CHAPTER 6. THERMOREGULATION.

Introduction.

Within the last 30 years there has been considerable interest in bat thermoregulation., with the majority of literature concerned with the Microchiroptera. The paucity of work on Pteropid temperature regulation is somewhat surprising, considering that a large proportion of daily flying fox activity appears to be in Jones' (1972) words "in response to,or correlated directly with temperature." He is apparently the only author to have recognized this fact, and stated it as such.

Before dealing with Megachiropteran temperature regulation, a brief review of Microchiropteran thermoregulation establishes the context for later discussion. The majority of work done on thermoregulation in this sub-order initially concentrated on temperate animals and their ability to tolerate low daily and seasonal environmental temperatures. Their response to these conditions was to undergo torpor and hibernation on a daily and seasonal basis with body temperature at these times falling close to ambient temperatures when activity ceased. The lability of body temperature in these animals prompted several authors (for example Hock, 1951, Eisentraut, 1960) to conclude that they lacked thermoregulatory ability at rest and were the most imperfect mammalian thermoregulators. This is far from the truth. When necessary they are capable of rewarming themselves quite rapidly through the sole use of endogenous heat. As Lyman and Wimsatt (1966) note, "the physiology of hibernation in bats....(includes) tolerance to very low body temperatures and precise control of circulation during arousal from hibernation. Thus this group has met the problems of small size and cold climate with definite specializations".

Early conclusions were further challenged by workers concentrating on animals from lower latitudes, animals with larger body size and non-insectivorous diet. Some of these animals demonstrated considerable ability in maintaining a reasonably constant body temperature.

The three major factors involved in regulating body temperature are thermogenesis, resistance to hypothermia and resistance to hyperthermia, as outlined by Stones and Weibers (1965). The level and efficiency of bat thermoregulation being determined by the interaction of body weight, basal metabolic rate and thermal conductance (McNab, 1969).

The activities reported to raise or maintain body temperature in Microchiropterans at low ambient temperatures included; elevated ventilation rate (Burbank and Young, 1934) some limb movement and shivering (Burbank and Young, 1934, Reeder and Cowles, 1951, Leitner 1966), Clustering to reduce the metabolic cost of maintaining constant body temperature (McNab, 1969, Leitner and Ray, 1964), migrating to warmer climates, or seeking warmer sections of the roost (Leitner and Ray, 1964). Many Microchiropteran species have been reported which do not use their wings to 'wrap up' and increase insulation, reinforcing Lyman and Wimsatt's (1966) contention that for small Microchiropterans wings are a liability rather than an asset in thermoregulati a very different situation to that seen in the Pteropids.

The major behavioural means for cooling the body recorded for Microchiropterans included; fanning with the wings partly, and later, fully extended (Reeder and Cowles, 1951), panting, salivating and licking the body, wings and uropatagium (Leitner and Nelson, 1967, Licht and Leitner, 1967) and seeking cooler areas within the roost (Stones and Weibers, 1965).

Looking now at the Megachiroptera, quite a different picture of thermoregulation emerges.

Within the Megachiroptera, the genus Pteropus has been credited with having "the most classic example of homeothermic regulation of body temperature" of all Chiropterans. Large members of the sub-order Megachiroptera, which form a majority, are very good thermoregulators on the homeothermic level. The smaller members of the group exhibit both homeothermic and heterothermic patterns of temperature regulation (Bartholomew et.al. 1970, Noll, 1979a). The full homeothermic capacity of larger species apparently is acquired within the first three or four weeks of life (Bartholomew et.al.,1964, Noll, 1979b).

Perhaps the most outstanding feature of Megachiropteran temperature regulation is that they do not enter daily torpor or seasonal hibernation, and maintain their body temperature even when quiescent or asleep.

As a group they are usually large, usually frugivorous, and mostly tropical. The majority of species roost in trees, often exposed to direct sunlight, wind, rain and temperatures at least as high as 40-45°C, (Lietner and Nelson, 1967) and occasionally, at least as low as 5°C. Bartholomew et.al. (1964) found Pteropus poliocephalus to maintain a body temperature between 35-39°C while ambient temperatures varied from 5 to 40°C. Noll (1979a) found that Pteropids demonstrate a circadian rhythm in body temperature. The six species studied had an elevated nightly body temperature 1.2 - 4.1°C higher than daytime body temperature.
P. poliocephalus was one of the species studied and had the lowest nightly temperature elevation of 1.2°C.
Due to their generally large body size, Megachiropterans require a relatively smaller energy expenditure per unit weight to maintain a constant high body temperature. Homeothermy is achieved through both physiological and behavioural means, many aspects of which are shared with Microchiropterans and have been mentioned previously. Some aspects of

particular interest are worth comment here. Firstly, it has been demonstrated by Noll (1979a) that the Megachiropteran Rousettus aegyptiacus, employs the hormone nor-adrenaline for non-shivering thermogenesis, as is found in Microchiropterans.

A second aspect of interest concerns the morphology of the Megachiropteran wing. The larger body size of these animals, notably members of the genus Pteropus, results in a more robust wing membrane. Wrapped around the body these wings form dead air pockets (Bradley and Deavers, 1981) providing good insulation for the body by greatly reducing thermal conductance; depressing the lower lethal temperature of P. poliocephalus by 4°C while keeping the air between the body and wings 10°C or greater, above ambient temperature (Bartholomew et.al., 1964). Furthermore, the wings, interfemoral membrane and ears are naked and well supplied with blood vessels. When the animal is overheated these become engorged with blood, the wing is fanned to move air across them and the heat load is reduced through convection. Furthermore the area of naked to furred skin is far greater in Pteropids than in other bats at a ratio of 11:1. In Nearctic microchiropterans this ratio varied from 4 to 8.5:1. (Bartholomew et.al., 1964).

A final aspect of interest here is the descent of the testes into the scrotal sac when the animal becomes overheated. This presumably helps protect the animal from heat induced sterility. A conclusion supported by Nelson's (1965a)findings that the surface of the testes was 4-5°C below the rectal temperature.

The reports of the thermoregulatory behaviour of Pteropus poliocephalus are incomplete. The activities reported whereby this animal seeks to gain or retain heat, include wrapping the wings around the body as previously mentioned, and shivering at virtually all temperatures below thermal neutral (Bartholomew et.al., 1964). To shed excess heat they are reported to fan with wings half extended, indulge in open mouthed panting, and salivate freely, licking wings, body and muzzle to facilitate evaporative heat loss (Bartholomew et.al., 1964, Leitner, 1966, Leitner and Nelson, 1967, Robinson and Morrison, 1957).

An alternative method of dealing with excessive heat, reported in the literature is to seek a cooler position within the roost (Bartholomew et.al.,196 Jones, 1972).

Before proceeding with details of the results of analyses made by this author, a few words should be said in relation to experimental procedure and complications. Prior to commencement of this study it was not appreciated that a large proportion of the Flying Fox day is concerned with the passive or active regulation of body temperature, through physiological and behavioural means. Consequently, the equipment and technique relevant to an accurate study of this phenomenon were not applied as well as would have otherwise been appropriate. The fact that environmental temperature is correlated to the time of day further complicates the interpretation of results. As the observations were made in the field rather than under controlled laboratory conditions, all references to temperature must be regarded as approximations to the ambient temperature which the animals in question were experiencing. Compounding this problem is the lack of any real measure of incident radiation, relative humidity or wind speed and direction. Observations were also clumped around a median temperature range - the majority of points falling within 10-20^{o}C. The majority of recordings were made under sunny conditions. The ratio of these sunny recordings to overcast, rain and miscellaneous recordings was 217:68:38:140 respectively. Where relevant this factor has been accounted for in mathematical analyses.

The fact that the animals are in a natural condition means their degree of exposure to direct sunlight and wind cannot be standardized. It was also found that the "recent" thermal experience of an animal affected its subsequent thermoregulatory behaviour. Therefore animals which had endured a night of low ambient temperature could be expected to behave very differently the following morning than if they had experienced a mild evening. Recent activity and its consequent thermogenesis obviously varied between individuals.

It is also presumed that individual variation would be found even in animals with similar thermal experience. Despite all these complicating factors, some important points did emerge, which indicate strongly that behavioural thermoregulation is more complex than previously reported.

Firstly, two passive activities or states should be discussed relative to their thermal significance.

Wrapped up Asleep / Wrapped up Awake -These two self-explanatory activities are often difficult to distinguish from one another.

As seen in Figs. 22, 23, 24, 25,

sleeping or inactivity predominate in early morning and late afternoon, the coldest parts of the day. This is most readily seen on the two histograms relating to sunny days. When not totally inactive, at least some proportion of the animals is covered by their wings, but showing some sign of wakefulness - swivelling, response to sound, eyes open, ears twitching etc. These two activities, or'states' are the most frequent of all diurnal activities. The insulative qualities of the wings when they enclose the body in this species, have previously been discussed with reference to Bartholomew et.al's(1964) findings. It is sufficient to say that for the period of structured observations 21/4/81 to 16/9/81 - covering the seasons, Autumn, Winter and Spring, the large majority of flying fox time was spent insulating the body against the effects of cold. This situation is

Fig. 22
Activity by both sexes on two overcast autumn days. 20-21/5/81.

