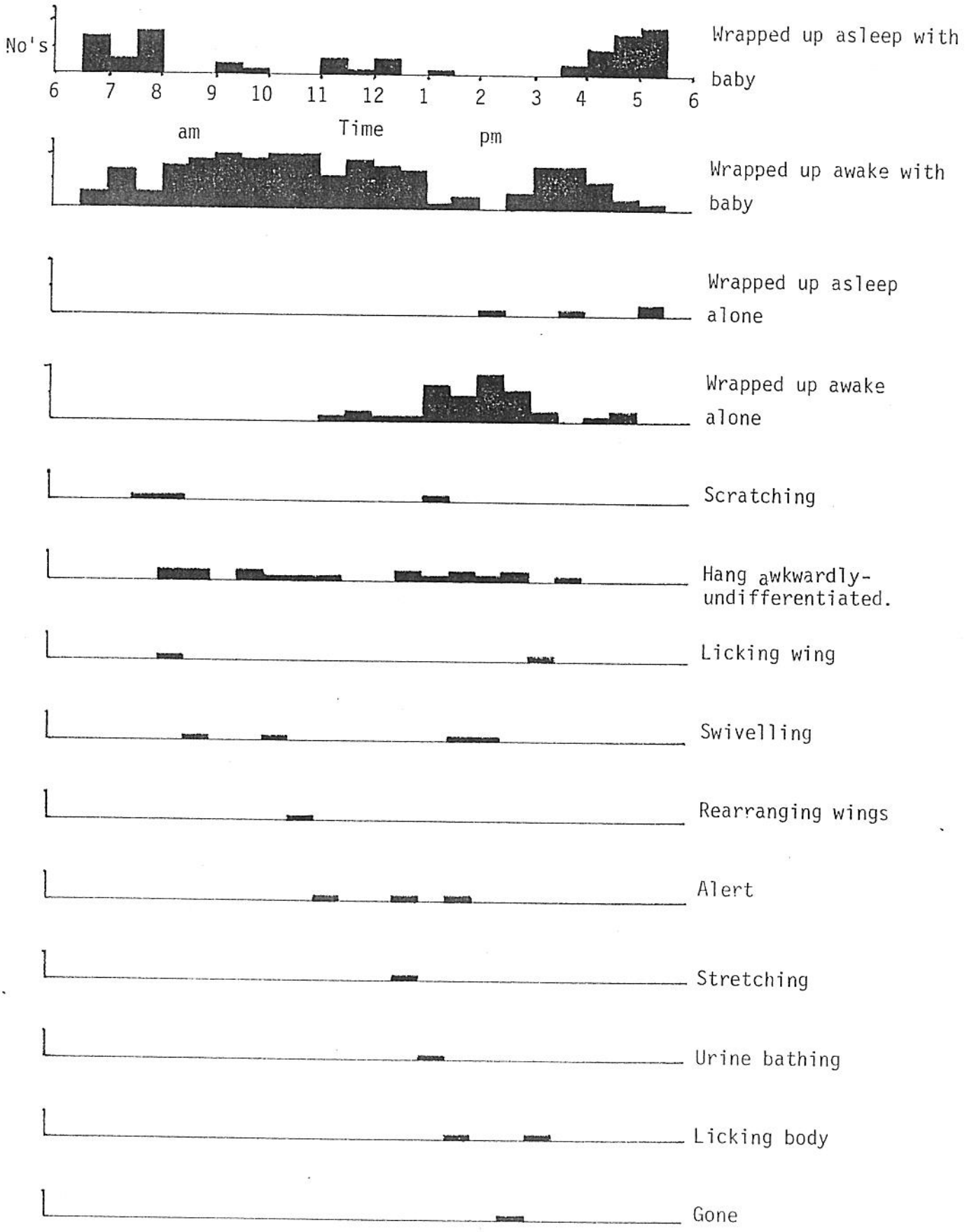
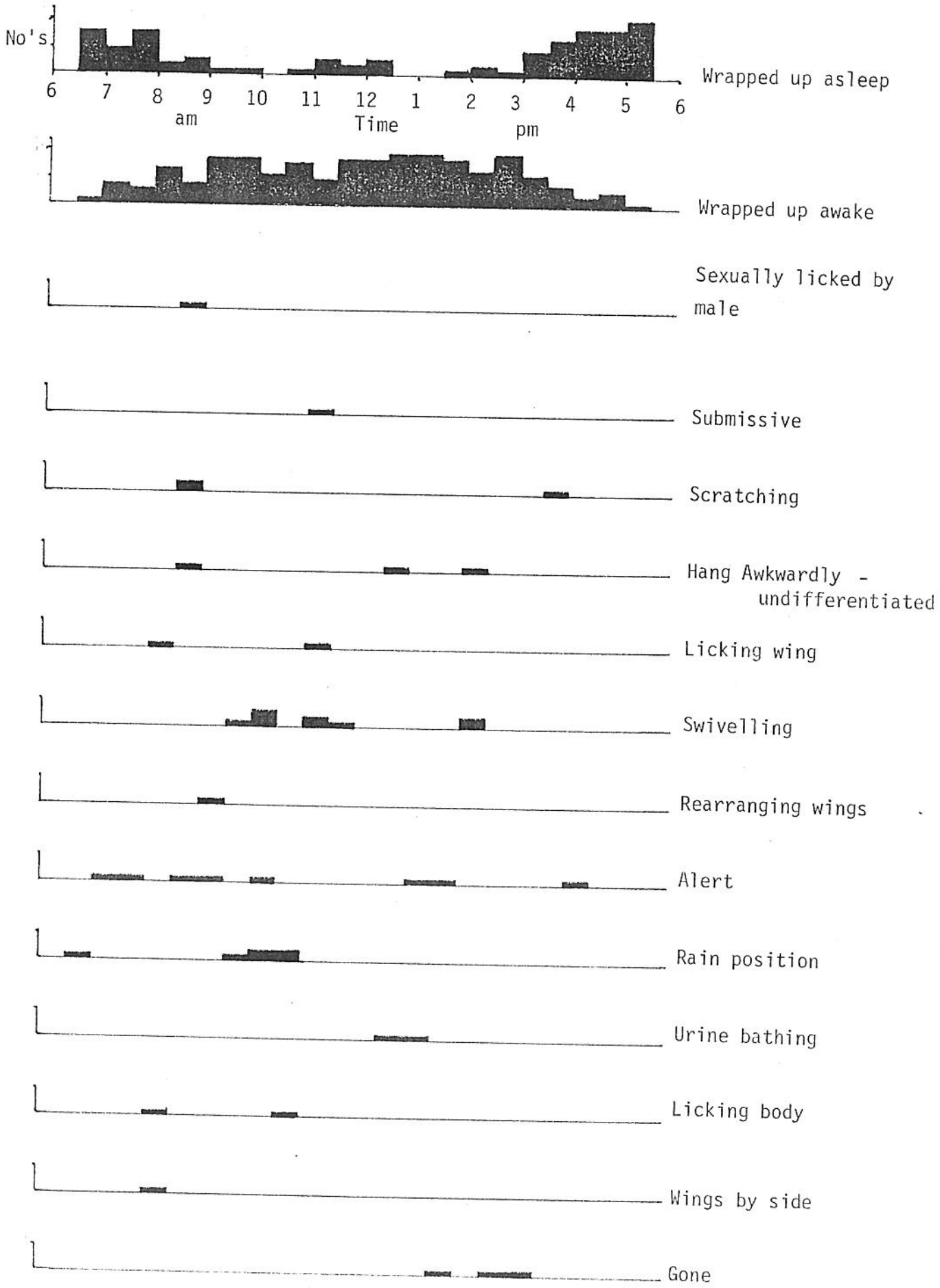


