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# Photoperiodism in House Sparrows: Testing for Induction with Nonphotic Zeitgebers

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### Abstract

In birds, as in other animals, the mechanism for photoperiodic time measurement is based on circadian rbythmicity. In models of this mechanism, the entrainment of circadian rbythms is a key feature. One can therefore ask whether any synchronizing agent (zeitgeber) that can entrain circadian rhythms could also induce photoperiodic responses. We addressed this question using known nonphotic circadian zeitgebers (playbacks of conspecific vocalizations, and nonspecific acoustic disturbance) in house sparrows. We subjected photosensitive male sparrows to stimulatory photoperiods (2L:10D:2L:10D and 12.5L:11.5D) and to similar "phonoperiods" in which part or all of the light of the photoperiods was replaced by a combination of conspecific vocalization playbacks and nonspecific acoustic disturbance. Direct observation with an infrared visionscope revealed that almost all birds remained alert during the sound presentation. Their circadian rbythms were also entrained to the sound. However, whereas sparrows exposed to stimulatory photoperiods experienced testicular growth (from 6 mg to 311 mg), sparrows exposed to the corresponding phonoperiods did not. These results suggest that nonphotic zeitgebers cannot mimic the photoperiodic effect of light. Conceivably, however, photoperiodic-like effects might still be obtained with stronger nonphotic zeitgebers, as yet undiscovered in birds, or with nonphotic zeitgebers whose action would reveal itself only when the zeitgebers occurred at circadian phases other than those at which light is effective.

# Introduction

In many bird species, the timing of reproduction is photoperiodically controlled. Gonadal recrudescence takes place only when day length exceeds a certain threshold. Birds are therefore able to measure day length, and for this they use a mechanism, or photoperiodic clock, located in the brain.

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Although its exact location is uncertain (but see Simpson and Follett 1981), many properties of this clock are well known. One such property is that photoperiodic time measurement is based on circadian rhythmicity (for reviews, see Follett 1973; Hoffmann 1981).

Two models exist to explain how circadian rhythmicity is involved in photoperiodism. In the *external coincidence* model (Bunning 1960; Pittendrigh 1966), a circadian rhythm of photosensitivity comprising both an insensitive and a sensitive phase is entrained by the daily light-dark (LD) cycle. The phase relationship is such that during most of the daytime, light coincides with the insensitive period, but when days are long some of the light may also coincide with the sensitive period, leading to photoinduction (gonad growth). In the *internal coincidence* model (Pittendrigh 1972), two undefined circadian rhythms are entrained, one by light onset and the other by light offset. Photoinduction depends on the phase relationship between these two rhythms, and only when days are long is this phase relationship stimulatory.

Entrainment is an important circadian feature of both models. For this reason, it has been asked whether entraining agents other than light could induce photoperiodic responses (Follett 1973). There is some evidence in the literature that nonphotic factors given at specific circadian times can lead to photoperiodic-like responses. For example, conspecific vocalizations and radio sound broadcast in the middle of the night caused gonad growth in Japanese quail (Guyomarc'h and Guyomarc'h 1982; Millam, El Halawani, and Burke 1985), and handling at dawn and dusk produced testicular regression in house sparrows (Meier and Dusseau 1973). It is not known, however, whether the nonphotic factors in these experiments could also entrain circadian rhythms. To our knowledge, no nonphotic agents known to entrain circadian rhythms in birds have been tested for photoperiodic effects.

It has recently been shown that both 2-h playbacks of conspecific vocalizations and 1.5-h bouts of periodic rattling sound (running one's fingernail along the side of the cages at 12–15-min intervals) can entrain the circadian activity rhythms of house sparrows, *Passer domesticus* (Reebs 1989). Those experiments took place in constant darkness (DD), and therefore the effects were truly nonphotic. Yet, despite being nonphotic, the two acoustic stimuli qualitatively mimicked light, in that phase advances and entrainment by phase advances were obtained when the stimuli coincided with the late subjective night (Eskin 1971; Reebs 1989). We therefore asked whether these two stimuli could also mimic the effects of light on the sparrow's photoperiodic system. House sparrows are ideal subjects for such an investigation; they have been used in many demonstrations of circadian involvement in photoperiodism (Menaker 1965; Menaker and Eskin 1967; Murton, Lofts, and Orr 1970; Farner et al. 1977). Here we report on two experiments in which we replaced the light portion of stimulatory photoperiods with a combination of conspecific vocalizations and rattling sound and looked for a possible effect of the resulting "phonoperiod" on gonad growth in house sparrows.

