The Whooping Display in Nilgiri Langurs: An Example of Daily Fluctuations Superimposed on a General Trend

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ABSTRACT. Field data on the whooping display in the Nilgiri langur were recorded in two ways: (1) the number of whoops heard while in the forest during a complete day; (2) the number of whoops heard by each of three troops while under constant observation from dawn to dusk for a total of 18 days. The temporal, visual, and auditory qualities of the display are described. Different methods of graphically representing the daily pattern of the whooping display are then exhibited. One method shows a main bimodal trend in whooping with a main peak in early morning and a smaller peak in the afternoon which is in accordance with other primate species. Secondarily, other ways of representing the data show that the morning peak is actually a series of peaks which decrease in magnitude after the initial peak. Additionally, the total amount of whooping is reduced during clear days and the initial morning peak is affected by the seasonal change in sunrise. The methods of representing data show that the gross trend of whooping is in reality a series of fluctuations which probably have relevance to the general activity as measured by the percent of individuals in the troop observed feeding. As in whooping the feeding activity when observed continuously in one troop for one day is a series of four to seven peaks rather than a bimodal distribution as represented by data of many days lumped together. A similar phenomenon of cycling in ontogenetic data is discussed.

INTRODUCTION

Methods of data collection and graphic or statistical representation of data varies with an individual scientist's view or his metaphysics (GOLANI, pers. comm.) and with the information being sought. Often, because of the difficulty and time consumption involved in collecting data on animal behavior and because of the desire to investigate species differences, behavioral scientists have opted to lump data from many individuals in order to have species trends emerge. This kind of information is very useful when employed toward a specific end point as ROSENBLUM (1971) does in comparing and contrasting behavioral development in two species of macaques. There are numerous other examples where gross trends in behavioral biology are pursued successfully. However, because these trends present themselves more boldly to the scientist does not mean that they show the complete picture nor even the most important biological significance of the behavior. I have recently uncovered fluctuations in data from two very different types of mammalian behavior (mother-infant contact and daily activity patterns) which document how biologically important fluctuations in behaviors have become masked by gross trends in these same behaviors. This concept is not new and in the field of business statistics, the analysis of time series is rudimentary and describes the interrelationship of five patterns of fluctuations: (1) basic trends which are long term movements, (2) seasonal fluctuations, (3) catastrophic movements caused by unusual events, (4) cyclical fluctuations which may be superimposed on the trend, and (5) residual variations which include chance variations (THIRKETTLE, 1968).

Before describing the aforementioned behaviors, there is one basic philosophical point which must be emphasized. An individual animal or an integrated group of animals does not act in allegiance to nor does it understand our concept of a species behavior. It behaves in a local manner with reference to its own inner biology and to the local external stimuli which include members of its own species. This is a simple concept which we as scientists live by since all of us act and live as independent units even though we may behave according to certain biological and species-specific principles. Generally, behavioral scientists, desiring to have enough data for statistical analysis, lump data from many separate animals, hiding individual trends which are in reality, the true way that individuals in the species are behaving.

I discuss the whooping display in the Nilgiri langur, *Presbytis johnii,* as an example of how the same data can be collected and represented in different ways. Some methods of representation mask the others. When taken together, they give a more complete pattern than any individual method. Two other examples of a general trend masking more subtle trends, in mother-infant contact in mammals and in daily feeding activity in langurs will be discussed briefly to add strength to the point.

METHODS

Observations were made on three troops of Nilgiri langurs which reside on a forested peninsula extending 4 km into Periyar lake in Periyar Sanctuary, South India. This peninsula is surrounded on the other sides of the lake by similar forested areas. For more details see TANAKA (1965) and HORWICH (1972). The three southern troops on the peninsula were observed for a total of 600 contact hours during two two-month periods, five and a half years apart in April–May, 1968 and again in January–February, 1974. When sighted, each troop was followed continually for as long as desired. For eighteen observation days (six on each troop) the troop was followed from dawn to dusk continuously. During these days, the times of whooping were noted for each troop. Because of the many years between the two study periods the three troops will be considered as six separate troops in analysis.

Data on whooping was collected in two ways. Each day in which I was on the lower peninsula for the complete day (dawn to dusk), I recorded one whoop. Every time a whoop or series of "hoo" sounds was heard. Since as many as seven whoops or "hoo" series may comprise a total whoop display, this meant that from one to as many as seven of these whoops could have come from one troop. It is possible that some of the troops had more than one whooping male although this is not common, and possibly some of the whoops could have come from lone males. My estimation during 1974 is that this data was being collected from about 15–20 troops or whooping males which were within my hearing range. Secondly, when I followed a troop for a complete day from dawn to dusk (18 days) I recorded the times at which that troop male whooped and also included his whoops in the total for that day.

