Role of social stimuli in the photoperiodic induction

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Abstract

Two experiments were performed to study of the effects of social interaction on photoperiodic induction in house sparrows. In the first experiment, short-day pretreated birds were exposed to stimulatory long day lengths (16L: 8D) for 4 weeks. The first set had a group of male and female birds kept individually in cages so that they could not see to each other. The second was similar to the first but the cages were separated by a transparent partition so that birds could see each other. In third four male and four female were kept together in the same cage. The second experiment differed from the experiment 1 in the sense that it housed individual birds and also included another variable, the noise. Birds were disturbed by the sound of a ringing bell for 15 minutes at three times of the day, ZT4, ZT8 and ZT12. Observations on body mass and gonad size were made at the beginning and end of the experiment. The pairing in the environment appears to affect the gonadal growth in females but not in males.

Keywords: *Social stimuli, Day length, Gonadal growth, Body mass, Zeitgeber time*

Introduction

The daily photoperiod has been widely investigated as the most potent 'primary timer' (Immelmann, 1971) or 'the initial predictive information' (Wingfield, 1983), which brings birds in a state of breeding readiness so that the actual reproductive effort could begin. This could be because the photoperiod can easily be manipulated and studied experimentally. Other social and environmental factors might also potentially affect the timing of actual reproduction. For instance, female birds do not respond to photoperiod as dramatically as males do, suggesting the importance of factors other than photoperiod contributing to the successful reproduction. It is evidenced that behavioral interactions act as strong force in regulating the timing of nesting in individual birds. Reciprocal interaction provides a secondary stimulus in female canaries: a female–male, but not female–female, pairing leads to quick gonadal growth and intense nesting activity (Hinde and Steel, 1978). Successful reproductive behaviors associated with male-male competition and courtship, as well as the production of gametes. By using predictive cues, such as photoperiod, to stimulate gonadal recrudescence, individuals can coordinate the physiological, behavioral, and neural changes necessary for the timely expression of reproductive behavior (Wingfield, 1983). Social attachment between mating partners is widely distributed among vertebrates. Reproductive pairing is most prevalent in birds, which may pair for the breeding seasons or longer. House sparrow is a social species. However, the underlying physiological mechanisms that mediate pair formation and maintenance are unknown in any bird species.

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Social interactions have been shown to influence sex steroids, neurobiology (Francis *et al*., 1993; Hartman and Crews, 1996; Tramontin *et al*., 1999), and reproductive physiology (Brzoska and Obert, 1980; Delville, *et al*., 1984; Cheng, 1986; McComb, 1987; Gudermuth, *et al*., 1992; Rissman, 1992).

Circadian and seasonal rhythms are dependent on environmental temporal cues, or zeitgebers, for steady entrainment to a 24-h cycle. Although the most ubiquitous zeitgeber is photoperiod, a number of nonphotic stimuli have been found to influence circadian rhythms by resetting the circadian clock, entraining rhythms, or facilitating re-entrainment following phase shifts of the light cycle, such as those experienced with transmeridian jet travel (Mrosovsky *et al*., 1989; Turek, 1989; Antle and Mistlberger, 2000; Aschoff *et al*., 1971; Goel and Lee, 1995a, 1995b; Amir and Stewart, 1996). Social influences on circadian timing might function to tightly organize the social group, thereby decreasing the chances of predation and increasing the likelihood of mating Governale and Lee (2001) routed odors from a housing unit containing entrained donor animals to a box containing phase-shifting animals. Recovery from the phase shift was equivalent to earlier experiments housing the donor in the same cage as the shifting animal. It is unclear whether male's apparent inability to accelerate re-entrainment when exposed to social cues is due to an absolute incapacity for social cue responsiveness or a decreased sensitivity to olfactory social cues relative to females. For some species, social cues can serve to synchronize circadian rhythms in the absence of other time cues or to amplify ambiguous light cues. This has been demonstrated to various degrees in fruit flies, fish, birds, bats and humans; however, studies in rats and hamsters have shown that social cues are less salient time cues for these species. Songbirds highlight the powerful influence of social cues on motor production during learning more generally, and reveal that motor output during learning may underestimate the actual progress of competency (Kojima and Doupe, 2010). Birdsong is a complex learned vocal behavior developed by motor practice in early life, with many striking parallels to human speech (Brenowitz *et al*., 2010). Social influences on circadian timing might function to tightly organize the social group, thereby decreasing the chances of predation and increasing the likelihood of mating (Davidson and Menaker, 2003).