# **Experiment 1**

### Material and Methods

Forty male house sparrows were mist netted in Toronto in late December 1987 and early January 1988. Day length (sunrise-sunset) was 8.9-9.2 h. The birds were not in reproductive condition; the average combined (left and right) testis weight of six males killed at this time was only 6.3 mg. After capture, the sparrows were brought to the laboratory and kept in individual cages ( $24 \times 35 \times 43$  cm) with free access to food (Purina Start and Grow), water, and a birdbath.

As they came in, the birds were randomly assigned to four different groups, each group being housed in a separate room. The first group (long photoperiod, n = 8) was kept in an 8L:16D regime until January 19. Then, during the next 8 d, light offset was gradually delayed until the photoperiod reached 12 h. At this point (January 27), the lighting regime was switched to 2L:8D:2L:12D. The first (or dawn) L of this skeleton photoperiod started at the same clock time as the previous full L. In the next 4 d, the second (or dusk) L was gradually delayed until, on February 1, the photoperiod was 2L:10D:2L:10D. This long skeleton photoperiod (fig. 1) was maintained for 50 d, at which point the birds were killed and their testes removed and weighed.

The second group (long phonoperiod, n = 11) was at first housed under an 8L:16D regime. Every day, they received two 2-h sound pulses (see below), one at dawn starting 10 min before light onset, and one at dusk ending 10 min before light offset. On January 18, the light bulbs in the room were removed and the birds were left in DD. The sound pulses remained, but every day the dusk pulse was delayed until, on February 1, the sound regime was the same as the light regime in the long photoperiod group (2:10:2:10). The birds were left in those conditions (fig. 1) for 50 d. The sound pulses were then discontinued, and the birds remained in DD for an additional 2 d, after which they were killed and their testes removed and weighed.

The sound consisted of a continuous playback of sparrow vocalizations recorded from wild flocks on the morning of June 15, 1986, and in the afternoon of January 4, 1988. In addition, during each 2-h playback an experimenter entered the room at 12–15-min intervals and observed the birds with an FJW infrared visionscope (infrared light is not photoperiodically stimula-



Fig. 1. Timing of the light and sound given to each group of house sparrows in the last 50 d (experiment 1) or 42 d (experiment 2) of the study. See text for details of the conditions that preceded this schedule.

tory, at least in starlings [Burger 1943] and ducks [Benoit and Ott 1944]). The observer noted whether any bird tended to sleep in spite of the playback. Before leaving the room, the observer also ran a fingernail five or six times along the side of each cage. Therefore, during a sound pulse, the sparrows experienced simultaneously both types of acoustic stimuli (playback and rattling sound) which had previously been used to entrain circadian rhythms in this species.

To confirm that entrainment had occurred, the activity of 10 birds in this group (and of 10 birds in the other phonoperiod group; see below) was monitored with hopping perches connected to an Esterline-Angus recorder located outside the room. In the case of the skeleton photoperiod group, entrainment was assumed to have taken place (see Takahashi and Menaker 1982).

Two control groups (short photoperiod, n = 10; short phonoperiod, n = 11) were treated as above, except that the photo/phonoperiod was 2:4: 2:16 from January 17 on (fig. 1).

Throughout the experiment, all birds within a room were visually, but not acoustically, isolated from each other. Temperature varied between 19° and 24°C. Light, when present, was 200–300 lx (measured by Gossen Profisix light meter) at perch level. Sound level from the playbacks was about 75 dB (Realistic sound-level meter) in the middle of the room. Cage maintenance



Fig. 2. Actograms (perch bopping) of bouse sparrows kept in DD (from day 0) and subjected to skeleton phonoperiods. Each borizontal line represents a 24-b day, with successive days below. Deflections on the lines (darkened with a pen on the original boards to assist photography) show perch bops. Boxes show time of sound. Changes in phase relationship between activity onset and "dawn" sound pulse may reflect changes in endogenous free-running periods, which often evolve from < 24 b to > 24 b in sparrows left in DD (Eskin 1971).

took place once a week, and was done when either light or sound was present. The infrared visionscope was used for cage maintenance in DD.