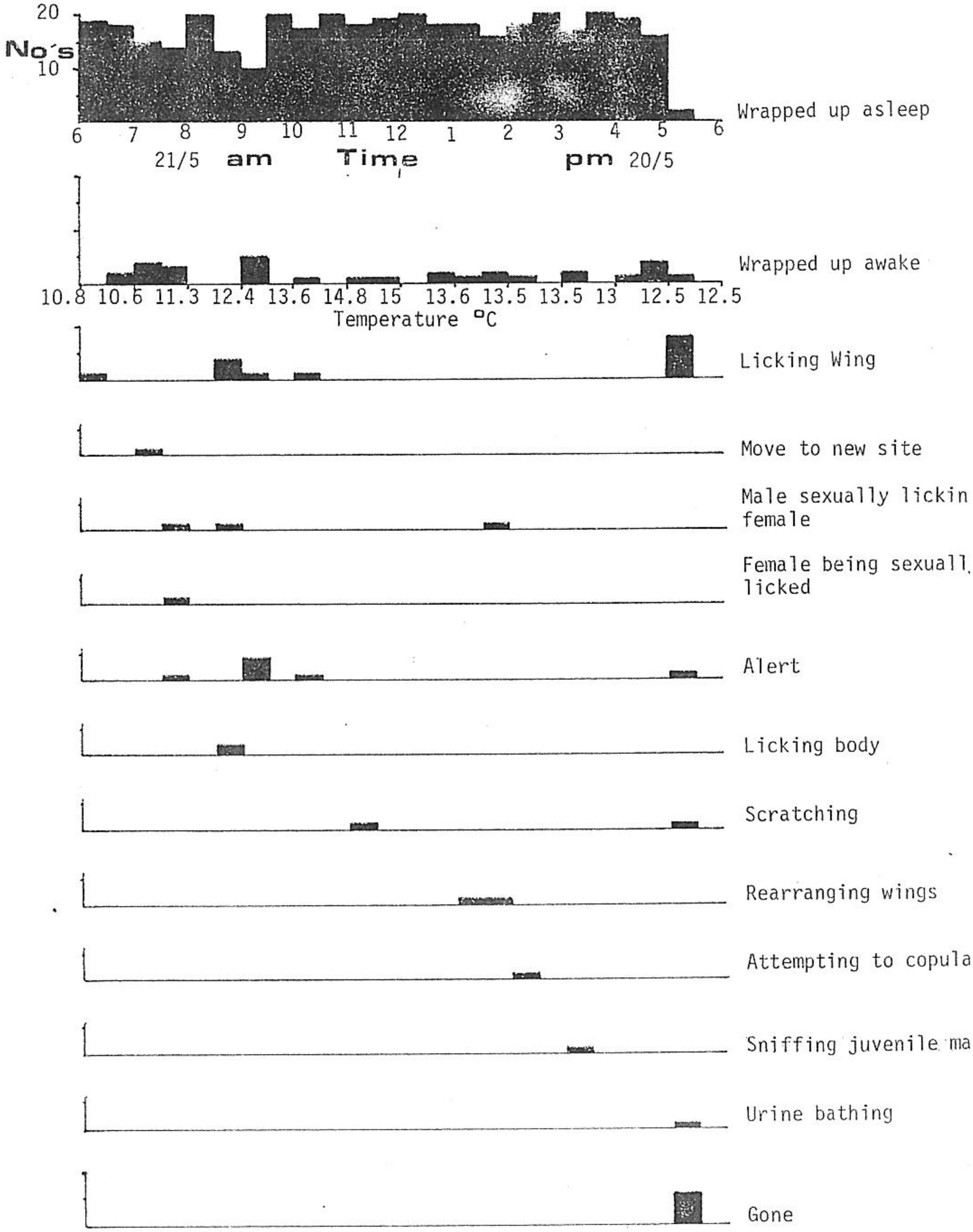


Fig. 23

Activity by both sexes on an overcast winter day. 31 8 81

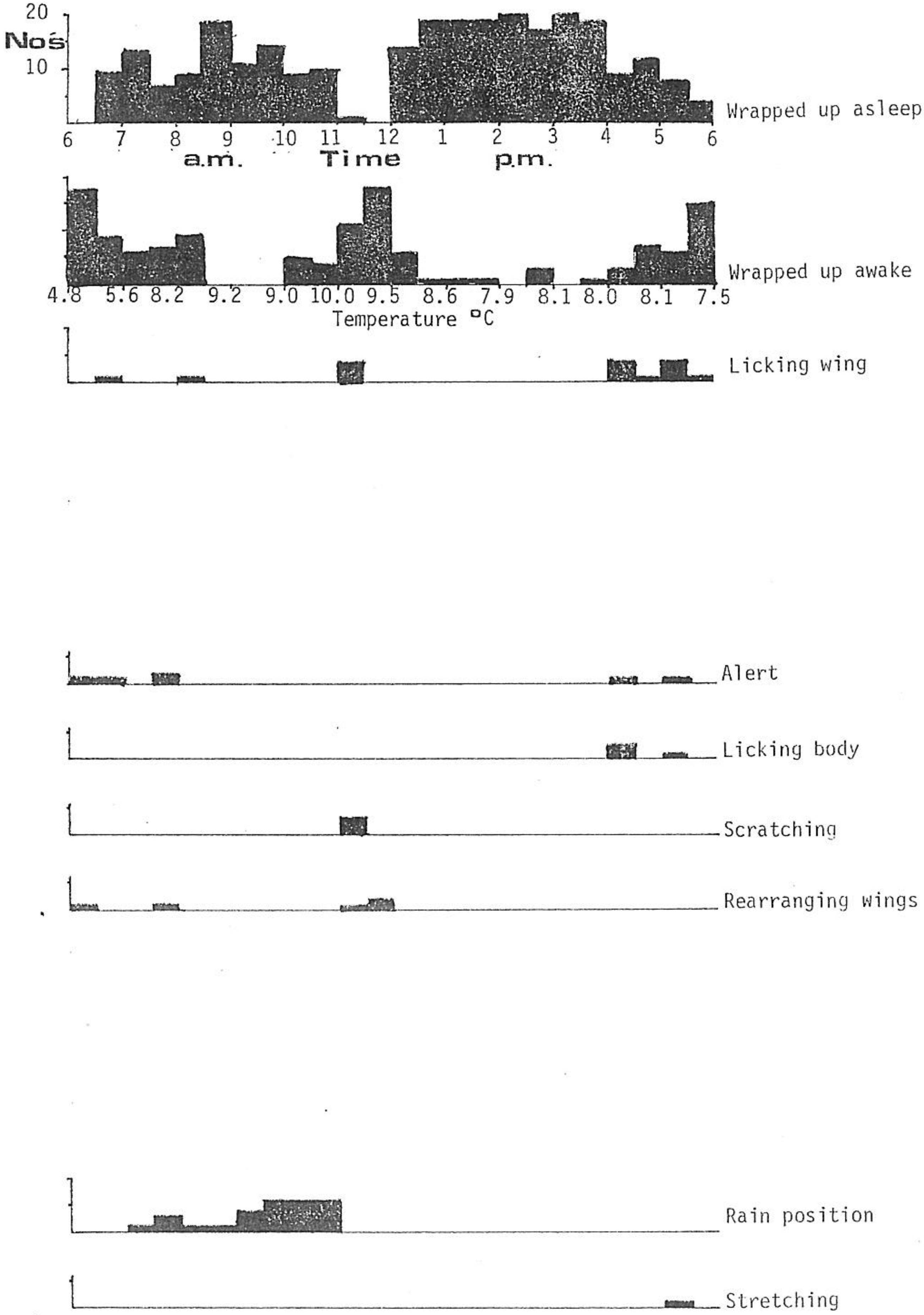


Fig. 24.