A large field of study in avian behavior is centered on the evolution and maintenance of different mating systems (Andersson, 1994). Although the distinction between monogamy and other mating systems in birds has blurred due to the discovery of extra-pair fertilizations found in presumed monogamous species (Mbller and Birkhead, 1992), general trends between mating pattern and certain behavioral repertoires remain. For example, polygamous systems often feature high levels of male–male aggression, and strongly monogamous species have high levels of paternal care (Ketterson and Nolan, 1994; Mbller and Birkhead, 1993; Schwagmeyer *et al*., 1999). The biological process addressed in this study is the control of seasonal reproduction in an adult subtropical avian species, the house sparrow by photoperiod.

In this study, we analyzed the effects of seasonal responses in the house sparrow birds of environmental disturbance. Birds exposed to stimulatory LD cycles were disturbed to assess the effect of disturbance on the physiological response. The other goal of this study was to address upon the question as to whether male-male or male-female interaction will influence the magnitude of photoperiodic response. In stimulatory LD cycles, birds were kept such that they could/ could not interact with the other individuals.

Materials and Method

Two experiments were performed on the adult male and female house sparrows (*Passer domesticus*) which were procured locally ($\sim 29^0$ N). They were then acclimatized to laboratory conditions for about 2 weeks.

Experiment 1: This experiment began in June 2004 to examine the effects of pairing of male and female (social interaction) birds. They were exposed to short day lengths (8L:16D) for 4 weeks ensuring their sensitivity to photoperiods before exposure to experimental long day lengths

(16L:8D). They were grouped in three sets. In the first set, a group (N = 4 each) of male and female birds were kept in separate cages in the same photoperiodic box but separated by a plywood partition so that they could not see each other. The second set had a group of male and female birds kept in separate cages in the same photoperiodic box but separated by a transparent partition so that they could see each other. In third set four males and four females were kept together in the same cage.

Experiment 2: This experiment began in December 2004, to determine the effects of disturbances on the seasonal responses. Birds exposed to stimulatory LD cycles were disturbed by noise to assess their physiological responses. At the beginning of the experiment, all birds had normal body weight and unstimulated testes and ovaries. This time birds were untreated with short days since at this time of the year they are found photosensitive. This experiment differed from the first experiment in being housed individually in the cage and in having experienced an additional cue, i.e. timed disturbance. Birds were exposed to stimulatory long day lengths (16L:8D) in three sets. In the first set, male and female birds were kept individually in cages that were separated by a plywood partition so that they could not see each other. The second set had male and female birds kept individually in cages but separated by a transparent partition so that they could see each other. In third set a male and a female were kept together in the same cage. In addition to this, birds were disturbed by sound of a ringing bell at three times of the day for 15 minutes at ZT 4, 8 and 12 (ZT0; zeitgeber time = time of light onset).

All experimental birds ere maintained under uniform husbandry conditions. Birds caged in groups of 4 wire-mesh cages (size-45 x 30 x 30 cm) were placed in the photoperiodic box (size- 75 x 70 x 60 cm); 2 cages were thus in one box. Birds under NDL were also similarly housed and kept in a room that received unrestricted environmental light and air from large windows. Food (seeds of kakuni, *Setaria italica* and paddy, *Oryza sativa*) and water were available *ad libitum,* and replenished once daily during daytime. Once every month, birds received in water glucose (Glucon-D, Heinz India Private Limited), vitamins (Vimeral, Glaxo-Smithkline Pharmaceutical Limited, Mumbai, India) and antibiotics (Tetracycline hydrochloride, Hoechst Roussel Vet. Ltd). Artificial light was provided by 14 watt fluorescent tubes (CFL) at an intensity of ~500 lux at the perch level, and the timing of light and dark was regulated by an automatic Muller electronic timer.