RESULTS

Qualitative Description of Whooping

The whoop display in Nilgiri langurs is a series of one to seven whoops integrated with body movements which lasts from one to three minutes. Records of the frequency of whoops per display recorded for all three troops in 1968 and 1974 for 18 complete days indicates usually only three or four whoops per display are given (Fig. 1).

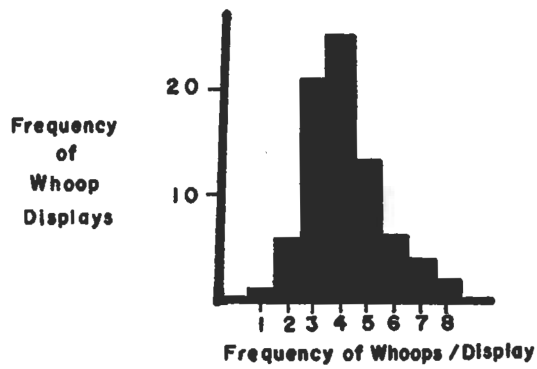

Fig. 1. The distribution of frequency of whoops per display.

The initial whoop is a series of sounds, expressed phonetically as "hoo", followed by a rapid aspiration caused by inhalation of air following the exhaled "hoo" sound. This initial whoop sound of about 15–17 "hoos" (based on three recorded displays) begins with a rapid series of "hoos" building up to a cresendo and then reducing the speed of the "hoos" at the end (Fig. 4). The dominant male who gives the call, rushes forward as he vocalizes, ending his locomotion in a stance with his arms bowed, his rump raised high with his tail looped over his back and head, and his head facing forward in line with his body (Fig. 2). He remains in this posture for 25–35 seconds then emits the second ejaculation of slower "hoos" preceded by a series of sounds which sound like HAH-ah-HAH-ah caused by rapid expulsion and inhalation with the emphasis on the expulsion sounds. He also bounds forward at this

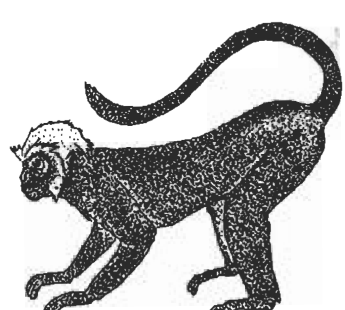

Fig. 2. The position a male langur remains in, following the initial whoop in a display.

time, rushing as much as 50 feet through the trees making a great deal of noise as he moves. Then, from 20 to 60 seconds later he gives a third whoop, a series of usually four slow "hoos" while he sits on a branch. This may then be followed by up to four additional series of slower "hoos" and an occasional kak or haha sound may be interspersed between them. Figures 3a and 3b show sonographs of two consecutive whoop displays recorded directly underneath troop 1 male on a Uher-4000-L tape recorder at 8:35 and 9:45 a.m. on March 4, 1974. A third whoop was recorded at 9:50 a.m. from the troop male just north of Troop 1.