Fig. 17. Female alone 2/6/81 - 8/7/81



its mother at lower temperatures the energetic costs of endogenous thermoregulation are reduced for both animals.

Rain position - This position represents a modification of the previous two. Both feet are used to clasp the branch, the wings are wrapped tightly around the body, the head is further withdrawn within the wings and the body is contracted ventrally, the animal is also completely immobile, see Plate 1i. This position is adopted during rain as a means of waterproofing the body, and keeping the fur of the head and ventral surface dry. When the rain ceases the animals almost immediately begin licking the moisture from their wings and body. Under constant rain this position will be maintained all day, and the colony is at its quietest. Females with young are unable to adopt this position.

The following eleven activities are all discussed in relation to their thermoregulatory significance in Chapter 6 so will only be briefly described here.

Hang Awkwardly - Wing Extended - the animal hangs by one or both feet in direct sunshine and extends one wing for 15 to 30 minutes, - see Figure 1c. This behaviour is usually performed only once at first sunlight and is proposed here as a heat-gaining activity.

Swivelling - the animal hangs by one or both feet with the wings wrapped around the body often with eyes closed - see Plate 1d & e. At quite regular intervals, even as often as once every 10 seconds, the animals twist around to present a different side of the body to the sun. The activity, in its thermoregulatory capacity, is only performed when

direct sunlight falls on the animals. The action is very brief (average 1.33 seconds, measured range .68 - 2.25). It is also performed by mothers with young enclosed in the membranes, but takes longer due to the lack of one central pivotal point (average 4.52 seconds, range 3.10-5.28). The action is also performed when the animal is listening for sounds but at these times the eyes are open and the pinnae are highly mobile.