#### Results

In the phonoperiod groups, some sparrows sometimes slept (eyes closed, or bill tucked under scapular feathers) during the sound pulses, but this was rare. The birds remained awake (both eyes open) during most of the sound pulses. In the long phonoperiod group, 8 of 10 sparrows whose activity was recorded were entrained to the sound (fig. 2a, 2b); that is, the period of their activity rhythms was 24 h rather than a period different from 24 h, as is usually displayed by free-running sparrows in DD (Eskin 1971; Reebs 1989). The other two sparrows were entrained at first, but 12–14 d before the end of the experiment their rhythms broke away from the zeitgeber and free-ran with a period > 24 h (fig. 2c). In the short phonoperiod group, 8 of 10 sparrows were entrained (fig. 2d). Of the other two birds, one appeared arrhythmic, and one free-ran with a period < 24 h. These observations confirmed that the acoustic treatment affected the circadian systems of most sparrows.

As expected, gonads at the end of the experiment were large in those birds exposed to a long photoperiod, and in general small in those birds exposed either to a short photoperiod or to a short phonoperiod (fig. 3). In the critical group (long phonoperiod), testes were in general small at the end of the experiment (fig. 3). A Kruskal-Wallis test followed by multiple comparison (Conover 1980) showed that the only significant differences were between the long photoperiod group on one hand, and each of the



Fig. 3. Combined (left and right) testis weight of house sparrows after 50 d exposure to various skeleton photo- and phonoperiods (see experiment 1 in fig. 1). Horizontal bars show medians.

other three groups on the other hand (T = 14.74, P < 0.005; P < 0.05 for the multiple comparison test). Skeleton phonoperiods, therefore, apparently cannot mimic the stimulatory effects of skeleton photoperiods on the photoperiodic system of sparrows.

# **Experiment 2**

## Material and Methods

Twenty-five male house sparrows were mist netted in late November and early December 1988. Day length (sunrise–sunset) varied between 9.2 and 9.4 h. All birds had yellowy or light gray beaks and therefore did not appear to be in reproductive condition. However, they were past their normal refractory period, which in this species ends in mid-November (Riley 1936). After capture, the sparrows were brought into the laboratory and put in individual cages under a 9.5L:14.5D regime. As they arrived, the birds were assigned to three groups, each group being kept in a separate room.

The experiment proper started on December 5, 1988. On that day, one group (long photoperiod, n = 8) had its photoperiod extended by 3 h in the

morning to yield a 12.5L:11.5D regime (fig. 1). The second group (short photoperiod and sound at night, n = 9) remained in a 9.5L:14.5D regime but received sound in the last 3 h of the night (fig. 1). The third group (short photoperiod and sound during the day, n = 8) also remained in a 9.5L:14.5D regime and received 3 h of sound, but this sound was given in the first 3 h of the day (fig. 1). The treatment lasted for 42 d, after which the birds were killed and their testes removed and weighed.

Birds within the same room were not visually or acoustically isolated from each other. For the second group (sound during the night), the acoustical treatment was the same as in experiment 1 (playbacks, rattling sound, and concurrent behavioral observations with the infrared visionscope). For the third group (sound during the day), only playbacks were used because the sparrows became too alarmed when they could see people entering the room. The sound level from the playbacks was about 75 dB in the middle of the room. Light intensity during the day was 100–150 lx at perch level.

### Results

Of the nine sparrows in the second group (sound during the night), one was found to be almost always asleep during the playbacks (although it was woken up each time its cage was rattled), three showed occasional signs of sleepiness (e.g., closing one eye), while the remaining five appeared continuously awake and alert.

As expected, sparrows in the long photoperiod had large testes at the end of the experiment, while birds experiencing sound during the short photoperiod had small testes (fig. 4). The critical group (short photoperiod and sound during the night) also had small testes at the end of the experiment (fig. 4). A Kruskal-Wallis test followed by multiple comparison (Conover 1980) confirmed that the only significant differences were between the long photoperiod group on one hand, and each of the other two groups on the other hand (T = 14.30, P < 0.001; P < 0.05 for multiple comparison). Therefore, 3 h of sound before the L portion of a 9.5L:14.5D cycle did not simulate the photoperiodic effects of 3 h of light given at the same time.