Activity by both sexes on two sunny Spring days 15-16/9/81

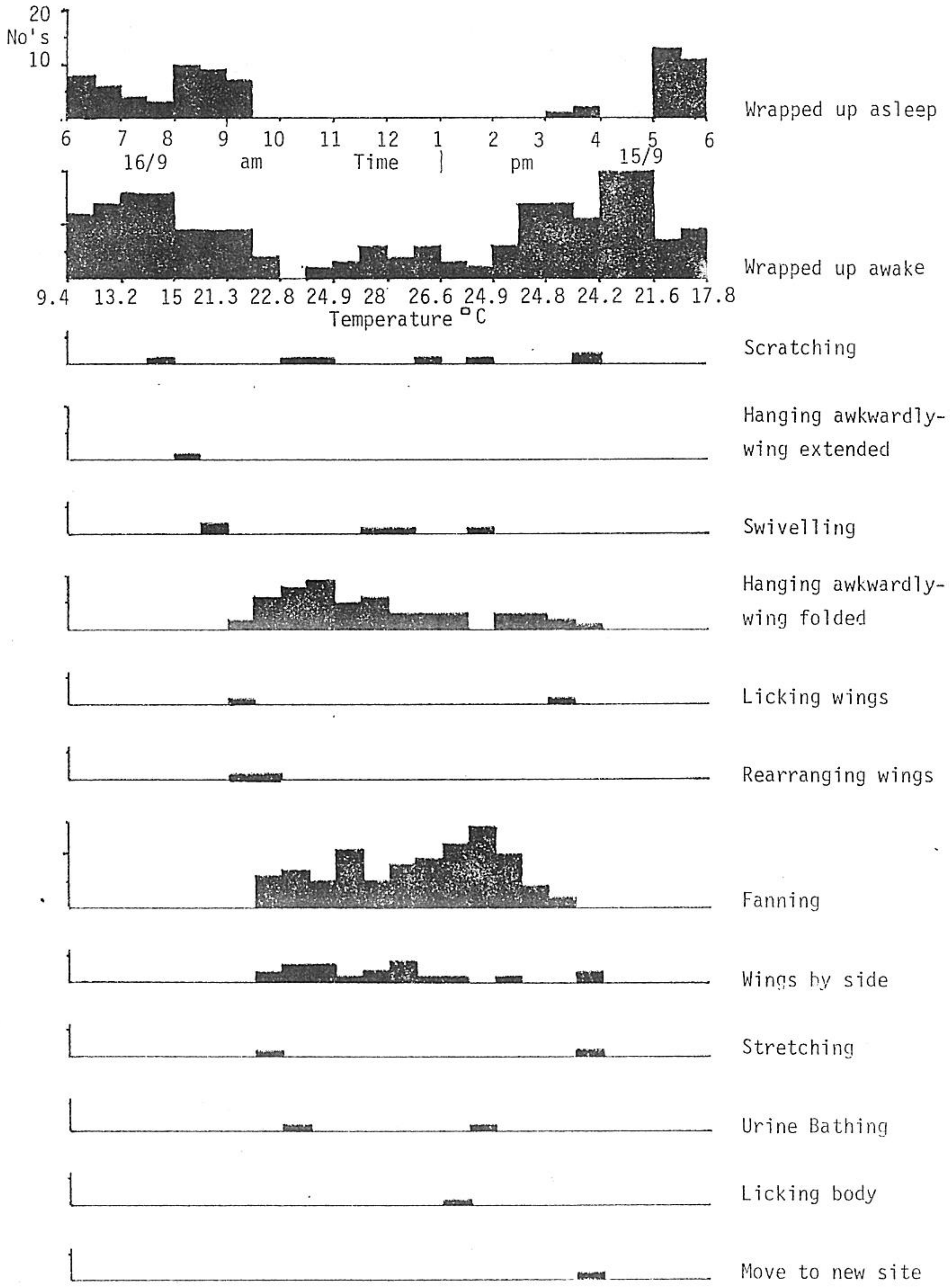
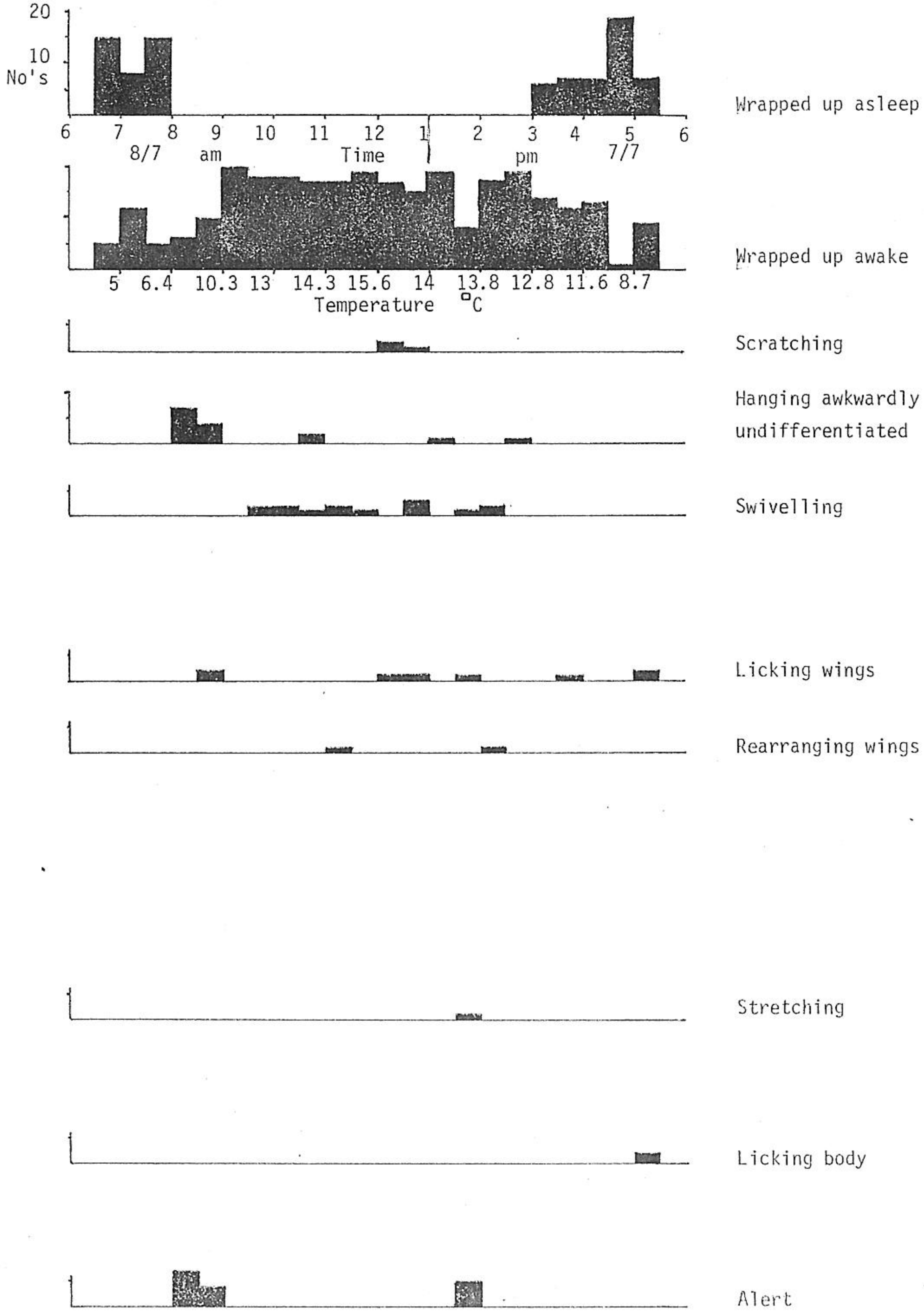


Fig. 25.
Activity by both sexes on two sunny Winter days 7-8/7/81



almost certainly different to that found under the higher ambient temperatures of Summer. Sleep appears to be strongly related to time, occurring at early morning and late afternoon and appears largely independent of temperature. Less animals are active under overcast conditions, so 'wrapped up awake' and 'wrapped up asleep' would occur with greater regularity at these times. Conversely, under sunny conditions, more animals engage in alternative activities, and the incidence of 'wrapped up awake and asleep' should decrease commensurately.

Eleven further activities which were reported in an earlier chapter were analysed graphically to determine their relationship, if any, to ambient temperature. Of these, hang awkwardly-wing extended, swivelling, hang awkwardly-wing folded, wings by side sunning, rearranging wings and fanning, are all believed to have considerable significance as activities specifically aimed at maintaining body temperature within a fairly narrow range. The remaining activities, stretching, licking wings and body, urine bathing and scratching are believed to be affected, quite strongly, in some cases, by ambient temperature and direct sunlight, but are not of themselves aimed at maintaining body temperature within acceptable limits. Each of these activities shall now be discussed in turn.

<u>Hang Awkwardly - Wing Extended</u>. This activity is employed early in the morning, often as soon as the sun's rays strike the sleeping or resting animals, or at any time of day after prolonged overcast conditions. The animals extend one wing - often stretching, or licking their wings beforehand, and may even seek a more exposed position. In this posture the venation of the wing membrane is clearly visible. It is quite likely that the wing is engorged with blood which is heated through the absorbtion of radiant heat,facilitated by the black wing colouring. It is proposed here that this heat is then transferred to the body, facilitating exogenous

heat gain and, elevating body temperature to 'acceptable' levels, e.g. from 35°(or lower) to 39°C.

Temperatures at Gordon were recorded as low as 3.4 C at first light. On these mornings the animals were noticeably lethargic in their movements. This may suggest that their body temperature is lower than Bartholomew et.al.'s(1964) 35°C - recorded in the laboratory for this species at an external temperature of 5°C. Under such conditions an energetically inexpensive method of elevating body temperature, such as proposed here, would be highly advantageous.