Hang Awkwardly - Wing Folded - the animal hangs by one or both legs but also uses one or both wing claws to hold onto nearby branches. The wing membranes are folded so that heat loss from the body is facilitated - see Plate 1g. This position may be held for an hour or more and is more pronounced at higher temperatures. If temperatures become 'excessive' this activity is replaced by fanning.

Wings by Sides - this is essentially the same as the prece-ding activity but the wings do not hold a nearby branch. Instead they are held folded beside the body, as seen in Plate 1i. Again this position allows heat loss from the body and may be maintained for considerable lengths of time, although generally it is less common than the prece-ding activity. This position is also adopted briefly by alert animals but in this case again, the animal is far more alert and the tips of the wings protrude behind the body - see Plate 2j.

Rearrange Wings - the animal is awake with the wings folded around its body, it momentarily unwraps its wings then folds them around the body again. This activity is displayed under a number of conditions as outlined in Chapter 6, with the most significant being as a pre-fanning activity. In this function it is an intention movement utilised prior to full fanning behaviour as temperature increases.

Fanning - the animal hangs by one or both legs. One wing is half-extended and used to fan the body. The remaining wing may be held folded against the body or used to hold a nearby branch - see Plate 1h. This activity is exhibited at relatively high temperatures and is used as a cooling mechanism. At constant high temperatures the bats will fan continuously unless ambient temperatures become excessive ($\fallingdotseq 40^{o}C$) at which time fanning ceases and licking of the wings and body is performed to facilitate evaporative heat loss.

Stretching - is usually seen after long periods of inactivity but also performs other functions as outlined in Chapter 6. One or both wings are stretched to their full extent as seen in Plate 1k. This activity has been observed being performed even by very young animals - i.e. less than one month old. In adults it may have a function in maintaining individual distance as outlined by Burton and Burton (1979) for the Common Cormorant.

Scratching - this activity is performed using the claws of one of the back legs. Flying foxes easily scratch their head, chest and back in this way. A more specialised form of this activity, not found in the literature, is the use of the claws of the hind feet to delicately scratch the teeth and nose, as seen in Plate 2e and f. The action in these circumstances is very slow and deliberate and may be aimed at dislodging food particles and mites respectively.

Urine Bathing and Combing - when urine bathing,the animal uses the arms to rub the neck and head, in the process the animals fur usually becomes wet , especially around the neck - see Plate 2a. The body and wings may also be licked at this time. The wetness apparently is urine and can be seen dripping off the animal during this activity. According to Robinson (pers. comm.) the liquid falling from the animal is an opaque

white colour. The activity has gone unrecorded to the author's knowledge although it is a relatively frequent activity being performed about once per day by each bat and is especially noticeable when the sun emerges after a long period of overcast conditions. It usually lasts 15 to 30 minutes.

Combing of the fur is done almost exclusively in conjunction with urine bathing. Combing is performed by slowly drawing the claws of the hind foot through the fur of the neck and body. Juveniles aged 6 months or less were regularly seen urine bathing and combing at the same time as their mothers. This trend of mother-young synchronised activities is very common and regularly seen in such activities as scratching, licking and defecation.

The significance of urine bathing and combing may be twofold, firstly as a means of cleaning the fur of the neck and upper back and removing loose hair, and secondly to permeate the body with the odour of urine or the scent from the scapular glands. The scent of flying foxes is quite strong and most pronounced at the colony on days with little or no wind.

Licking Wing - this activity is self explanatory. It is most frequently observed being performed by virtually all animals just prior to flying out to feed at dusk. Bouts of wing-licking may last up to 30 minutes or more. Each animal probably spends an average of 30 minutes per day licking the wings, considerably less than Nelson's (1965b) estimate of several hours. Nelson (1965b) states that it is important to keep the wing membranes clean as they would otherwise "become less supple due to interference with the production of the oily secretion from the epithelial glands".

After licking the body and wings, bats were sometimes seen to rapidly

flick their wing which shook off a small 'object'. This presumably is accumulated hair which the animal is unable to spit out. By depositing it on the wing and then rapidly flicking it the 'object' is effectively removed. Again this action has not been encountered in the literature.

Licking Body - this activity is practised daily and is again self explanatory - see Plate 2b. The flying fox usually concentrates on the chest, abdomen, legs and particularly the anus and genitals. Apart from the interface between the wing membrane and the back,they were not seen to lick their upper dorsal surface and may be unable to do so. However, the back of the legs and lower dorsal surface were routinely licked.

The following behaviours are not discussed elsewhere;

Allogrooming - Scratching or combing of one bat by another was never seen. Licking of one bat by another was observed in four contexts. Firstly a mother licking her young, secondly a male licking a female prior to attempting copulation, thirdly between two male juveniles and fourthly by one juvenile licking water off another after rain.