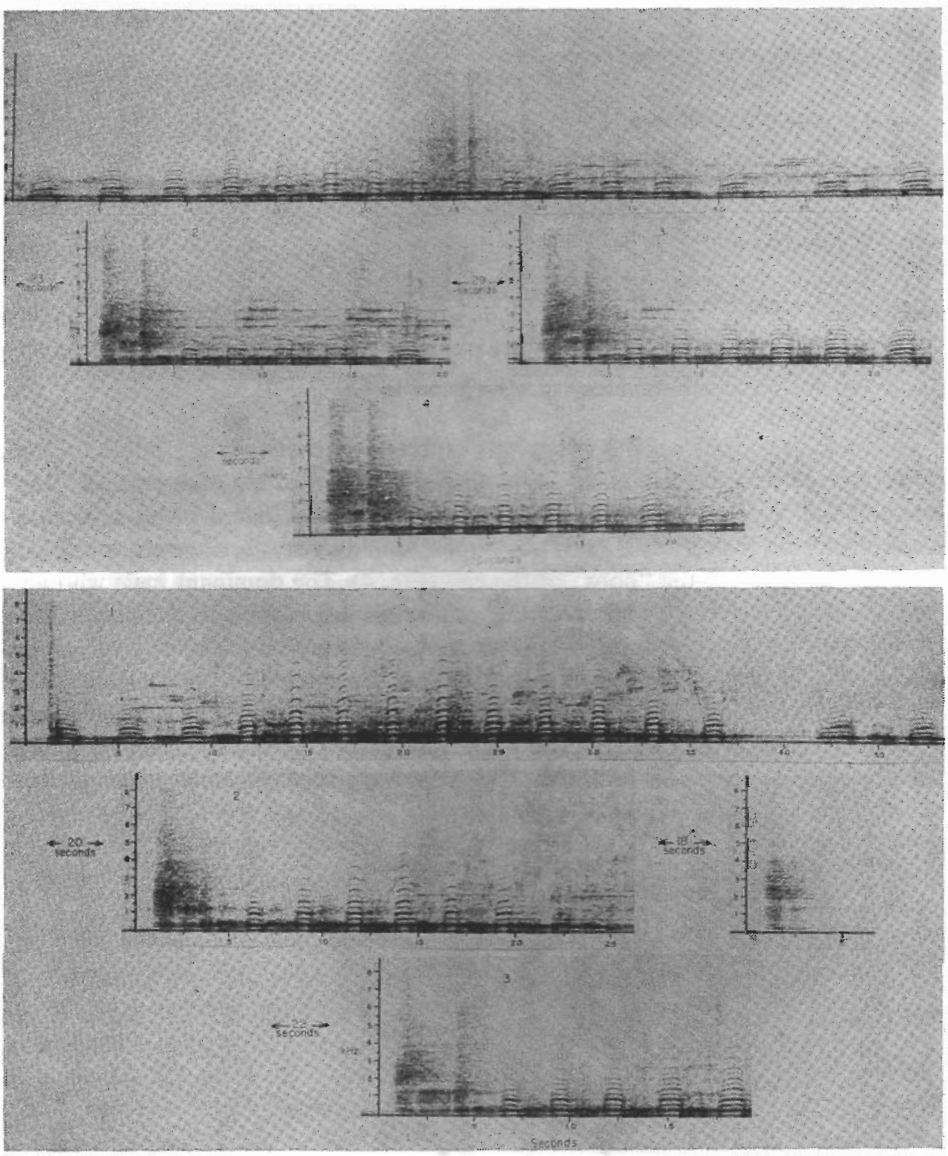

Fig. 3. Sonographs of two complete whoop displays given successively by the same male.

Whoop display 1 (Fig. 3a) includes four whoops. The first whoop consists of 16 "hoos" interspersed by intervals of .078–.383 seconds. The second whoop 23 seconds later is composed of two exhalation—inhalation haha sounds followed by five "hoos" which are separated by intervals of .109–.234 seconds. The third whoop, 29 seconds later has six "hoos" with intervals of .109–.211 seconds. The fourth series of seven "hoos" following the haha has .086–.187 second intervals.

Figure 3b shows a second display given two hours later by the same male. The initial whoop cresendo is composed of 15 "hoos" separated by intervals ranging from .078–.476 seconds. The second whoop 20 seconds later has six "hoos" following the haha with intervals of .078–.179 seconds. A kak follows 18 seconds later. Notice its visual similarity to the haha components. A third whoop 22 seconds after the kak has five "hoos" interspersed by intervals of .109–.187 seconds. In all "hoos" recorded the main energy band was at .3 kHz with a series of harmonics about every .33 kHz to about 8 kHz.