# Discussion

It has been known for some time that nonphotic factors such as sound can entrain the circadian activity rhythms of birds (Gwinner 1966; Menaker and Eskin 1966; Lohmann and Enright 1967). That this effect of sound is truly nonphotic has been demonstrated recently with house sparrows kept in DD (Reebs 1989). The entrainment we observed in our experiment 1 (in DD)



confirmed these previous findings. However, in spite of this circadian effect, no photoperiodic influence of sound was detected in either experiment 1 or experiment 2. The conclusion must be that sound, even when capable of entraining circadian activity rhythms, cannot imitate the effect of light on the photoperiodic system.

The idea of nonphotic influence on the photoperiodic clock is not new. Soon after discovering photoperiodism in vertebrates, Rowan (1929, 1938) proposed that light might act on the photoperiodic system of birds by increasing their daily activity time—an essentially nonphotic characteristic. This hypothesis was later falsified in studies where mechanical devices (Riley 1940; Kendeigh 1941), sound (Thornton and Cummings 1945), and temperature (Farner and Mewaldt 1955) were used to artificially increase wakefulness without any photoperiodic-like effects. Inasmuch as our combined acoustic stimuli also interfered with sleep, our results confirm that increased wakefulness is not involved in the day-length-measuring mechanism. Our experiment 2, moreover, provides additional information. In all of the previous studies for which its timing could be determined, enforced wakefulness took place after a short day. Yet, within the framework of the external coincidence hypothesis (see Introduction), one can conceive that entrainment of the photosensitive rhythm is caused by light onset (see Menaker and Eskin 1967; Follett 1981) and that it therefore takes place at the beginning of the day. To test for similar entrainment by extra wakefulness, the sleep-interrupting stimulus has to be given before dawn on a short day. This is what we did in experiment 2. That no photoperiodic response was secured with this treatment confirms that sleep interruption is not an element of the photoperiodic system, even when it takes place immediately before light.

Although when considered on a group basis sparrows exposed to sound remained reproductively quiescent, some individuals within these groups had relatively large gonads by the end of the experiment. In our first experiment in particular, five birds from the short photoperiod and short phonoperiod groups had gonads > 200 mg. The responsiveness of some individuals to treatments that are normally nonstimulatory is a puzzling phenomenon that has been observed in many other studies (e.g., Middleton 1965; Menaker and Eskin 1967; Murton et al. 1970) and especially in house sparrows (Middleton 1965; Farner et al. 1977). The reasons for it are unknown. In our experiment 1, the five birds with gonads > 200 mg in the nonstimulatory treatments were also the heaviest individuals of their respective groups (28-29 g vs. 23-28 g in the other birds). However, these few responders did not appear to differ from the other birds in other respects, including their propensity to become entrained, the length of their activity period on the last day of the experiment, or the site of their capture. This remains true even when birds with gonad weights between 100 and 200 mg are added to the responder category. It is interesting to note, however, that exceptional responders did not appear in experiment 2. Birds in experiment 2 were captured and studied slightly earlier in the season (November-December) than those in experiment 1 (December-January). Middleton (1965) has shown that exceptional responses under nonstimulatory photoperiods are more likely to occur after long periods of exposure. Perhaps long exposure to unnatural conditions upsets the photoperiodic system, or permits the expression of an as-yet-undiscovered endogenous program. Whatever the explanation, the presence of a few exceptional birds with large gonads does not affect our conclusion that in general phonoperiodic treatments do not substitute for equivalent photoperiodic schedules.

Failing to obtain gonadal responses with acoustic factors known or suspected to entrain circadian rhythms does not constitute a refutation of circadian involvement in photoperiodism, or of the models depicting this involvement. There are several explanations that could account for the lack of effect of sound and still be consistent with the concept of circadian-based photoperiodism.