Unfortunately, the implications of this behaviour were not appreciated until late in the series of observations. Consequently, this behaviour was no recorded separately from 'hang awkwardly folded' - a proposed heat dissipating mechanism. As a result, substantive quantitative data is lacking. However, support of this theory is found in the very different sequence of activities found on mornings following nights of low or relatively high ambient temperatures. This is discussed in a later section of this chapter.

Hanging awkwardly with the wing extended, was recorded at temperatures as low as 7°C. Of interest is the fact that one particular bat, which typically displayed this behaviour at first sunshine, did not display it on one occasion at 3.6°C but climbed up to an exposed position and hung in direct sunlight but with wings folded. Presumably, the considerable ability they exhibit for absorbing radiant heat does not exceed the amount of heat lost through lack of insulation at temperatures as low as this. Finally, care must be taken with the recording of this activity, as overheated animals may on occasion be seen to hang in shade with one wing drooping to facilitate heat loss. This obviously represents a very different case to that under discussion.

Swivelling. This behaviour has been reported as being simply an alert response to external stimuli. This is the cause in only a minority of cases. Under these circumstances the animals are noticeably alert, as evidenced by open eyes and highly mobile pinnae. Discarding these cases it becomes clear that swivelling is strongly correlated with sunny conditions and is almost totally absent under overcast conditions, as demonstrated by fig. 26.

Swivelling was recorded at a wide range of temperatures (4.8 - 27°C) but reaches its highest rate, expressed in actions per animal per minute within the range 12-19°C as illustrated by fig.27. The degree of correlation between this activity and time of day (expressed as minutes since sunrise for a.m. records, or before sunset for p.m. records) and temperature was ascertained through linear regression analysis. This test was applied separately to all records less than 16°C., and again for those greater than or equal to 16°C. The significance for the correlation between temperature and swivelling were better than .001 in both cases. Similarly, the significance of the linear regression slope as a tool for the prediction of the relationship between ambient temperature and swivelling was also highly significant at the .001 level.

Multiple linear regression analysis was also applied to the relationship between time, temperature and swivelling for all records - divided into a.m. and p.m. This determined that only 29% of the variability in swivelling for the p.m. records and 22% for the a.m. records, could be explained by its dependence on time and temperature. For the a.m records the effect on swivelling of both time and temperature showed a very large standard error. For the p.m. records, the standard error for time was 55.5% i.e. $.0009 \pm .0005$ while the standard error for temperature was 24.5% i.e. $.1649 \pm .0405$.

July 1981 - Average swivels per animal per minute plotted against ambient temperature under sunny and overcast conditions.

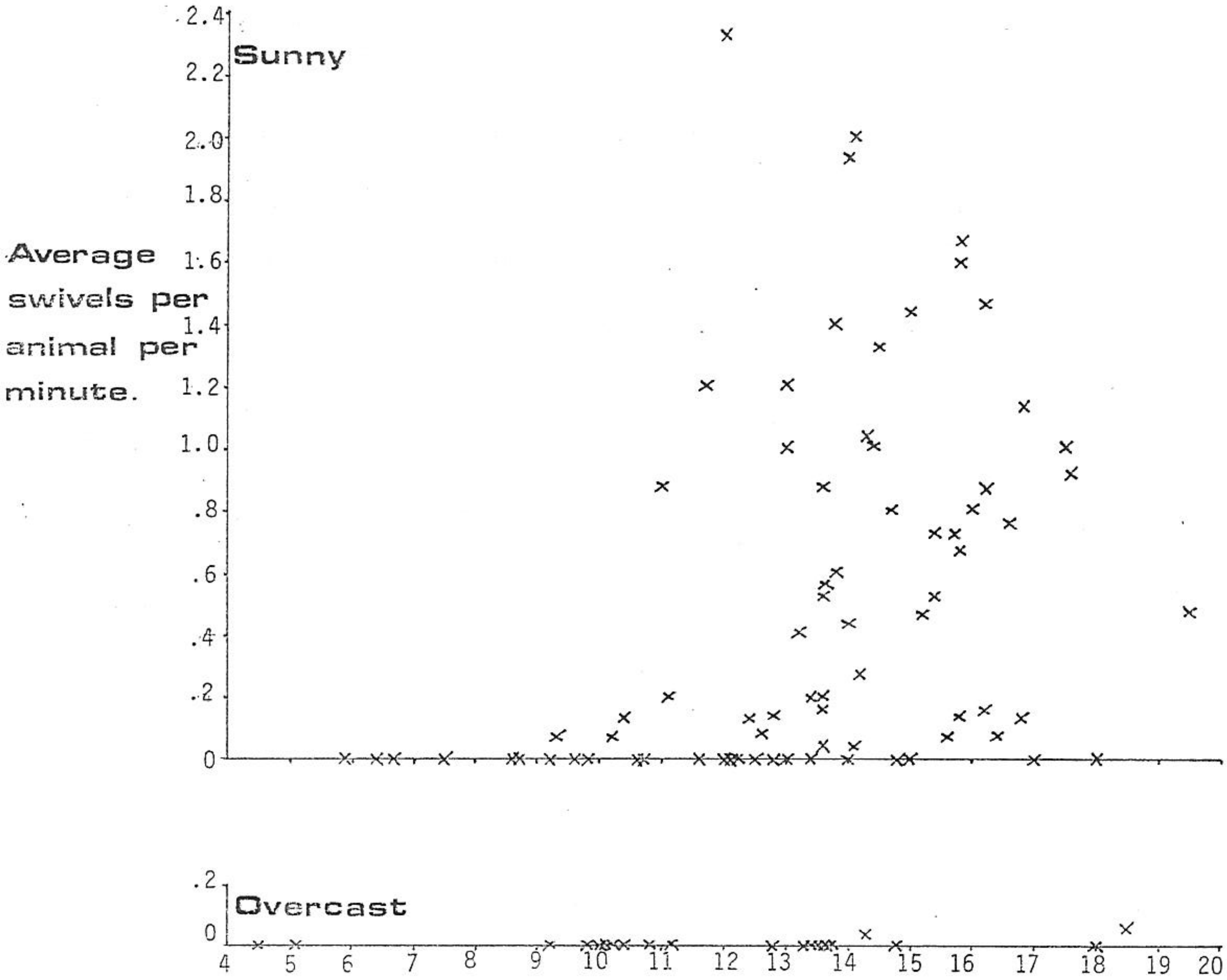
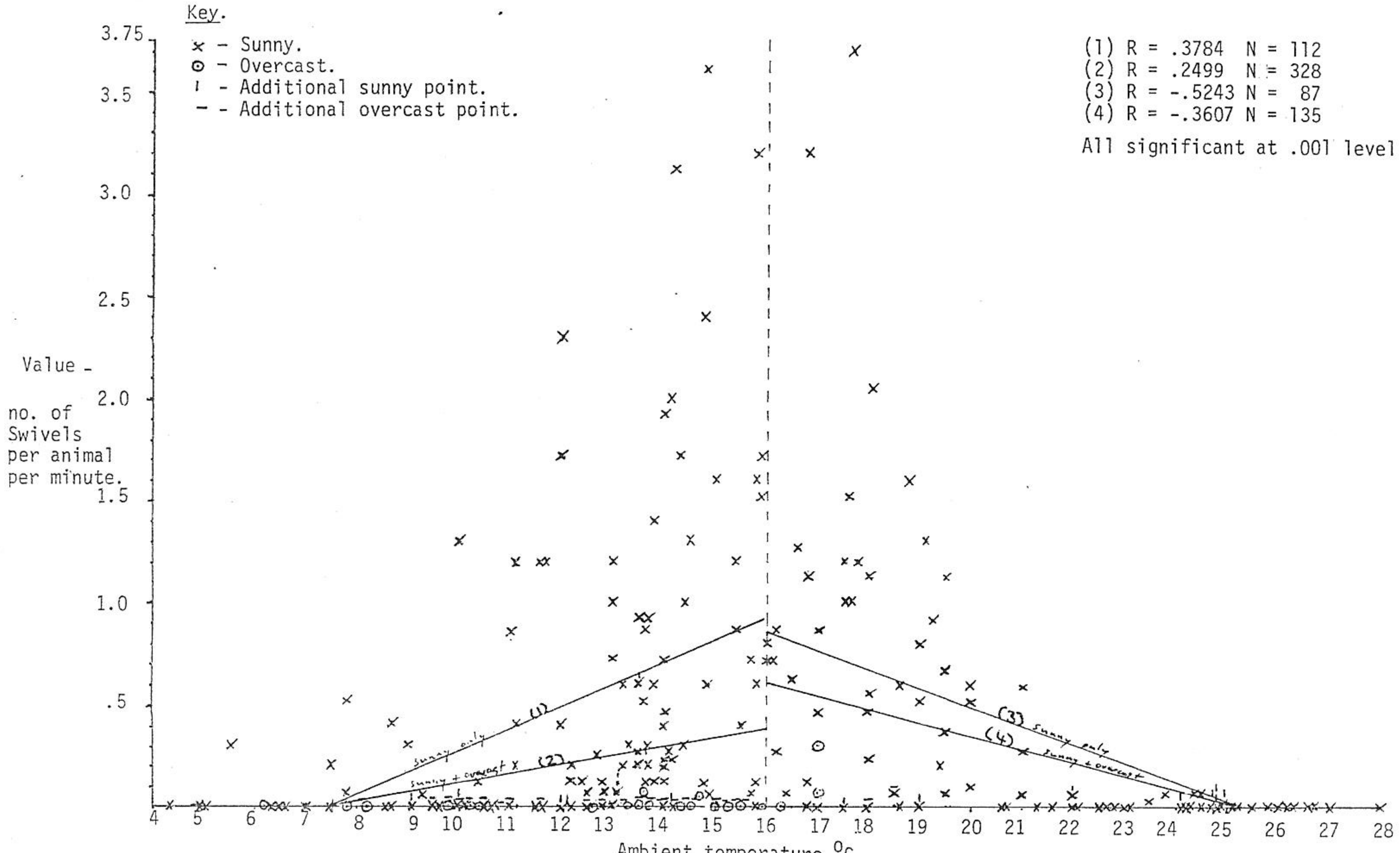


Fig. 27.