The photoperiodic effects, assessed as changes in body mass and testis volume or follicle diameter, were measured at the beginning (day 0) and end (day 30) of the experiment. Body mass was recorded using a top pan balance to an accuracy of 0.1g. The testicular growth was recorded by laparotomy performed under local anesthesia as per procedure described by Kumar *et al.*, 2001. Briefly, a small incision was made between last two ribs on the left flank, and the left testis was located within the abdominal cavity with the help of a spatula. The dimensions of the left testis were recorded and testis volume was calculated from $4/3\ \pi\ ab^2$, where a and b denote half of the long and short axis, respectively. In females, an ovarian follicle of a small or regressed ovary with indistinct follicles was scored as 0.1 mm in order to make the data statistically comparable. Data generated from experiments are presented as mean ± SE. They were further analyzed statistically to produce more meaningful results. One-way analysis of variance was employed to examine the effect of a photoperiodic treatment over a period of time. In these experiments, before and after means of the same group were compared using paired t-test. Significance was always taken at $P<0.05$.

Results and Discussion
Experiment 1: The mean body mass among the three groups of male and female birds was not significantly different (fig. 1a, c). Male birds of set 1, set 2, and set 3 showed a significant gain in testicular volume (day 0 vs day 30: $P<0.05$, paired t-test). Testes were not significantly different among the three groups of male birds ($F_{2,11}$ = 0.9268, P = 0.4246; 1-way ANOVA). Female birds of set 1, set 2, and set 3 showed a significant gain in

follicle diameter (day 0 vs. day 30: P < 0.05, paired t-test). The follicle diameter were not significantly different among the three groups of male birds ($F_{2,11} = 0.7143$, P = 0.5129; 1- way ANOVA).

Experiment 2: The mean body mass among the three groups of male and female birds was not significantly different (fig. 2a, c). Male birds of set 1, set 2, and set 3 showed a significant gain in testicular volume (day 0 vs. day 30: P< 0.05, paired t-test). Testes were not significantly different among the three groups of male birds ($F_{2,11}$ = 0.8690, P = 0.4518; 1-way ANOVA). The follicle diameter of set 3 birds was significantly greater than the set 1 and 2 birds ($F_{2,11}$=8.561, P= 0.0083; 1- way ANOVA).

Studies have shown that paternity rates (proportion of young fathered by the male parent) are relatively high in species where males make relatively large contributions to incubation and nestling care (Ketterson and Nolan, 1994; Mbller and Birkhead, 1993; Schwagmeyer *et al.*, 1999).