First, it is possible that only light could entrain the relevant rhythms. Because in birds the pacemaker for circadian activity rhythms and the mechanism for day-length measurement have not been proved to be the same (Follett 1982; Saiovici, Nicholls, and Follett 1987), one cannot assume that an agent affecting one will necessarily affect the other. Certainly our results seem to speak against such a commonality of effect.

Second, it is possible that acoustic or other nonphotic factors can entrain the relevant rhythms, but only if they are strong enough. In the circadian realm, acoustic zeitgebers do not always entrain the activity rhythms of all individuals (Menaker and Eskin 1966; Lohmann and Enright 1967; Reebs 1989; our experiment 1). This means that acoustic zeitgebers are weaker than light. This weakness may also operate in the photoperiodic realm, translating into a failure to entrain the appropriate rhythms. According to this view, only nonphotic circadian zeitgebers as strong as light could have photoperiodic effects. Such nonphotic factors have not been found in birds yet.

A third possible explanation for the lack of photoperiodic-like effects of acoustic zeitgebers is that, although sound may be able to entrain a rhythm of photosensitivity, light still has to be present for direct induction (external coincidence model). Once present, light may have incidental entraining effects with which sound cannot compete. For example, in our experiment 2, the critical group received sound 3 h before light onset. Every day, the rhythm of photosensitivity may have been phase shifted one way by sound onset, only to be phase shifted back by the light onset that occurred 3 h later. As a result, the last light of the day (9.5 h later) would not have coincided with the sensitive phase. The conclusion would be that sound cannot compete with light in entraining rhythms of photosensitivity. (See Saiovici et al. [1987] for an example of how powerful light is in providing dawn signals that generate photoinducible phases in quail.)

Fourth, it may be that acoustic stimuli can entrain the relevant rhythms, but at a phase completely different from that observed when light is the zeitgeber. Meier and Dusseau (1973) reported that house sparrows experienced testicular regression when handled by humans at the beginning or end of a long day. On the basis of this finding, Meier and Dusseau (1973) developed a model in which two photosensitive rhythms could be differentially driven by adrenal corticoid–releasing (stressful) events such as handling. Only when the stressful events were in the middle of the day or the middle of the night would the sensitive phases of both rhythms coincide with the light of a long day, leading to photoinduction. Unfortunately, this model was based on a finding that could not be repeated in other species, such as the white-throated sparrow (Meier and Dusseau 1973) and the Japanese quail (Meier et al. 1973).

Other researchers have had more success in influencing reproductive states with nonphotic factors in Japanese quail. However, these results are also controversial. In a study with female Japanese quail kept under an 8L:16D regime, 4-h playbacks of male crowing given in the middle of the night caused a significant increase in ovary weight (from 65 mg to 100 mg), but not in oviduct and uterus weight (Guyomarc'h and Guyomarc'h 1982). In male Japanese quail, 3 h of radio sound starting 6 h prior to the light onset of a 9L:15D cycle caused a significant increase in testis weight, as compared to that of males that experienced the sound either 3 h prior to or concurrent with light onset (Millam et al. 1985). This latter experiment lasted a long time (63 d), and in many birds the sound caused increased activity in the middle of the night. However, the actual change in gonad weight was small: individual gonad weight was about 20 mg on average for the unresponsive groups, and about 31 mg for the responsive group (see fig. 2 in Millam et al. [1985]). Such a small difference, albeit statistically significant, is probably not biologically meaningful. At the very least, it is not typical of a photoperiodic response. Photoperiodically stimulated house sparrows, for example, commonly experience individual gonad growth from 2 mg to 200 mg (Meier and Dusseau 1973; this study).

In the wild, nonphotic factors such as weather, presence of a mate, and food have modulatory effects on the expression of photoperiodic responses, especially in females (see, e.g., Farner 1964; Morton 1978; Wingfield 1985). For example, the rate of growth, rather than its induction threshold, is faster when conspecific song is present (Morton, Pereyra, and Baptista 1985). However, gonad growth in anticipation of breeding still seems to be triggered by light only. Our results suggest that nonphotic factors cannot mimic the photoperiodic influence of light, even when those nonphotic factors are effective circadian zeitgebers. Our results also confirm that this effect of light is not mediated by the nonphotic characteristic of extra wakefulness. In birds, photoperiodic responses are aptly named since, in practice, light remains the only physical factor known to induce them.

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