Swivelling - plotted as average 'swivels' per animal per minute against ambient temperature.

It is proposed that the function of this activity is either to maintain or 'fine-tune' the animals body temperature at an equable rate. By repeatedly rotating the body, the animals alter their orientation with respect to the sun, and are evenly warmed on all sides. The black wings, although wrapped around the body almost certainly absorb some radiant heat energy. On partially cloudy days, the animals cease swivelling as soon as the sun is obscured and resume when the sun reappears. The drive to perform this behaviour is apparently strong as it is even exhibited by females with large young enclosed in their wing membranes. This is quite a strenuous exercise as the young's grasp of the branch means there is not a single point of revolution, but two. The female must use both feet and considerable body torsion to expose all sides of her body to the sun's rays.

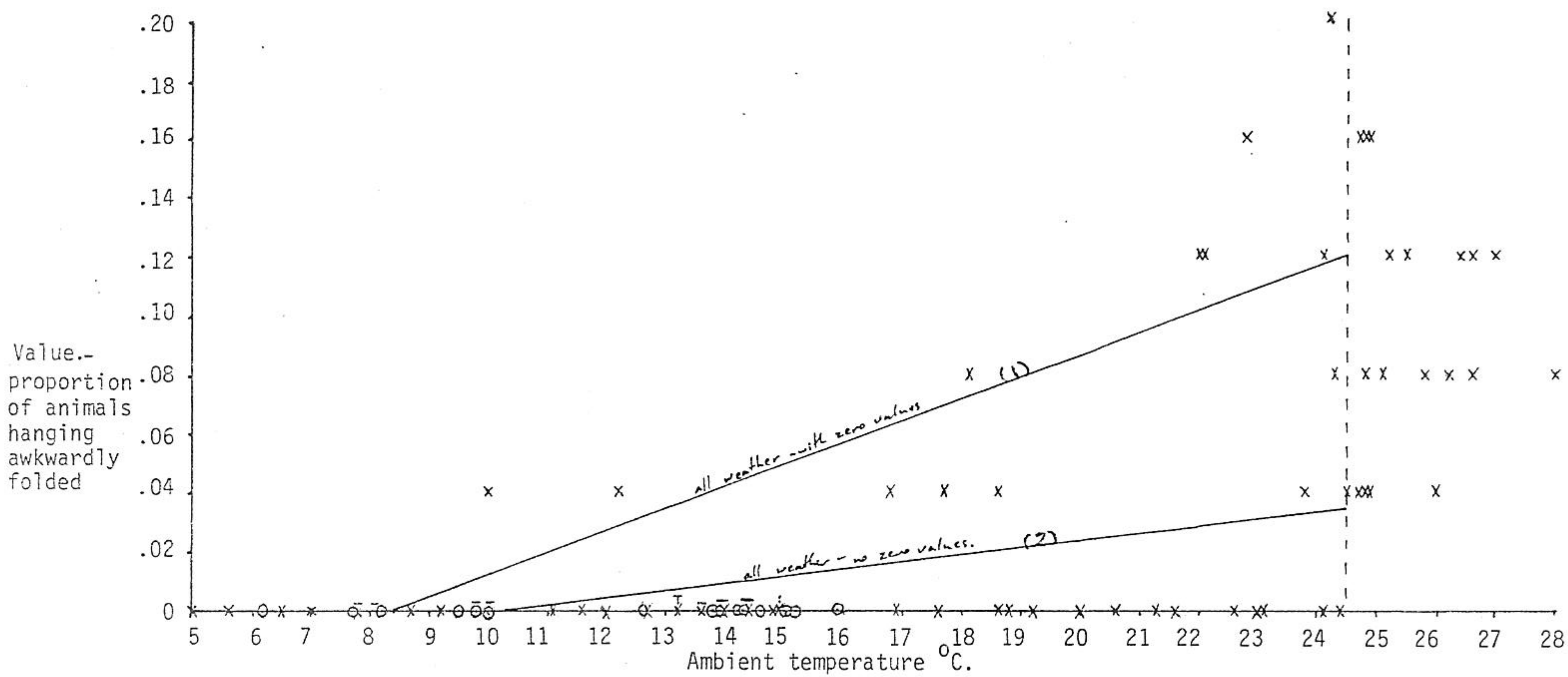
Hang Awkwardly - Wing Folded. This activity is proposed as a heat dissipating mechanism. Obviously, with the wings not wrapped around the body, their insulative qualities are lost. The wing membranes are folded to present the minimum surface area for heat uptake. In this position the animal hangs by one or both legs but also uses the thumb claw of one or both wings to hold on to a nearby branch. This means the wings are not in close contact with the body, further facilitating heat loss. As stated previously, this behaviour was not differentiated from 'hanging awkwardly with the wing extended' until late in the observation period. However, the few records obtained, demonstrate the activity to be present at ambient temperatures between 10 and 28^{o}C., with its greatest frequency being at around 22-27^{o}C. as illustrated in fig. 28. It is positively correlated to temperature (R= .440, significant at the .001 level) up to 24.5^{o}C. After this temperature it begins to be replaced to a large extent by active fanning of the wings and is not significantly correlated to temperature.

Fig. 28.

Key.

× - Sunny.
⊙ - Overcast.
ı - Additional sunny point.
– - Additional overcast point.

