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DIURNAL RHYTHMS IN THE VOCALIZATIONS OF BUDGERIGARS

ROBERT FERRELL

AND

LUIS F. BAPTISTA

Photoperiod is an important stimulus of gonadal growth in Budgerigars (*Melopsittacus undulatus*; Pohl-Apel and Sossinka 1975, Shellswell et al. 1975). However, actual breeding activity in these parrots and other avian inhabitants of the xeric Australian hinterland is triggered by rainfall or the lush vegetation that follows (Immelmann 1971, Pohl-Apel 1980). In some species, e.g., the Ring Dove (*Streptopelia "risoria"*; Lott et al. 1967), Budgerigar (Brockway 1969), and Canary (*Serinus canaria*; Kroodsma 1976), vocalizations may act synergistically with photoperiod to accelerate ovarian growth.

The pituitary exhibits a daily rhythm of sensitivity to light in two temperate species (Farner 1965, Meier 1973), and tropical Budgerigars also exhibit a circadian sensitivity to light (Shellswell et al. 1975). Budgerigars show an additional diurnal sensitivity to recorded conspecific vocalizations (Gosney and Hinde 1976), but the "song"-sensitive rhythm is not in phase with the light-sensitive rhythm. Budgerigars are sensitive to light about 12 h after dawn, but sensitive to song sometime during the first seven hours of the morning. Gosney and Hinde (1976:410) stated that little is known about diurnal variations in male Budgerigar vocalizations, but that a morning peak is common for the song of many passerines. They added that if this were true for the Budgerigar, it might well be adaptive for females to exhibit a sensitivity to song in the morning when males were most likely to be singing. Although diurnal rhythms in vocal behavior are known in passerines (Armstrong 1963, Holmes and Dirks 1978), we are aware of no detailed study in nonpasserines. We document herein diurnal rhythms in the warbling behavior of Budgerigars and discuss its biological significance.

Two mated pairs of Budgerigars were placed in an anechoic chamber measuring 50 × 50 × 75 cm on the inside. Two fluorescent lamps provided an L:D of 14:10, and a fan circulated fresh air into the chamber. Feeding time was varied from day to day to prevent possible entrainment on stimuli other than photoperiod. The chamber was fitted with a Shure Cardioid Uni-Directional Dynamic microphone whose signal was channeled through a threshold limiter and a band pass filter attenuated to the frequencies approximating those of the birds' vocalizations (1.0–4.0 kHz). A pre-amplifier provided about a 50 dB gain so that the fidelity of weak AC signals from the microphone would be preserved on their way to a main amplifier. Sound signals (vocalizations) triggered responses in an Esterline Angus chart event recorder. The detailed schematics of our apparatus are available.

Brockway (1969) catalogued 10 types of vocal behavior in the Budgerigar. Two of these types, the loud and soft warbles, are used in courtship and are thus functionally equivalent to the passerine song. Warbling is performed by both sexes, but males warble much more and longer than females. We observed, as did Brockway (1969:145), that males of isolated pairs performed virtually no warbling. Single pairs rarely breed if isolated from others. The sight and sounds of other conspecifics stimulate courtship activity, which in turn is correlated with gonadal activity. Copious warbling activity ensued only when we put *two* pairs of birds in our chamber.

Data were recorded over an 18-day period, from 9 March to 27 March 1979. Mean numbers of vocalization bouts are summarized in Figure 1. A vocalization bout is here defined as the smallest discernible period during which birds were vocalizing and thus producing a mark on the chart. Each bout could last from less than a second to several minutes. A bimodal, diurnal rhythmicity in vocalizing is evident, with one peak in the morning and a smaller one in the evening. Vocalizations were few (mean of 0.06 to 0.38 bouts) between 22:00 and 07:00 when the lights were off. A significant rise in number of vocalizations followed the onset of light at 07:00 (from a mean of 0.22 to 6.06).