Figure 4 shows graphs of "hoo" lengths and the lengths of the intervals between

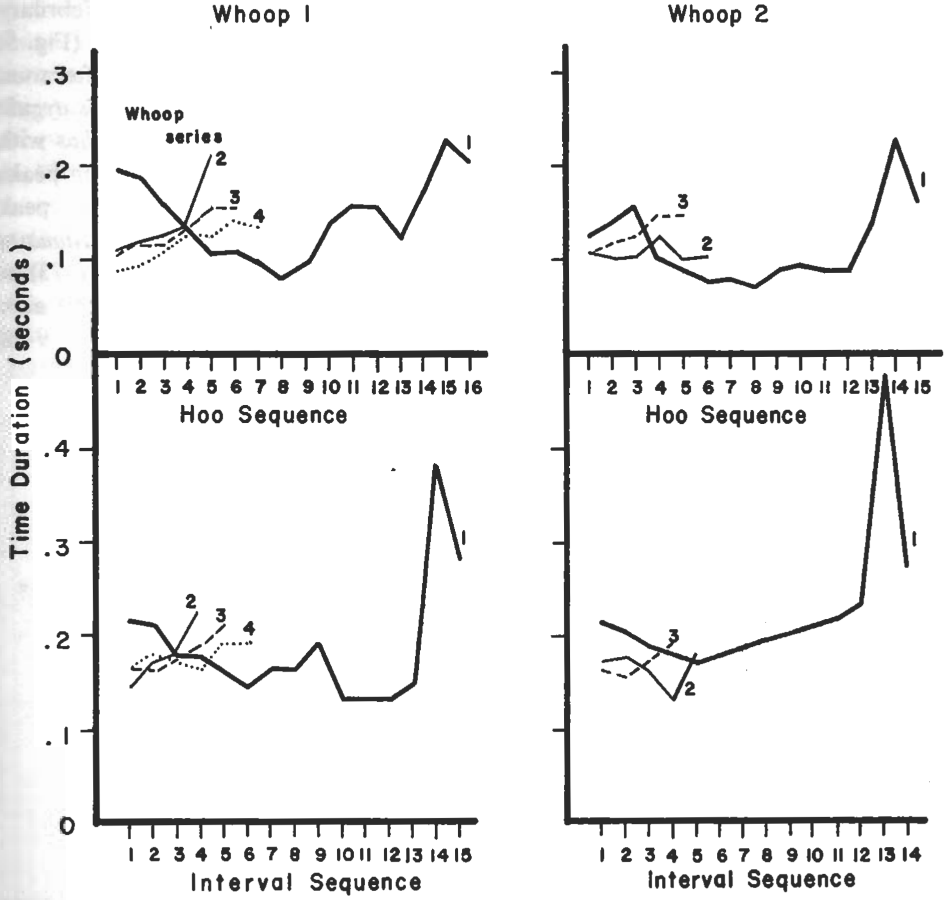

Fig. 4. The temporal changes in duration of hoo sounds and the intervals between hoos for two successive whoop displays given by the same male.

"hoos" for each whoop. The initial whoop shows a decreasing "hoo" and interval length building up to a cresendo then slowing down with a lengthening of the "hoo" sounds and one very long penultimate interval.

POIRIER (1970a, b) gives some description of the whoop vocalization which seems unclear relative to the sonographs. One main difference that he mentions is a hiccuping which lasted as long as 10 minutes. I never saw this in the troop males at Periyar nor did I see any immediate response to these vocalizations by other troop males. However, the data of Figure 6 does indicate a possibility that troop males are in some synchrony with each other perhaps due to immediate response or a similar daily cycling.

QUANTITATIVE DESCRIPTION OF WHOOPING

The daily profile of whooping in the Nilgiri langur has been described by POIRIER (1967, 1970b) and from his graphic representation of data collected during September through December, whoops are much more prevalent in the morning than in the afternoon. There is a large peak at 7:30–10:00 a.m. and a smaller peak at 2:00–3:30 p.m. with a depression at 0–2 p.m. My daily profiles for 23 days in January–February 1974 and 31 days in March–May 1968 offer a similar graphic representation (Fig. 5) except that the main morning peak occurs between 6–9 a.m. and the smaller afternoon peak occurs at 3–6 p.m. Similar primate curves in calling occur for *Presbytis aygula* with peaks at dawn and dusk (MACKINNON, 1974) and *Presbytis melalophos* with peaks at 5 a.m. and 6–8 p.m. (CHIVERS, 1973). Species with similar morning peaks without any slight afternoon increase include *Presbytis obscurus*, 6 a.m. peak (CHIVERS, 1973), *Colobus polykomos*, 9:30–10:30 a.m. (SABATER-PI, 1970), *Alouatta villosa*, 5:30–6:00 a.m. (ALTMANN, 1959), *Hylobates lar*, 7–8 a.m. (CHIVERS, 1973) or 8–9 a.m. (MACKINNON, 1974) or 7:30–8:30 a.m. (CARPENTER, 1964), or 6–10 a.m. (CHIVERS, 1972), and *Symphalangus syndactylus*, 8–10 a.m. (CHIVERS, 1973) or 9–10 a.m. (MACKINNON, 1974) or 8–12 a.m. (CHIVERS, 1972).

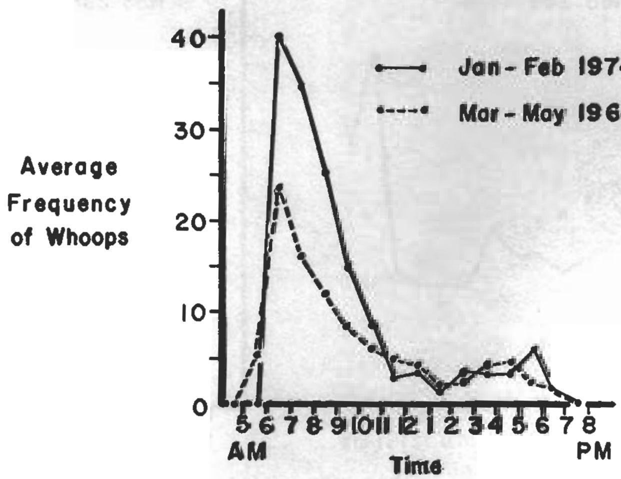

Fig. 5. The distribution of whoops during the day. The data is a lumped compilation from 23 days in 1974 and 31 days in 1968. Points plotted represent hourly totals.