Mothers regularly lick the wings and body of their young, paying particular attention to the anus and genitals. Nelson (1965b) reports that young can clean themselves at 3 to 4 weeks of age, but mothers were seen to lick their young as late as the 8th July, 1981, when the young should be approximately 8 months old. Females were also seen to lick their young prior to leaving them, either to go on feeding flights or simply to allow the mother to groom herself.

Males were always observed licking the females genitalia prior to copulation. This activity was often quite prolonged,typically taking

20 minutes or more. Females were never seen to lick the males.

On one occasion only, two juveniles (males) were seen to engage in wrestling, with sexual overtones, after which one began to clean itself. The second male then briefly licked the head of the first.

Finally, after rain, one juvenile was observed to lick water off the fur of two other juveniles. Each of these repelled the bat after a short time.

Carroll (1979) reports that allogrooming is common among all age and sex classes of Pteropus rodricensis in captivity, occupying 2% of their time. It is quite probable that the extent of allogrooming varies between individual flying fox species. For example P. scapulatus do not maintain the same strict individual distance as P. poliocephalus, often clumping together, so we would expect allogrooming in P. scapulatus to be more pronounced.

Defecating - Urinating - this activity is always accomplished by the animal inverting and hanging by its thumb claws as seen in Plate 2c. The animal urinates or defecates and then shakes its legs several times rapidly, after which it swings up to resume its normal position. This activity is most frequent early in the morning to the extent where it is significant at the .001 level using Chi-squared analysis ($n = 64$). This fact is further reinforced by the rapid food passage time typical of the species. Nelson (1965a) established a food passage time of 40 minutes for P. poliocephalus in captivity, with solid materials such as seeds and stamens being little affected during their passage.

Locomotion - travelling horizontally within the tree the animal may use either its back legs alone or use both legs and wing claws in a sloth-

like fashion. Using only the back legs the animal effectively walks upside-down. This locomotion is relatively slow and used only for short unhurried movements along the branch. Use of all four limbs allows much faster movement and is more common than the other method.

Climbing vertically up and down limbs and tree trunks is always accomplished head first and can be quite rapid - see Plate 2g and h. Climbing up the trunks is accomplished mainly by using the wing claws in a man-like climbing fashion, the legs playing a minor role in simply preventing the animal from slipping down. The chin may also be pressed against the trunk to allow an 'arm' to be moved upwards. Climbing down the trunk the back legs are usually wrapped around the tree trunk and allowed to slide downwards in a controlled manner with the 'arms' assisting to a lesser degree. Smooth limbs and tree trunks of large diameter provide the greatest barriers to free movement within the tree, being too large to encircle with the limbs and providing no grip on their surface. As a consequence roosting is largely confined to limbs of small diameter.

The purpose of the majority of movement within the tree is to investigate or expel intruders, approach females prior to mating or to seek a more, or less, exposed position in relation to sun, wind or rain. Daytime flying from tree to tree is usually a result of a disturbance, a relatively common occurrence at the Gordon colony, or by females escaping the unwanted advances of amorous males.

The young learn to fly at about 3 months of age (Nelson, 1965b). Prior to this they are left behind as the adults fly out at night to feed. As the adults leave, the young flap their wings but do not let go of the branch. This activity undoubtedly conditions them for true flight. Static flight was also observed occasionally with adults but usually as an intention

movement prior to moving to a new site or when being expelled by territorial animals. Prior to takeoff the animals usually flap once or twice to gain lift so that there is no dropping after release of the perch.

Alert - excepting when temperatures are very low the alert animal has its wings folded by its sides with the wing tips protruding obviously behind the animal. This is probably a means of informing other bats of possible danger - see Plate 2j. The eyes are open and the ears are mobile or directed to the source of the disturbance. When cold the animals may remain wrapped within their wings but still face the direction of the disturbance. Flying foxes are highly reactive to the sound of breaking sticks. Whether this is because it may warn of an approaching predator or because it signifies a breaking perch is not clear. Branches were often heard to break at Gordon. Ogilvie and Ogilvie (1964) report that 12 fruit bats were killed by a falling branch during high winds, lending some emphasis to the second theory.

Vocalisations sometimes accompany this activity, presumeably when the animals are more alarmed. When vocalisations were made the majority of bats in that local area became alert and often took wing.

Wing Spread Alarm - this activity was observed to varying degrees in three situations. Firstly when the animals were (spontaneously) startled. Their reflex action was to open their wings very briefly and usually not to their full extent. This is analogous to the human reaction of 'jumping' to similar surprising stimuli. Sounds reacted to in this fashion included splitting branches and loud nearby bird calls. The second situation was when the display was used by bats at night time in trees within the colony to ward off other bats flying nearby and was accompanied by loud vocalisation. The 'intruders' repeatedly approached the tree as if attempting to attack the residents and when they occas-ionally landed,quite savage fighting

resulted between the two groups. No explanation was ever found for these raids, nor is there any reference to them in the literature.