These data do not distinguish between warble and other (non-courtship) vocalizations. We therefore quantified the duration of continuous bouts of vocalizing as recorded on the chart (Table 1). Short clicks were eliminated from this analysis as representing mostly social calls. By occasionally monitoring vocalizations through a loudspeaker we satisfied ourselves that most of the vocalizations in the continuous records were indeed courtship warbles. Birds began warbling as soon as lights came on. The first bouts of the day ranged in duration from 40 to 220 min ($\bar{x}$ = 129 ± 49.9 SD). This was followed by 20 to 80 min of silence ($\bar{x}$ = 32 ± 19.89 SD), and then a second period of warbling lasting 10 to 30 min ($\bar{x}$ = 21 ± 7.0 SD). This was followed by a third and sometimes a fourth bout. However, after day 4 of the experiment, only two bouts of warbling were recorded in the morning (Table 1). A long silence ensued, followed by a period of warbling beginning about 16:30. Periods of afternoon (12:00 to 16:30) warbling grew gradually fewer and disappeared entirely after day 7 of our experiment. Warbling during the early evening (16:00–20:00) disappeared entirely after day 5. Only the long morning bouts and a relatively short bout after lights out lasting 10 to 70 min ($\bar{x}$ = 35 ± 19.83) persisted throughout the experiment. The gradual disappearance of warbling activity during the afternoon and early evening (Table 1) may be due to the birds gradually entraining to the L:D 14:10 light regime. After lights out most of the vocalizations heard through the speaker were social calls rather than warbles. Intense warbling was thus restricted to one or two hours in the early morning.

These data do not permit us to isolate the relative contribution of each individual bird to the total amount of warbling. Although crude, our data are biologically sig-

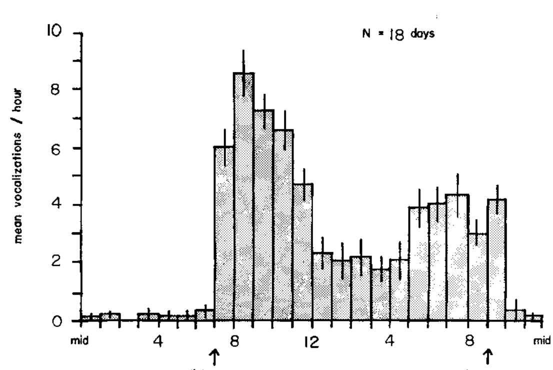

FIGURE 1. Diurnal rhythms in vocal behavior in the Budgerigar. Each vertical bar represents mean number of vocal bouts at that particular hour, with two standard errors above and below the mean represented by the short vertical line. These data include all types of vocalizations.

TABLE 1. Duration of warbling bouts (minutes).

Day of experiment	Morning 07:00–12:00				Afternoon 12:00–16:30			Evening 16:30–21:00			Night 21:00–22:00
1	70[a]	10	10	20				20	10		10
2	160	20	40		30	80	30	20	80	50	10
3	40	20	20		10			40	60	30	40
4	90	20	20		20			40			30
5	130	30			20			30			70
6	140	30			20						30
7	180	20			40						20
8	130	30									40
9	130	10									30
10	220	20									—[b]
$\bar{x}$	129	21	9	20	14	80	30	15	15	40	35
±SD	±49.9	±7.0	—	—	—	—	—	—	—	—	±19.8

[a] Reading from left to right, durations of single continuous warbling bouts are listed consecutively as they occurred within each time block. Note period of afternoon quiescence after day 7. Values in minutes rounded off to nearest 10.
[b] Bouts of vocalizing were too sporadic during this period to qualify as "continuous" on this day.

nificant since it is warbling activity of the colony and not the individual that stimulates gonadal recrudescence (Brockway 1969).

In summary, as predicted by Gosney and Hinde (1976), most warbling activity is confined to the early morning. A small amount occurs after lights out, so that the distribution of warbling activity through the day could be considered bimodal as has been reported for song of some passerines (Armstrong 1963). Reports of field investigators indicate that activity of Budgerigars in the wild is also bimodal in distribution. Forshaw (1969) and Wyndham (1980) noted much flying and intense foraging in the morning followed by a long period of quiescence. Immelmann (1972) cited the 19th century naturalist John Gould, who reported that Budgerigars were inactive for hours at a time, remaining almost motionless during the hotter hours of the day, probably a method of reducing evaporative water loss in their xeric environment. Birds become active again in the evening. It is noteworthy that the quiescent afternoon period is retained in the more "favorable" conditions of the laboratory.

The long morning bouts of warbling activity correspond to the diurnal rhythm of sensitivity of the Budgerigar pituitary: the two diurnal periodicities must have evolved in parallel. Perhaps the first two hours after lights come on, the period of peak vocal activity, may correspond to the period of maximum sensitivity of the Budgerigar pituitary.

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Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, Texas 77843. Address of second author (reprint requests): Department of Ornithology and Mammalogy, California Academy of Sciences, San Francisco, California 94118. Accepted for publication 29 July 1981.