Observations of the 54 daily profiles show that the bimodal curves from Figure 5 are in reality a series of peaks about one half to one hour apart which gradually decrease after the initial peak at 6:45–7:00 a.m. In most of the daily curves these fluctuations can be seen although in some they are more obvious than in others. Field data of howlers also indicates this multiplicity of peaks. CARPENTER's (1965) observations on a single troop indicate peaks at 6, 10, 2:30 and 4:30 p.m. Other data indicates peaks at 5–6, 8–9, and 5 p.m. (CHIVERS, 1969).

Figure 6 shows samples of the original whooping data. They exhibit the daily curves for the number of whoops observed between April 27 and May 3, 1968 (Fig. 6b) and January 14 to 17, 1974 (Fig. 6a). Peaks are clearly indicated although they are not noticeable when the days are lumped together and when the whoops are totaled on an hourly rather than quarter hourly basis (Fig. 5).

These daily curves show that the same phenomena is occurring during each day but that the peaks are not occurring at the same exact time each day so that *lumping the data destroys the individual fluctuations and displays only the gross trend of a major morning peak and a minor afternoon peak.*

Another method of data representation also brings out these peaks and depressions. From the original daily curves of whooping I defined a peak as a 15-minute-interval rate which was greater than five whoops in frequency and which is over twice the value of the depression preceding or following it. Figure 7 represents a plot of the frequency of peaks during any 15-minute interval for a total of 23 days of observation in 1974. Figure 7 indicates an uneven distribution of the data into favored peaks. The morning peaks are about a half hour apart.

Figure 8 displays yet another way of representing the data which again indicates clustering of the whoops. For the nine days in 1968 in which each troop was continuously observed, I recorded the time of each whoop display. When these are totaled for each 15-minute interval, definite clustering occurs. Figure 8a displays peaks at about 6:30, 7:15, 7:45, 8:30, 9:15, 10:15, 12:15 and the afternoon whoops are too few to indicate

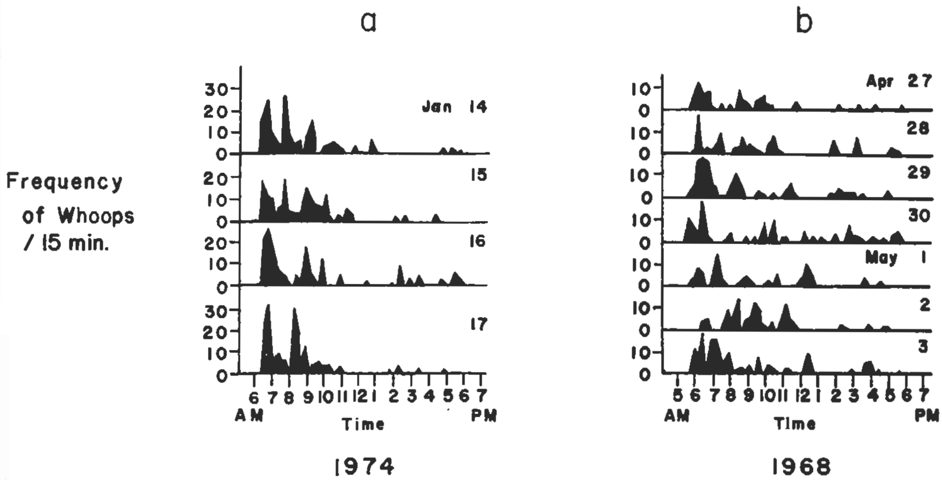

Fig. 6. Daily data of distribution of whoops during the day. Points plotted represent quarter hourly totals.