The third occasion on which the wing spread alarm posture was adopted was in the presence of large birds either perched or flying nearby. Unlike the previous two occasions the wings remain spread to their fullest extent for some time - see Figure 18

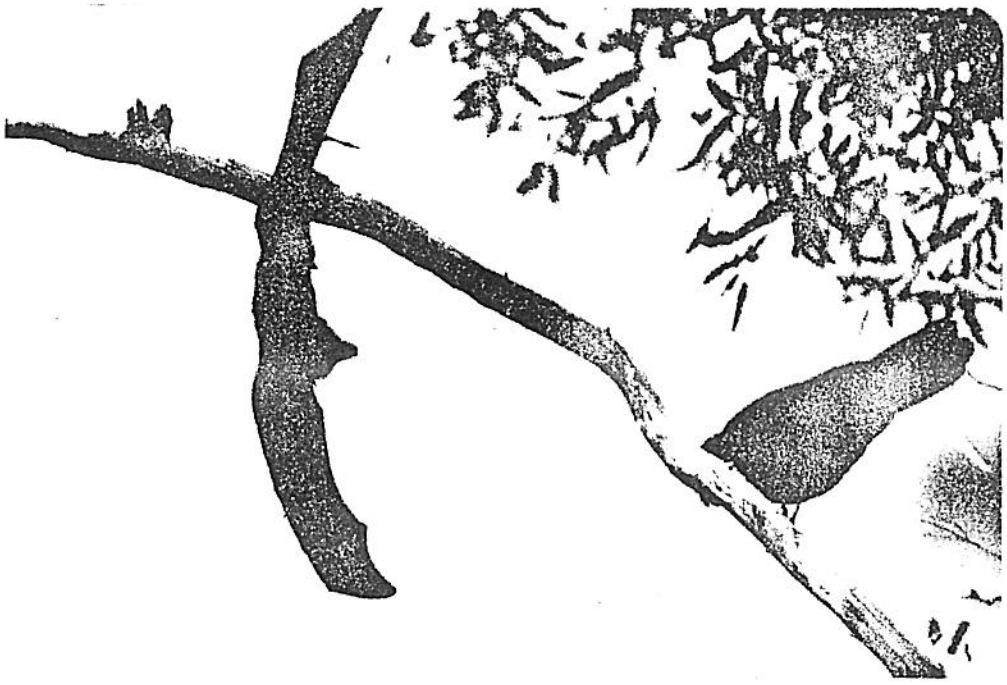


Figure 18. Wing spread alarm display by P. poliocephalus against the Australian Raven, Corvus coronoides.

This display was seen directed to the Australian Raven, Corvus coronoides and the Kookaburra, Dacelo gigas - the only two bird species observed feeding on young flying foxes. These displays may serve to confuse and disorient the predator by seemingly increasing the size of the flying fox, and thereby act as a specific antipredator device. (Humphries and Driver, 1967). In both cases the birds flew off after some time and did not appear at all concerned by the display. (Once the crow had left, the

bat moved to where it had been, sniffed the perch and then flew off).

Discussion and Conclusion.

Although the preceding text is concerned almost solely with daytime activity a few important points from the literature should be made in relation to night-time behaviour, and their bearing on observations made in this study.

Bats of the genus Pteropus have been demonstrated to have a circadian rhythm of activity which is maintained under artificial conditions of continuous light, and is also capable of following seasonal changes in the light-dark cycle. When the dark period was artificially extended, the bat's activity period increased but did not expand to cover the entire dark period - activity began well after 'sunset' and ceased well before 'sunrise'. [(Erkert, 1970), quoted in Zack et.al. (1979)]. This finding corresponds very nicely to the changing seasonal relationship between exodus time and sunset demonstrated for P. poliocephalus in the previous chapter. Erkert (1970) further found that this night-time activity consistently demonstrated bimodal peaks. This occurred even in the shortest nights of mid-summer, the pause being reduced in length but still present. The work of Carroll (1979) on Pteropus rodricensis also showed this bimodal pattern. A final point made by Erkert (1970) was that activity onset prior to sunset was not always clearly demarcated, while activity offset at sunrise was consistently clear. These bimodal activity patterns were not observed in the large majority of Microchiroptera species studied by Brown (1968).

From observations made in this study there is almost certainly no bimodality in daytime activity. Under fine weather conditions the animals are awake at all times of the day except early morning and late afternoon when they usually sleep.