This correlation between mating system and male parental care can be further expanded by adding a third dimension, seasonal male testosterone (T) profile. Wingfield *et al.*, (1990) found that annual T peaks are short-lived in males of strongly monogamous and paternal species compared to the peaks in males of polygamous species. However, hormone data are rare for species that exhibit high levels of both paternity and male parental care. Male woodpeckers both incubate and feed nestlings at similar rates as females (Winkler *et al.*, 1995). Few data are available on extra-pair fertilizations (EPFs) in woodpecker species; however, existing studies have found very low frequencies of EPFs, even among the cooperatively breeding red-cockaded woodpecker (Picoides borealis; Haig *et al.*, 1994; Michalek, 1998). Acorn woodpeckers (*Melanerpes formicivorous*) also maintain genetic monogamy when nests are cared for by a single male-female pair (Dickinson *et al.*, 1995). In accord with these behavioral patterns, limited hormone data show that male woodpeckers have low circulating levels of T during breeding periods relative to species with greater extra-pair paternity and less male parental care (Khan *et al.*, 2001).
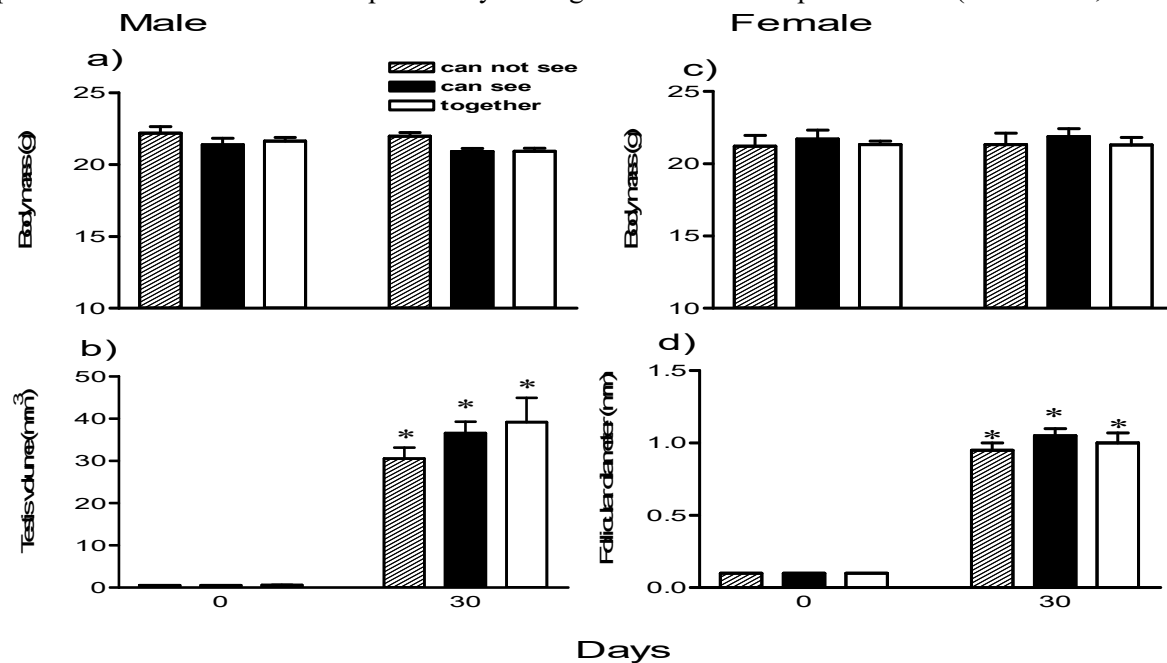

Figure 1. A group (n=4 each) of male or female birds were kept individually in cages separated by a plywood partition so that they could not see each other (Set 1) or kept individually in cages but separated by a transparent partition so that they could see each other (Set 2) or kept together in the same cage (Set 3). Each point symbol represents mean (± SEM) response in male (a, b; left panel) and female (c, d; right panel).

Wingfield *et al.*, (1990) classified species into three groups according to weather male showed low, moderate, or high levels of aggression during the breeding season. Males in species with low levels of aggression rarely interacted and tended to have high levels of parental care. They also had relatively low levels of T throughout the year. Males in species with moderate levels of aggression interacted frequently before the parental phase, but the frequency of interactions dropped after nestlings hatched. Those males, on average, showed seasonal T peaks approximately five times the breeding baseline levels. Wingfield *et al.*, 1990 and Hirschenhauser *et al.*, 2003 showed that males had a greater hormonal response to social challenges than males with different combinations of life history traits. Therefore, male house sparrows show a considerable increase in testis size in all groups. Wingfield (1994) showed that the sexes in sexually monomorphic species have similar T levels (Archawaranon *et al.*, 1991; Hegner and Wingfield, 1987; Wikelski *et al.*, 2000; Wingfield *et al.*, 1982, 1989). In males in monogamous but sexually dimorphic species often have T concentrations three times higher than females (Schwabl and Sonnenschein, 1992). The reason for this pattern is not certain, but Wittingham and Schwabl (2002) showed that circulating T in females during the breeding season is correlated with the rate of competitive interactions among females. As we showed here, house sparrow females, which are together and can see the male bird showed greater response, male birds showed equal response against all three schedules.
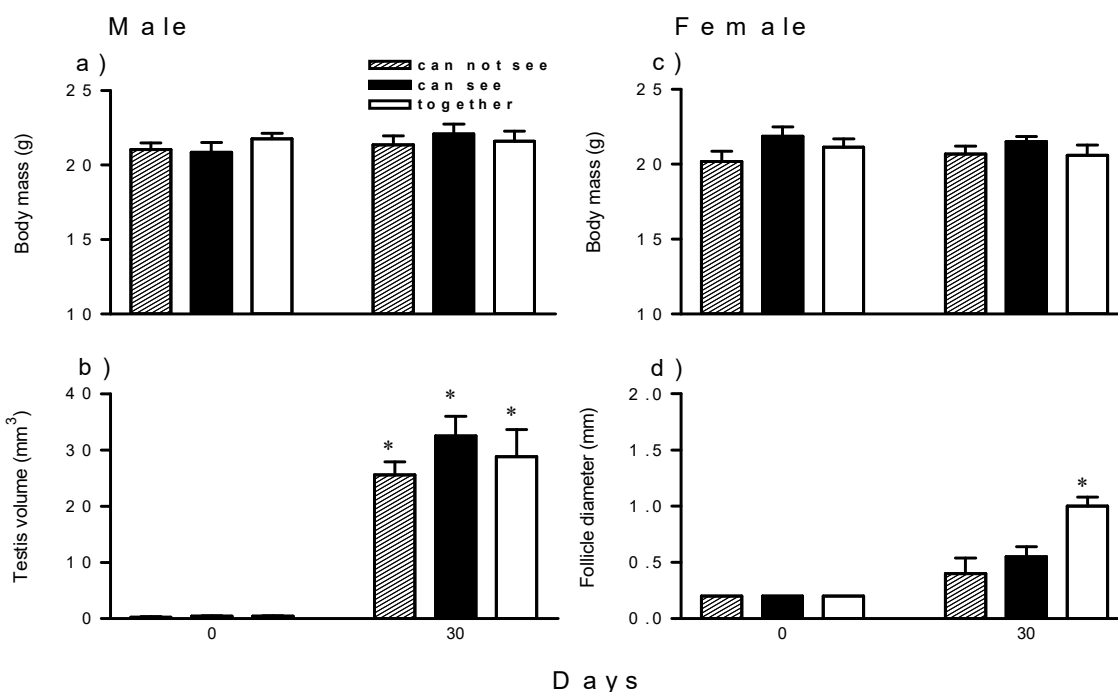