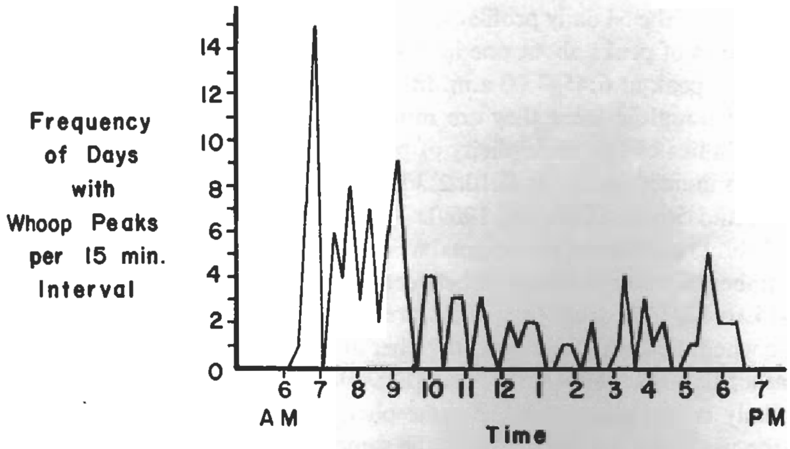

Fig. 7. Frequency of days with observed whoop peaks at quarter hourly intervals as a function of the time of day.

any peaks. Figure 8a shows fluctuations despite the use of whoop displays instead of individual whoops, and therefore the fluctuations are not an artefact of totaling the whoop components of the display. If one plots these same whoop displays as a function of the time after the initial display (Fig. 8b) then a slightly different pattern emerges, re-emphasing the fluctuating nature of the data. In this case the curves degenerate in peak frequency, time between peaks and solidarity of peaks. This degeneration seems very similar to data on behavioral development of primates (HORWICH, 1974).

One variable which seems to play a part in first reducing the fluctuations and in generally reducing whoops during a whole day is the degree of cloud cover and mist over the forest. Although the data is not conclusive due to lack of very objective means of assessing cloud cover, it is quite suggestive and on the few very clear days available the lack of whooping was very pronounced. Of 21 days in which the cloudiness or mistiness was assessed, only five were clear days. The Mann-Whitney U test comparing total whoops per day between misty and clear days indicates a significance at .02 level that a greater frequency of whooping is likely to occur during cloudy and misty days. It is my suspicion that days of intermediate cloudiness result in an intermediate amount of whooping and general depression of fluctuation. In contrast in howlers (CHIVERS, 1969) the onset tends to be later, duration shorter and fewer howls are given at a faster rate on cloudy days.

Figure 9 indicates that weekly averages of the number of daily whoops increases to a peak during mid February and decreases to a low point in mid April only to increase again at the end of April.

Another light variable which effects whooping and general activity is the time of sunrise. Figure 10 shows that the initial morning peak occurs earlier from January to April. Superimposed on these peaks is the effect that the mist and clouds have in essentially reducing the light intensity during the time of sunrise until about 9:00 a.m. each morning. On clear days the sun may rise over the forest at Thekkady as early as 7:00 a.m. during January–February. At other times it may only show through the clouds at 8:00 or 8:30 a.m. Howler monkeys also show a later chorusing with later sunrise (CHIVERS, 1969).

The question which must be asked is which interpretation is the more important

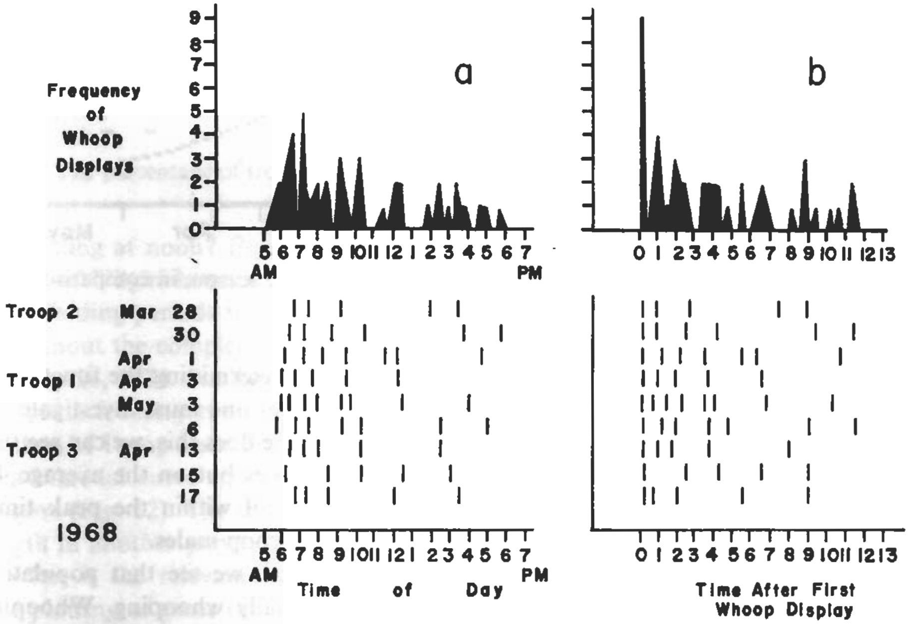

Fig. 8. (a) Frequency of whoops per 15 minute intervals for 9 days of data recorded in 1968 from three troops under constant observation. (b) The same data as (a) transposed so that the initial daily peaks of whoops are aligned.