Activity is affected to varying degrees by a wide variety of factors including ambient light, season, rain, direct sunlight, temperature, time of day, age and sex of the animal, the presence or absence of young and the reproductive status of the animal. The majority of these factors will be discussed in Chapter 6 but a few important points are worth comment.

For the eleven activities assessed for their correlation to temperature, it was found that, if the minimum range of 10 of their highest points was plotted as shown in Figure 19 then 8 of these ranges overlapped between 13.2 and 17^{o}C. This provides a good indication of the temperature range in which the flying foxes are most active. The three activities outside this range are all directed at shedding heat at high ambient temperatures. (The figures for hang awkwardly-wing extended were the only 10 points available of this activity. From previous observations it appears certain that more information would shift this range significantly towards lower temperatures).

Comparing differences in activity between sexes by reference to Figures 14 and 15, we see that there are no major differences in any activity, and there are few sex-specific activities. This allows generalisations to be made when the sex of animals being observed is unknown. However, due to the small numbers involved in this comparison no real conclusions can be drawn. Activities where some difference would be expected between the sexes include movement to new sites, stretching - when used as a mild threat or spacing activity, and possibly the amount of time spent alert - with males expected to be more active in each of these areas.

Similarly, comparison of females with and without young, Figures 16 and 17, show no real differences, although hanging awkwardly - both extended and folded seems more pronounced in the females with young. As already stated, females with babies are unable to adopt the 'rain' position.

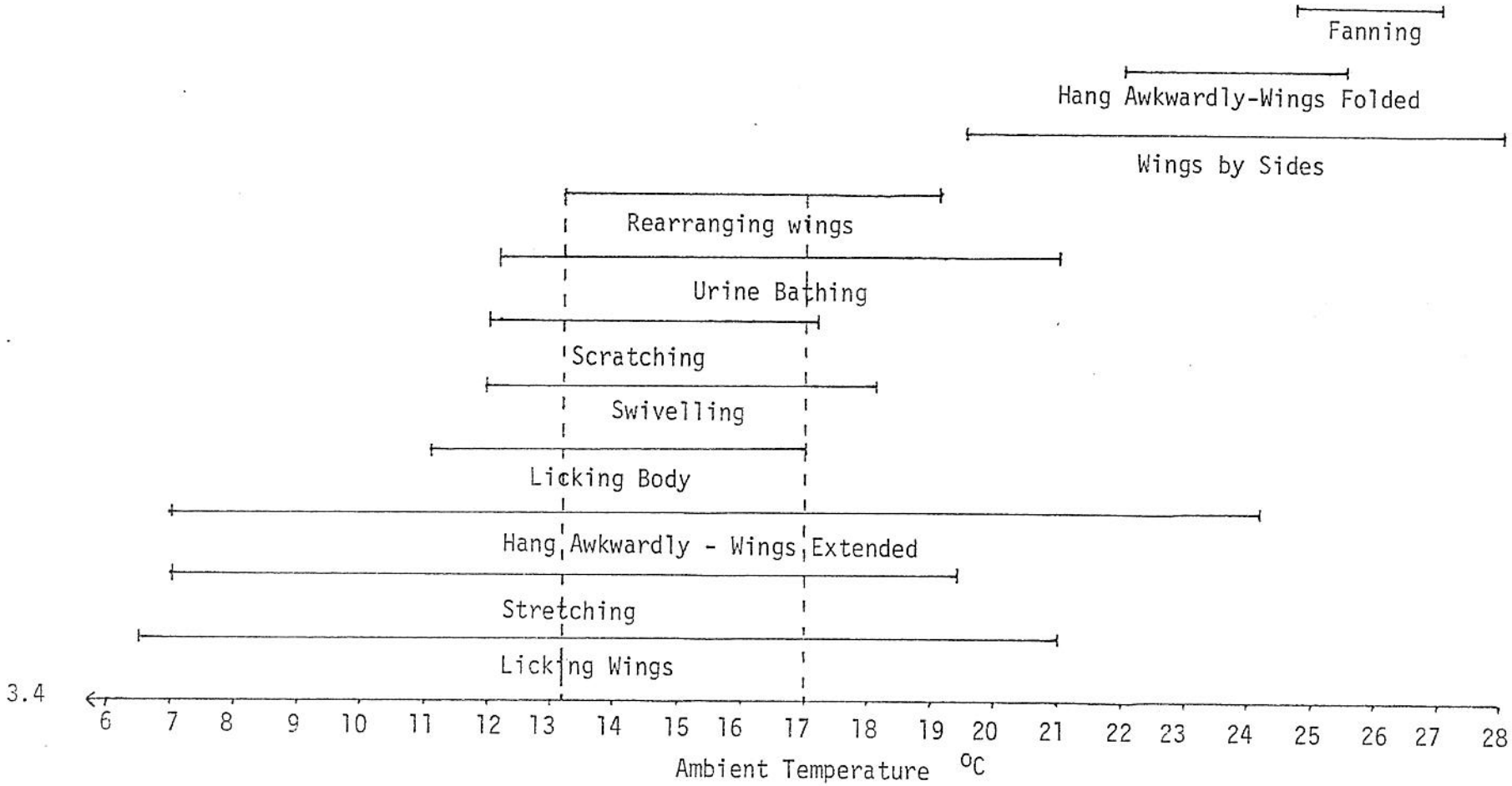


Fig. 19 - Smallest temperature range in which 10 highest values for each activity fell.