(1) R = .4398 N = 130 Sig. at .001
(2) R = .6529 N = 14 Sig. at .01

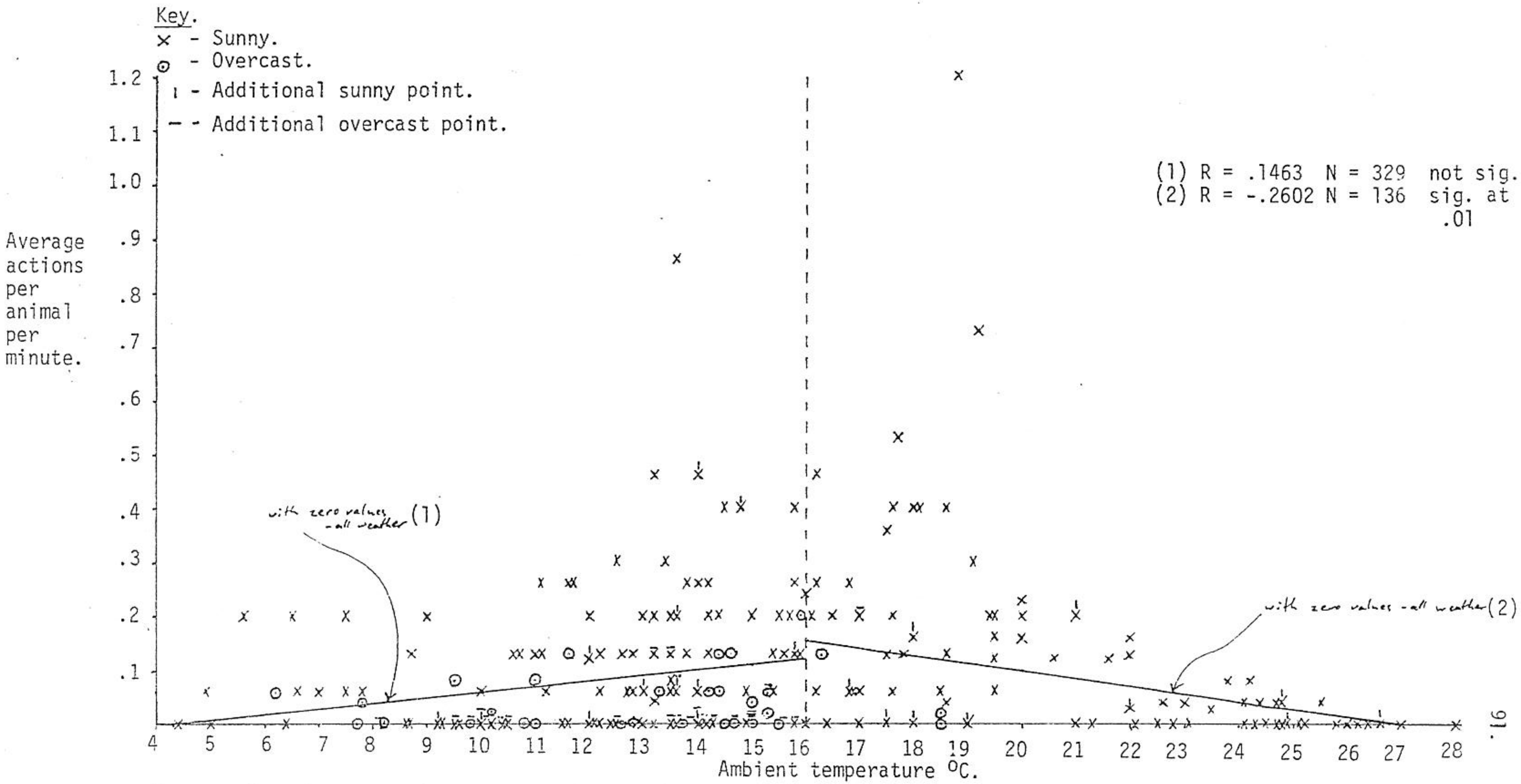


Hang awkwardly folded - plotted as proportion of bats hanging awkwardly folded, against ambient temperature.

Wings by Sides. This activity is essentially the same as the preceding one, excepting that in this case both wings are held folded at the sides, exposing the body to radiative and convective heat loss. The animal is essentially in the alert position but the lack of obvious ear or body movement and closed eyes distinguish this behaviour. Furthermore, the 'flags' of the wing tips do not protrude as obviously behind the animal as they do when the animal is alert or alarmed. The fact that the wings are held at the sides rather than out from the body, means that less body surface is exposed for heat loss. This position may therefore be used when the required heat loss is fractionally less extreme than for the previous posture.

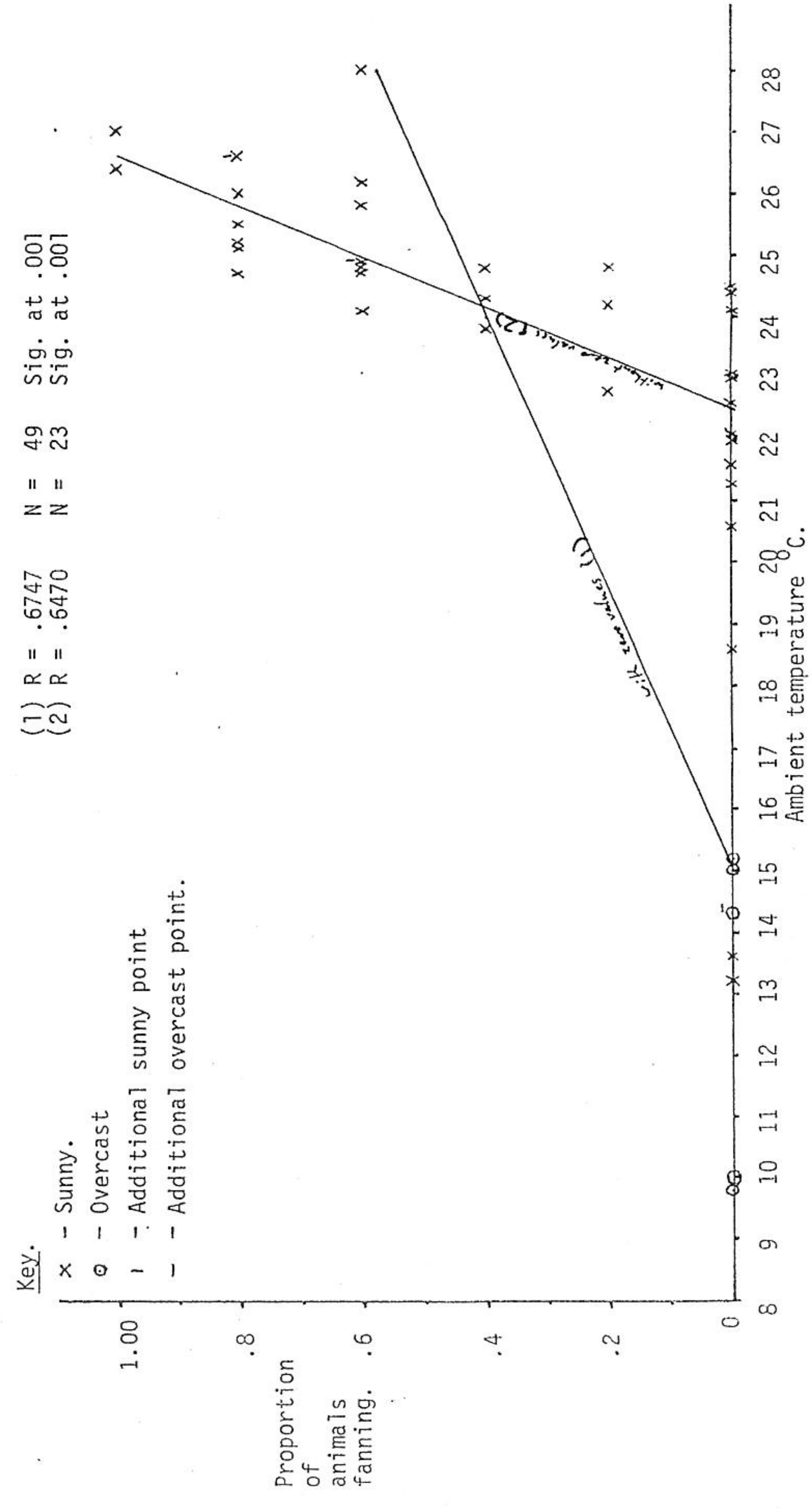
Rearranging Wings. This behaviour is exhibited for different reasons at different times and is difficult to correlate to any particular feature of time, temperature or solar radiation. It is seen early in the morning when the animal 'wraps up' to improve insulation, or after some activity. It is seen under windy conditions when the wings have been partly blown open by the wind and the animal rearranges them for comfort and to restore their insulative qualities. Mothers with young enclosed within their wing membranes, rearrange their wings after the young is seen to move within them. It is exhibited by females in an attempt to thwart a male's advances, or after mating, to prevent further contact. Finally, it is exhibited as a pre-fanning behaviour, at uncomfortably warm temperatures. In this last case, the wings are unfolded, then folded up again, presumably to dissipate the heat build-up between the body and wings as reported for Microchiroptera by Burbank and Young (1934). As ambient temperature increases, this behaviour becomes more frequent until it evolves into full fanning behaviour. As can be seen in fig. 29., this activity is exhibited at temperatures ranging from $4.8^{o}C$. to $25.5^{o}C$ but reaches its peak frequency between 12 and $20^{o}C$. It is displayed under both sunny and overcast conditions, but is more pronounced under sunny conditions.

Fig. 29



Rearranging wings - expressed as average actions per animal per minute plotted against ambient temperatures.

Fig. 30.



Fanning - expressed in the proportion of bats fanning plotted against ambient temperature.

so may have uncomfortably elevated her body temperature. This observation raises an interesting point. Noll (1979b) states that a female and young enclosed within the female wings form a single thermoregulatory unit. Sydney lies in the southern section of this animal's range. Nightly winter temperatures, especially when accompanied by westerly winds must approach the animals' lower limits of tolerance. The retention of the young by females would confer a selective advantage by reducing the cost of maintaining body temperature for both female and the smaller young. It was noted that some females retained their young far longer than others. Whether this simply reflects later birth time, or whether the female-young association was more prolonged in these animals is not known, but further study of this phenomenon could yield interesting results.

In autumn, fanning was observed to begin at temperatures around 21-22^{o}C. and cease at around 18-19^{o}C. During winter fanning was observed on only two occasions, once at 19.8^{o}C. and again at 18.6-19.1^{o}C. For the spring records mentioned before, fanning was initiated at 22.8^{o}C. and ceased at 23.8^{o}C. Although the information is too sparse to allow solid conclusions to be drawn, it could be that animals acclimatize to cold ambient temperatures during winter and consequently become overheated, and fan, at lower ambient temperatures. Temperatures above 28^{o}C. were not experienced in this study. Consequently, the pronounced salivation and wing and body licking reported earlier as extreme temperature regulatory mechanisms were not observed.