Figure 2. Individual male and female birds were kept individually in cages separated by a plywood partition so that they could not see each other (Set 1) or kept individually in cages but separated by a transparent partition so that they could see each other (Set 2) or kept together in the same cage (Set 3). In addition to this birds were disturbed by sound of a ringing bell at three times of the day for 15 minutes at ZT 4, 8 and 12 (ZT0; zeitgeber time = time of light onset). Each point symbol represents mean (± SEM) response in male (a, b; left panel; N = 4) and female (c, d; right panel, N = 4). Asterisk (*) indicates significance of difference at P<0.05.

Wingfield *et al*., (1990) hypothesized that increases in T level between the non-breeding and breeding baselines facilitate sexual interactions. While individuals of many species of birds do not have the opportunity to interact sexually with a former or future mate during non-breeding periods, individuals of other species do. With increased association frequency, other more courtship like behaviors such as solicitation poses and the exchange of visual, vocal, and acoustic signals could occur. Our results revealed no significant relationship in males and females, who cannot see each other, they can contact vocally. But because of sound disturbance, their signals were not clear. Another two groups, which had visual contact, they were less effective by sound disturbance. Social cues are of the product of interactions between individuals, and in such cases it can be difficult differentiate the effect of the reception of cues from the production of responses (Burmeister and Wilczynski, 2000). Social interactions, especially competitive ones, are often stressful (Fox *et al*., 1997) and may be especially so in cases where the individual is unable to exert control. The interaction between the auditory system and vocal production pathway may be related to acoustically evoked mate calling. Not surprisingly, many of these same brain regions that are involved in reception and production of social signals are also responsive to circulating sex steroids (Kelley *et. al*., 1975; Morrell *et al*., 1975; Kelley, 1981). Social relationships between males are likely to go beyond neighbours with whom territory boundaries are shared (Naguib, 2006).

The pairing in the environment appears to affects the gonadal growth in females but not in males. All male groups whether they were separated or remained together with females had almost similar testicular volume but females when put in company of males had grown significantly ($P<0.05$; 1-way ANOVA) larger follicles. This is adaptive since females this way can limit the reproduction when the chances of survival are greatest. Males on the other hand cannot adapt to such social cues since testicular growth and development to when there is full spermatogenesis requires a period of at least 6 to 8 months. The present findings are therefore significant in showing the importance of pairing between males and females.

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