Fig. 20.

Polygamous male 10-24/6/81

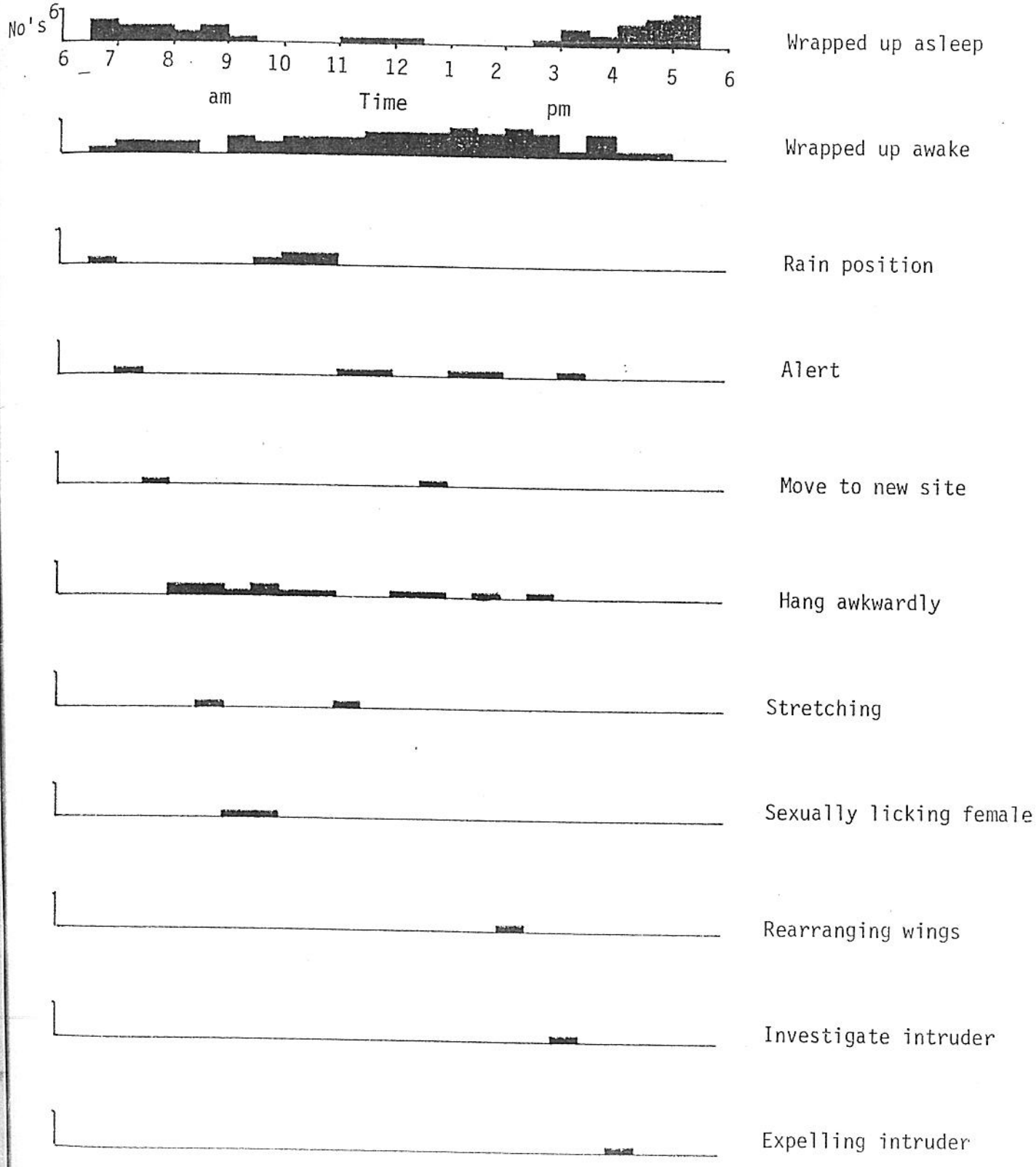
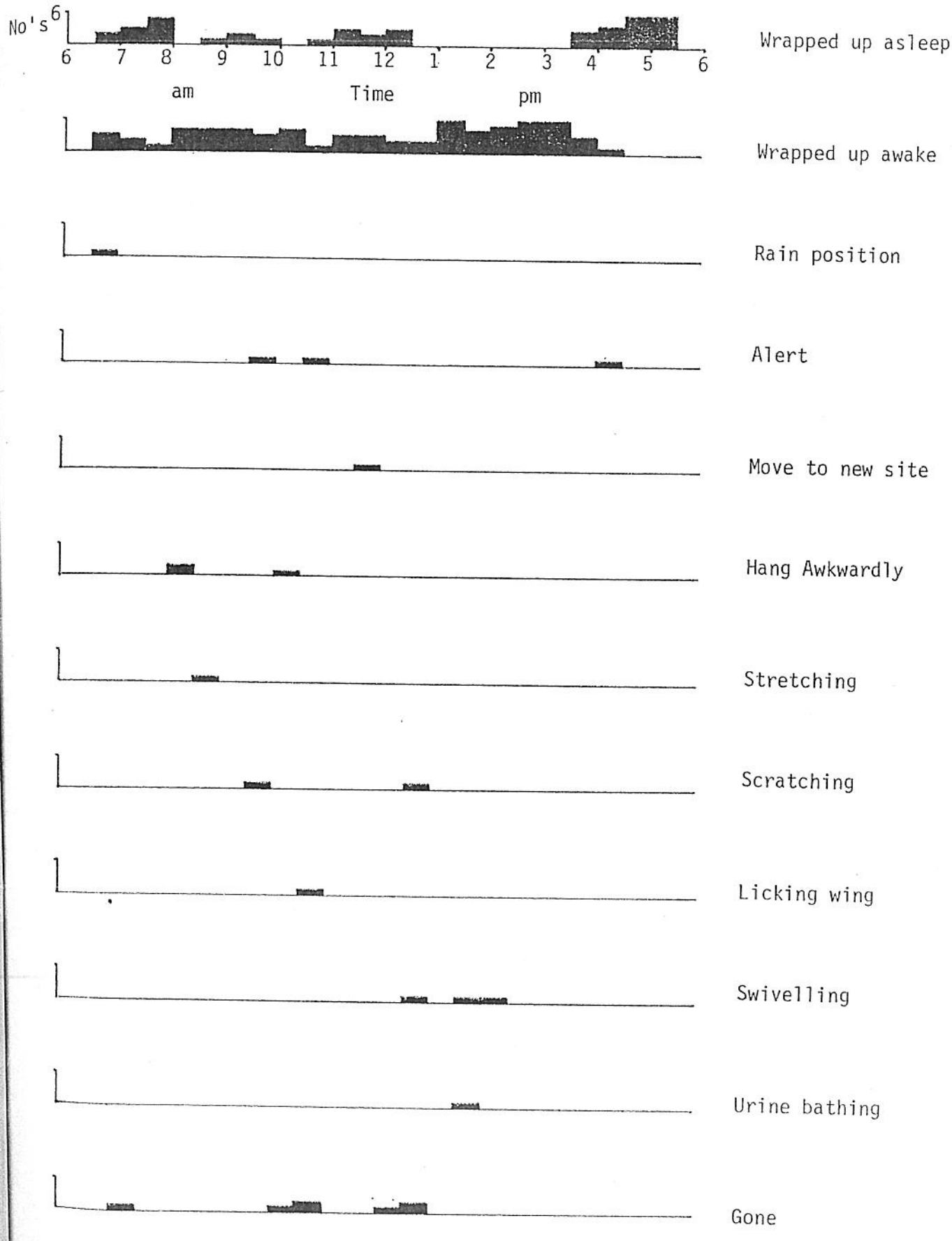


Fig. 21.

Monogamous male 10-24/6/81



Again the numbers of observations are very small and allow no significant comparison.

A final comparison made was between monogamous and polygamous males - see Figures 20 and 21. Here again unfortunately the figures are too small to allow real comparisons to be made. Furthermore these results refer to a single male in each case so differences seen could easily be attributed to individual variation alone. This factor probably accounts for the considerable difference in "hang awkwardly". The areas where greater activity would be expected on the part of the polygamous male would be in alertness, sexual activity, the repulsion of intruders and movement to new sites. All of these areas point to heightened levels of energy expenditure for polygamous males which, from general observations appears to be the case.

Considering each of these alternatives it seems that observations of the activities of animals of unknown sex (and probably age) would provide at least an approximation to the levels of these activities in a group of 'balanced' sex and age composition (in relation to their proportions in the population). Presumeably this would introduce only minimal unintentional bias to the results. The differences that do exist however, indicate that it is more desirable to observe animals of known sex and age. This would allow an estimate of bias to be made. If possible, steps could then be taken to remove this source of error.