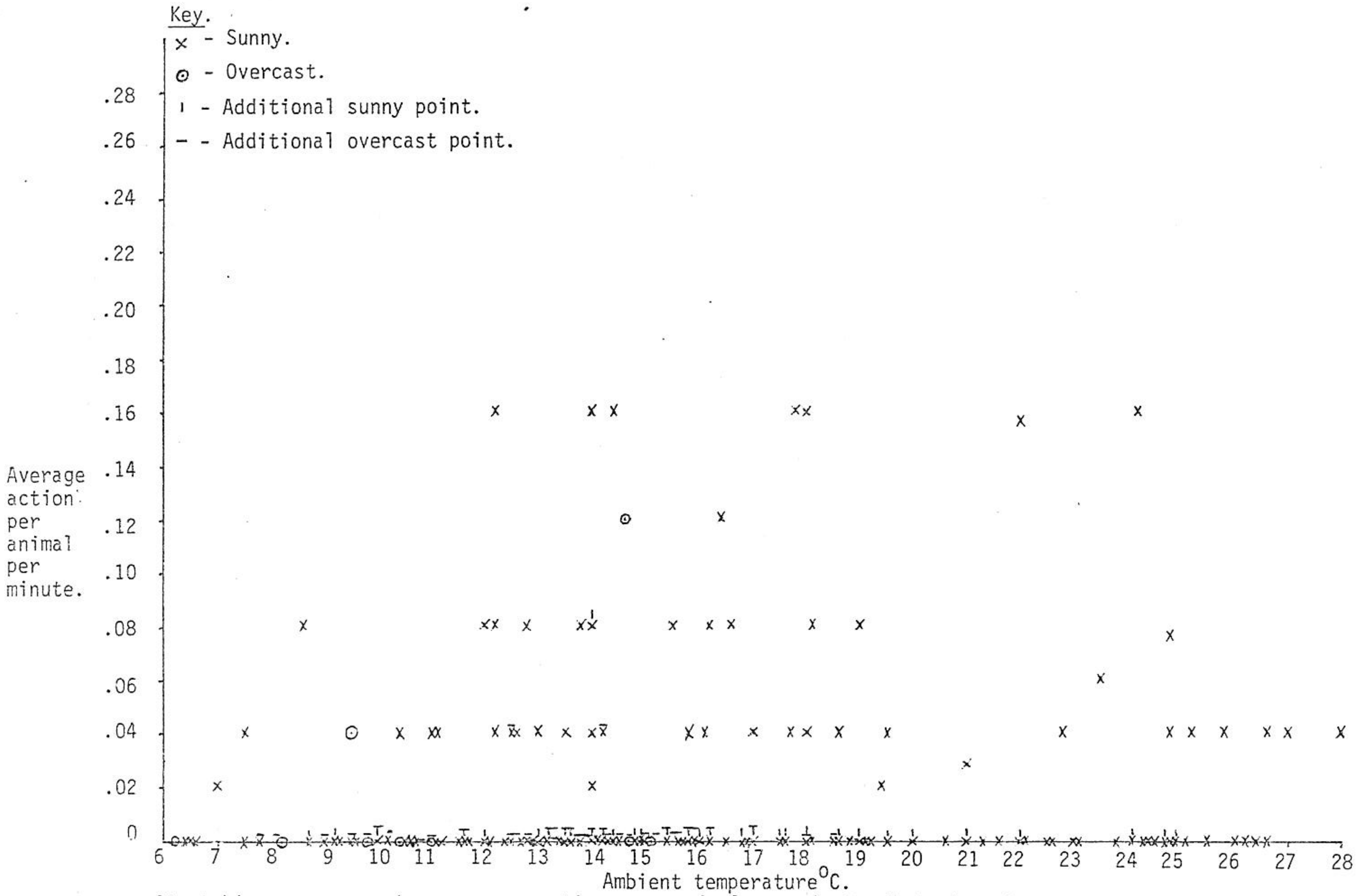
The following activities were found not to be directed at temperature regulation within the range of temperatures experienced in this study, but in some cases a relationship was found to exist between activity and temperature, so are worthy of mention here.

Stretching. This activity appeared at all ambient temperatures between 7 and 28^{O}C. and was not significantly correlated to ambient temperature. Marginally higher rates of stretching were observed between 14 and 16^{O}C. A relationship does exist between this activity and sunny conditions (significant at the .001 level by Chi-squared analysis), as evidenced by fig. 31.

The lack of a significant relationship with temperature, would in part be explained by the fact that this activity has several functions. Firstly, the activity is simply a means of stretching muscles after a period of inactivity. It is often done prior to hanging awkwardly with the wing extended and may reduce the need for muscular action to keep the wing extended, that is, in effect to temporarily exceed the elastic limit of the flight membranes. Finally, it appears to be a mildly assertive behaviour used to maintain individual distance between animals or demonstrate dominance by a male over a female. The wing in these cases is extended towards, and briefly held quite close to a nearby animal. The major thermoregulatory significance of this transient activity is that when the wings are unwrapped or stretched, their insulation is immediately lost, resulting, presumably, in a small drop in body temperature as demonstrated for Microchiropterans by Burbank and Young (1934).

Licking Wings. This is a cleaning activity except at very high ambient temperatures (greater than 40^{O}C.) where it becomes of thermoregulatory significance, as previously discussed under 'fanning'. It is not correlated significantly to temperature. It was observed from 4.8 - 26.4^{O}C. under both sunny and overcast conditions, although it predominates under sunny conditions (significant at .01 level by Chi-squared analysis). The lack of a highly significant correlation here is no doubt partly due to the fact that the wings are often licked immediately after rain

Fig. 31.



Stretching - expressed as average actions per animal per minute plotted against ambient temperature.

to remove water - when conditions are still overcast. This activity is also strongly related to time of day - being extensively performed by all animals immediately prior to exodus and upon return to colony from feeding areas. Mathematical substantiation of this is lacking as records were not taken at these times due to low visibility. Multiple linear regressic analysis was applied to records of daylight hours to ascertain the importance of time ,(as minutes since sunrise for a.m. and as minutes to sunset for p.m. records)and temperature on wing licking. These two aspects were found to be of very minor importance, explaining only approximately 4% of the total variability in wing licking for both morning and afternoon records. Undoubtedly the inclusion of data for immediate pre-flight licking of wings would significantly raise this figure.

Licking Body. This cleaning activity is very similar in many aspects to the preceding one. Licking the body is used as a cooling mechanism at extremely high temperatures and was not observed in this context in this study. This activity was observed at all temperatures between 4.8-25.2^{o}C. Its highest incidence occurred between 11 and 17^{o}C. It was displayed under both overcast and sunny conditions, but was far more evident under sunshine conditions (significant at .001 level with Chi-squared analysis).

Urine Bathing. The animals usually become moistened by this activity, so we would expect it to be correlated with both medium to high temperatures and sunny weather conditions. Of the twenty recordings made of this activity, only one was made during overcast conditions. Fourteen were made in sunny conditions. The remaining five were made under unknown or unsettled conditions. All recordings fell within the temperature range 8.6 - 22.1^{o}C. The activity is most pronounced when the sun emerges after a long period of overcast. It is a relatively infrequent behaviour, probably performed only once, or at most twice, by an individual per day and not at all on cold, overcast or rainy days. This is understandable as the water loss as urine is quite pronounced for an animal which does not drink between dawn and dark unless rain falls. Repetition of such an activity, especially on hot days, would considerably stress the animal's water balance.