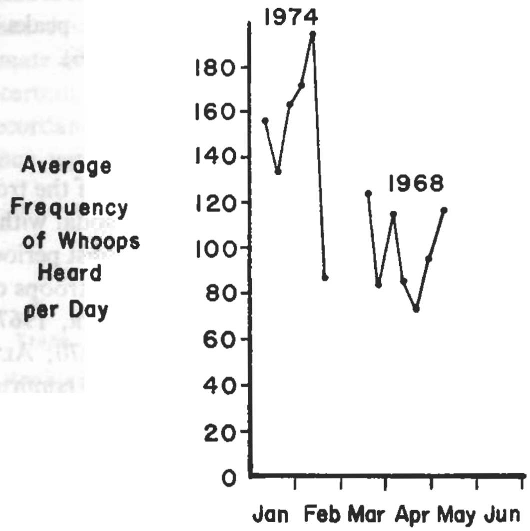

Fig. 9. Average frequency of whoops per day as a function of the season. (Data from 1974 and 1968 probably represent different numbers of troop males).

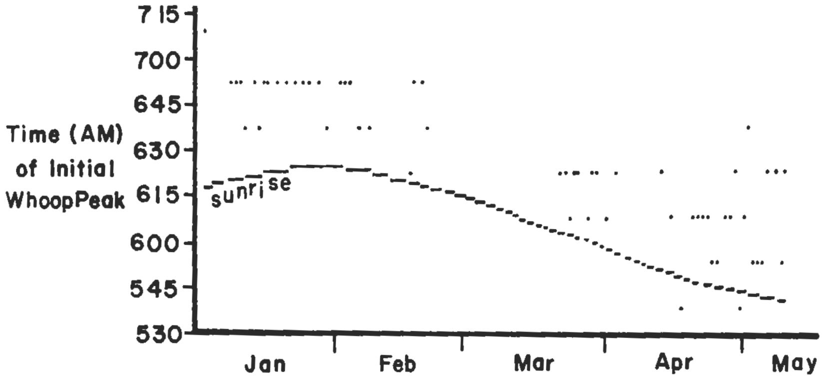

Fig. 10. The time of the initial whoop peak as a function of the season, in comparison with the seasonal change in sunrise.

trend in terms of the animal's biology and in ultimately determining the function of the whooping display. In order to look in even finer detail one must investigate the daily whooping of each troop male for each day. When one does this, we can see that each troop male (18 days) whoops from zero to eight times but on the average 4.4 times per day (Fig. 8). These whoop displays usually fall within the peak times exhibited by the daily fluctuations for the population of troop males.

When the above bits of data handling are synthesized, we see that population lumping techniques have masked a definite pattern in daily whooping. Whooping follows a bimodal distribution trend with a greater morning peak and a lesser afternoon peak (POIRIER, 1967; Fig. 5). More subtly it shows a fluctuation whereby there is a greater probability that whoops will occur at specific peak times than at times preceding or following these peaks periods. Additionally, there is a decaying of the whooping display as designated by the first three morning peaks at 6:45, 7:45, and 8:30 descending in frequency in the order mentioned (Fig. 6).

DISCUSSION

How do these ideas of whooping fit in with the biology of the troop or the species? Generally, activity in primates has been described as bimodal with a peak of feeding in the morning and a peak in the afternoon with a major rest period in midday. Most of these activity profiles have been determined by lumping troops or ad lib sampling. (ALTMANN, 1959; SCHALLER, 1963; RIPLEY, 1965; POIRIER, 1967; YOSHIBA, 1967; VAN LAWICK-GOODALL, 1968; CHIVERS, 1969; RIPLEY, 1970; ALTMAN & ALTMAN, 1970; MACKINNON, 1974). BECK and TUTTLE (1972) have confirmed this profile in the common langur by taking a different measure of activity (frequency of common langurs at a waterhole) and have shown that this measure of activity fits the same general pattern as other scientists have found in the common langur. POIRIER's (1967) data on the Nilgiri langur conforms quite well with the common langur's bimodal curve.

Is this then how a troop of monkeys acts, by feeding in two major activity periods

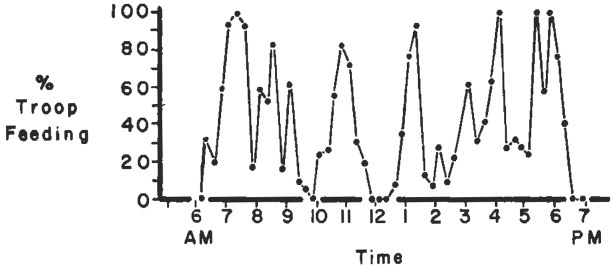

Fig. 11. The percentage of troop members feeding for one complete day in the life of troop 2.

and resting at noon? Eighteen complete days of recording feeding activity in three troops of Nilgiri langurs show that each troop actually feeds in from four to seven small feeding periods with rests and moves interspersed between the feeding periods throughout the complete day. Figure 11 shows a selected sample from troop 2 on January 26, 1974. Similar observations have been made by HUNT-CURTIN (in prep.) on Spectacled langurs and by YOSHIBA (1967) on common langurs. However, when the six days of Troop 2 and 3 in 1974 are lumped, a similar masking effect occurs resulting in a bimodal curve similar to the gross activity curves in the common and Nilgiri langurs (Fig. 12). The interactions of these and other behaviors will be discussed at length in another paper.

What is the relevance of these subtleties to the biological processes involved? The plotting of gross trends tells the scientist the direction a behavior is taking over time but it may fail to show what are the subtle but very important fluctuations which the individual is pursuing and reacting to. One important example is in development of behavior. Most researchers studying ontogeny have lumped all infants in their studies to produce a species trend which shows a general decrease in mother-infant contact as an infant develops. However, data on 15 species of primates and four species of non-primate mammals show that regressive periods of closermo ther-infant contact occur at certain periods within each infant's life which occur at the same relative time in accordance with the species age scale, although there is considerable individual difference within a species (HORWICH, 1974). This error in describing

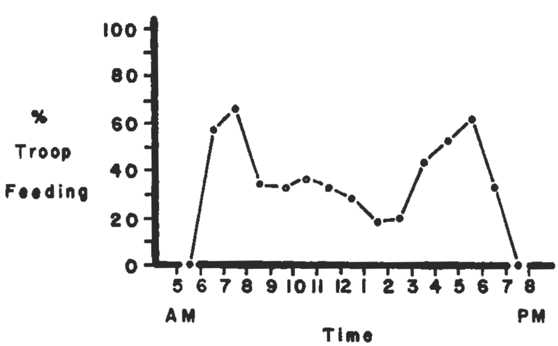

Fig. 12. The percentage of troop members feeding for each hour in the day. This graph is a compilation of three days from troop 2 (including Fig. 11) and three days from troop 3.

baseline developmental trends could lead to serious mistakes in experimental work. For example, if certain experimental groups in ontogenetic studies are picked which conform to high and low periods in a cycle, then the conclusions drawn from the experiments may be entirely a result of the ontogenetic trends rather than the experimental factors.

The main point to be made can be summed up as follows: life processes, of which behaviors are a final product are extremely complex, and as more answers are sought to questions about life, we must adopt more ways of investigating these processes and we must increasingly look for more subtleties. One way to do it is to approach behavioral studies from a holistic point of view such as studying species at the individual level and attempting to exhaust the possibilities in examining patterns or in attempting to see the interactions of many behaviors in the individual. There are already some scientists who have been doing this and made some progress. NELSON's (1974) analysis of individual patterns of bird song and GOLANI's (1973) frame by frame analysis of jackel movements are examples of this.

Acknowledgements. I wish to thank the Kerala Forest Department and the Chief Conservator of Forests for the permission to use Periyar Sanctuary for my study. I also thank Mr. JAMES VARGHESE and Mr. NANNU NAIR, Wildlife Officers in 1968 and 1974 for their encouragement and help during my study. I am grateful to LINDA LERESCHE for the criticism of the manuscript and to MARY NICHOLS for typing it. Thanks also go to JOHN LINNEMEIER and BOB and ANDREA SNOYINK for their help and use of their tape recorder. The 1968 phase of the study was done with the encouragement of Dr. HELMUT K. BUECHNER, under the auspices of the Office of Ecology, Smithsonian Institution. The 1974 work was done while employed by The Chicago Zoological Society with the aid of a grant from The Institute of Micro-ontogenetic Ethology and Macro-cosmological Ecology.

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—Received *March 24, 1975*; Accepted *May 24, 1975*

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