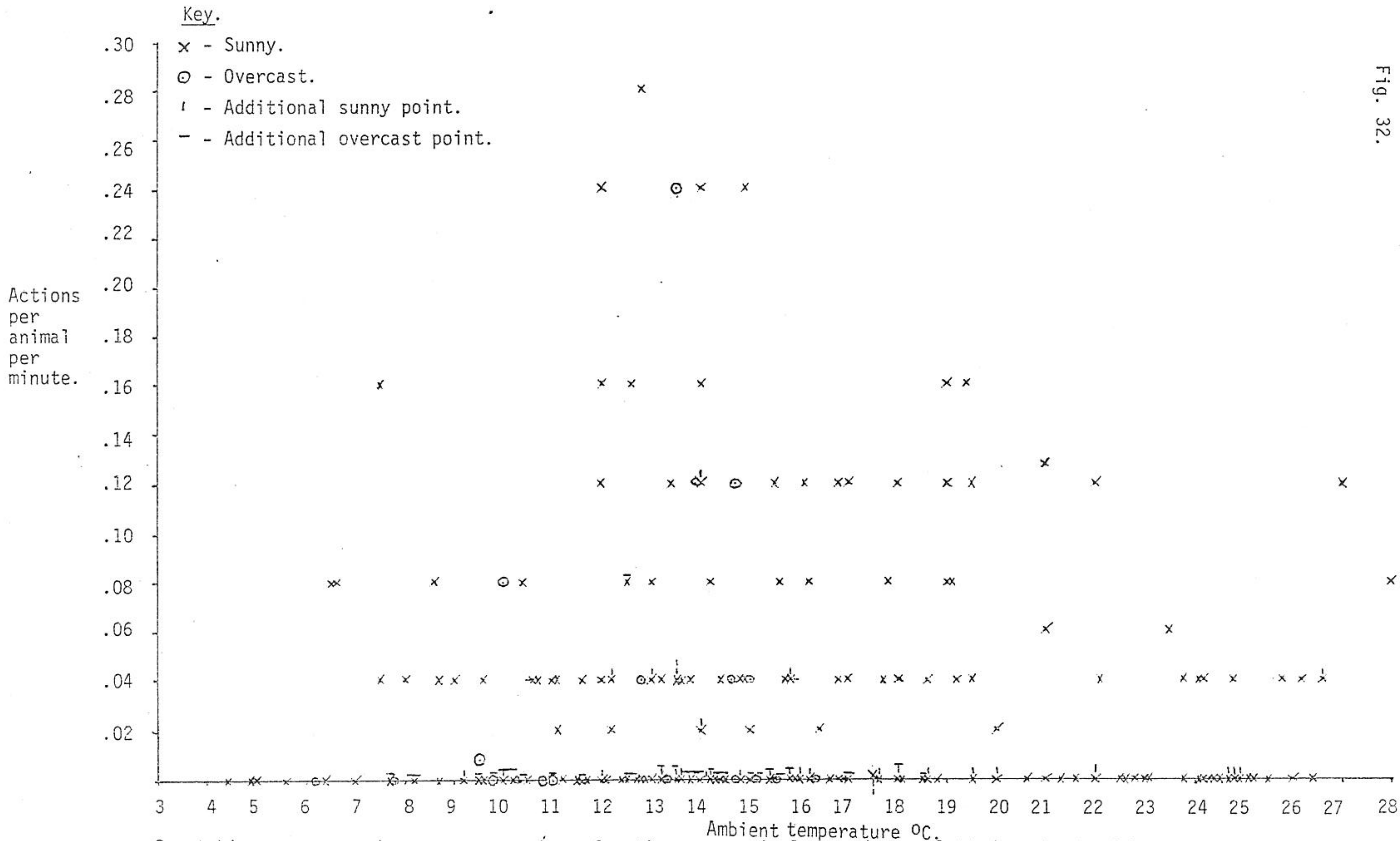
Scratching. This activity was found to occur at all temperatures between 3.4-28^{o}C. - the total range of observed temperatures. The highest incidence of this activity occurred between 12 and 17^{o}C. as seen in fig. 32. It was performed under both sunshine and overcast conditions. However, very few high rates of this activity were observed when overcast. This perhaps suggests that the animals are reticent to unwrap their wings and lose the temperature gradient between the enclosed body and the atmosphere, under overcast conditions.

Rain Position. This posture is assumed under conditions of moderate to heavy rain. It may also be seen when precipitation is only very slight but is accompanied by low ambient temperature or cold wind. Flying foxes are least active during rain and may remain motionless all day if the rain is continuous. Should the rain slacken or ease, activities such as scratching, licking wings and body to remove moisture are immediately seen.

This posture is really a refinement of 'wrapped up asleep'. It is unclear if the animals are awake or asleep when displaying it, however, as they are motionless. Presumably some effort is required to maintain it.

Testes Descent. Nelson (1965a) reports that the testes of *P. poliocephalus* descend at an ambient temperature of 26^{o}C. or greater. In this study, testes were seen exposed at ambient temperatures ranging as low as 14^{o}C. Furthermore testes were not seen at temperatures as high as 19^{o}C. See fig.33.

Fig. 32.



Scratching - expressed as average number of actions per animal per minute plotted against ambient temperature.

the ambient temperature reached approximately 8^{o}C. Their sex was unknown.

A note should be made here concerning a reported aspect of P. scapulatus' thermoregulatory behaviour. Bartholomew et.al. (1964) state that P. scapulatus are less prone to wrap up within their wings than are P. poliocephalus, though they "may occasionally do so". The scapulatus seen at the Gordon colony and captive specimens kept by this author, were routinely wrapped up when awake at moderate temperatures. The only exception to this is when the animals are overheated/alert or frightened, which may provide an explanation of the observations of Bartholomew et.al. (1964).

Moving to less exposed conditions. This behaviour was not observed when the animals were maintaining territories. After this period, roughly from mid-July, it was noticed that there was a distinct vertical movement, so that all animals were roosting much lower in the trees throughout the day. The surrounding shrubs and better foliated lower portions of the trees provided considerable protection from the strong, cold winds evident at that tir i.e. mid-July-August. Prior to the establishment of territories for breeding purposes, it may well be that animals escape uncomfortably high ambient temperatures by moving to less exposed sites. At temperatures in the high 20's some movement was evident that may be explained by this fact. Conversely, in the winter months animals were seen to move into exposed positions where they would be exposed to direct sunshine.

Thermoregulatory behavioural sequences. If the suppositions about the significance of the thermoregulatory behaviours are correct, we would expect to see a sequence of behaviours as ambient temperature rises from below optimal levels to above optimal levels. This is indeed the case. Reference to Fig. 24, shows that initially the animals are wrapped up - either awake or asleep - resting after the nights feeding and insulating against the cold. The first active thermoregulatory behaviour seen is hanging awkwardly-with the wing extended, to raise body temperature. Within the next 30 minutes, swivelling begins, indicating that the animal is comfortable or possibly a little cooler than ideal. The next thermoregulatory behaviour exhibited is hanging awkwardly with the wing folded to negate the insulative qualities of the wings and lose body heat to the atmosphere.

At the same time, the pre-fanning activity, rearranging wings, is exhibited by some animals. This activity is, in effect, a series of intention movements, exhibited prior to full committed fanning behaviour. The less common thermoregulatory behaviour, wings by sides, is seen in the next 30 minutes. Simultaneously, some animals begin fanning to prevent body temperatures becoming too high.

Although these spring days i.e. 15-16/9/81, do follow the suggested thermoregulatory pattern, the degree of warming up activities - hang awkwardly, wing extended and swivelling is minimal, in marked contrast to that seen for winter days. On the other hand, the heat shedding activities, hang awkwardly, wings folded and fanning are reduced or absent from winter records, due to lower ambient temperatures.

The absence of warming up activities from warm spring records is best explained by overnight ambient temperatures. During winter, the animals are subjected to low nightly temperatures (6.2 - 10.7°C for mid-June from Bureau of Meteorology records). Undoubtedly at these times their body temperatures fall at least to the reported minimal level of 35°C. Consequently, when direct sunlight falls on the animals they act to increase their body temperature through exogenous, energetically inexpensive means. However, in the spring and summer, with accompanying higher night-time temperatures (11.6-15.8°C for week leading up to 16/9/81) the animal's body temperature would not be expected to fall as markedly. (In fact, on extremely hot nights, the thermogenesis resulting from flying may subject the animal to some heat stress). Consequently, after having returned to the roost, the animals are already 'warm' and have no need of further warming. The animals remain relatively inactive, presumably until such time as ambient temperatures rise above thermal neutral maximum, at which time, cooling activities are employed. This explanation fits neatly to the observations of the 15-16/9/81.

Factors affecting activity. Apart from season and food availability, the major factors affecting activity appear to be, in order of importance; night or day, rain or fine, presence of direct sunlight, ambient temperature and finally wind.

Justification for this conclusion is as follows:

Firstly, regardless of all other factors, if it is night-time, the animals will be engaged in feeding behaviour away from the roost, if daytime, they will be at the roost. During the day, if it is raining, the animals will be virtually inactive, becoming active only when the rain stops or slackens off to a very light rate. If it is not raining, then the animals wil be more active if the sun is shining than if the sky is overcast. This last relationship is true to some degree for the majority of activities. Lastly, the presence of strong wind tends to depress the level of activity.

Variations in the nature of Megachiropteran and Microchiropteran behaviour are explicable in part, by the factors outlined above. Microchiropterans roost by day in caves, hollow trees and similar protected sites. As they are largely shielded from the direct effects of weather, their daytime behavioural repertoire is confined largely to cleaning and sexually related activities, or is greatly reduced as the animals enter torpor.

The tree roosting Megachiropterans on the other hand, are exposed to the full effects of direct sunlight, rain and wind. Their usually large body size allows them to tolerate extremes of weather whilst maintaining a relatively stable body temperature. It is argued here they have adapted behaviourally to a large degree to cope with, and benefit from these conditions.

Future Work. Confirmation of the thermoregulatory significance of the activities discussed here came largely from observation of the sequential activities of individuals. Future work on the thermoregulatory behaviour of Pteropids should concentrate on the continuous study of the behavioural sequences of individuals under natural or near natural conditions, with animals directly exposed to sun, wind and rain. Careful attention should be paid to the nervous state of laboratory animals. The results of many studies on bat thermoregulation are open to interpretation as a result of using animals which are obviously stressed by their confinement and handling.

An area of particular interest, is the histology of Pteropid wing venation and the control of wing blood flow under various combinations of temperature, sunlight and activity.

Utilizing insights gained from this study, the work of Bartholomew et.al. (1964) in this area, could be significantly extended.