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Original article

The development of photorefractoriness in termination of the breeding season in the tropical brahminy myna: role of photoperiod

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Summary — Gonads of brahminy myna *(Sturnus pagodarum)* spontaneously regress in July/August when the daylength is still stimulatory. Experiments were conducted to investigate if photoperiod was involved in the timing of gonadal regression and if photorefractoriness terminated the breeding season in this species. The observations obtained in the present study clearly show that: i) increasing photoperiods of spring/summer programmed for eventual gonadal regression in the late summer; ii) the birds developed photorefractoriness to all stimulatory daylengths and consequently the breeding season could not be extended by providing more stimulatory photoperiods; and iii) exposure to short daylength treatment failed to overcome the onset of refractoriness in birds after they had attained full gonadal growth and development. These results suggest that refractoriness is a process used by the brahminy myna to terminate the breeding season, and that this species becomes totally photorefractory.

photorefractoriness / breeding / photoperiod / bird / myna

Résumé — Développement d'un état photoréfractaire à la fin de la saison de reproduction chez le mainate brahmane tropical : rôle de la photopériode. *Les gonades de mainate brahmane* (Sturnus pagodarum) *régressent spontanément en juillet–août, alors que la durée du jour est encore de nature stimulante. Des expériences ont été conduites pour rechercher si la photopériode intervient dans la programmation de la régression des gonades et si un état photoréfractaire met fin à la saison de reproduction dans cette espèce d'oiseaux. Les résultats de ces travaux montrent que :*

- *des photopériodes croissantes données au printemps et en été programment une éventuelle régression gonadique en fin d'été,*
- *un état réfractaire se met en place quelle que soit la durée quotidienne de la photopériode stimulante et la saison de reproduction ne peut donc pas être prolongée en poursuivant le régime photostimulant et*
- *les traitements de «jours courts» ne peuvent pas empêcher l'établissement de la phase photoréfractaire lorsqu'ils sont donnés après que les gonades des oiseaux ont atteint leur plein développement. Ces résultats suggèrent que l'état réfractaire est un moyen utilisé par le mainate brahmane pour mettre fin à la saison de reproduction au cours de l'année et que cette espèce devient totalement photoréfractaire.*

reproduction / photopériode / état réfractaire / oiseau / mainate

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INTRODUCTION

In seasonally breeding animals, the breeding season is restricted to the optimum period for raising young, which varies widely to suit the ecological needs of each species. In most species of birds from temperate latitudes, in which reproduction usually begins some time during spring, the breeding season ends by the development of a state of refractoriness which results in spontaneous gonadal collapse and loss of response to stimulatory daylengths; once the birds are photorefractory, exposure for a time to short daylengths is necessary to render them photosensitive again (Murton and Westwood, 1977; Farner *et al,* 1983; Follett, 1984; Stokkan and Sharp, 1984; Nicholls *et al,* 1988). Similar results have been found in some spring/summer breeders that reproduce at high latitudes but overwinter in the tropics (Tewary and Kumar, 1982; Kumar and Tewary, 1983; Tewary and Tripathi, 1983).

In the tropics, breeding seasons among birds are spread out over the entire year and correspond to existent favourable conditions, but reproduction in individual species is essentially seasonal (for review see Chandola *et al,* 1983). A number of species breed during spring and summer, and some of them react to photoperiods similar to those of temperate species (Thapliyal and Tewary, 1964; Epple *et al,* 1972; Lewis *et al,* 1974; Thapliyal, 1981; Dittami and Gwinner, 1985; Gwinner and Dittami, 1984; Tewary and Tripathi, 1985; Tewary and Dixit, 1986). However, the mechanisms controlling the termination of the breeding season in these photosensitive species are divergent and remain controversial. While photorefractoriness is lacking in some long-day breeders (Thapliyal and Saxena, 1964; Miller, 1965; Epple *et al,* 1972; Lewis *et al,* 1974), a few birds are reported to undergo spontaneous gonadal regression under continuous long day-lengths (Lofts, 1962; Thapliyal, 1981; Tewary and Tripathi, 1985; Tewary and Dixit, 1986).

Therefore we sought to study the importance of refractoriness in the reproductive cycle of a subtropical spring/summer breeder, the brahminy myna *(Sturnus pagodarum),* which is a widely distributed resident species in India. It has a distinct annual gonadal cycle with breeding periods varying according to the locality, between March and August (Ali and Ripley, 1972). At Meerut, India (latitude 29 ° 1 N; longitude 77.45' E), the gonads begin to recrudesce in March/April when daylengths increase (≈ 12–13 h), and reproduction ends in July/August when daylengths decrease (≈ 13.7–13 h) but are still longer than the inductive photoperiods. Under laboratory conditions long daily photoperiods (14–16 h) induce a gonadal growth-involution cycle within 3–4 months, but not during sexually quiescent periods (Kumar, 1988; unpublished observations). This indicates that in brahminy myna the end of the breeding season is marked by spontaneous gonadal regression as well as by failure to respond to further photoperiodic stimulation, similar to temperate species, including European starlings of the same genus (for refractoriness in starlings, see in particular Dawson and Goldsmith, 1983; Dawson *et al,* 1985; Dawson, 1987; Nicholls *et al,* 1987).

The present experiments were designed to determine whether refractoriness was a process used by the brahminy myna to terminate its breeding season. We also investigated whether: i), the breeding season could be extended by exposure to stimulatory photoperiods before the onset of gonadal regression; and ii) responsiveness to long photoperiods could be maintained by the short-day treatment when the birds had attained full gonadal maturation.

MATERIALS AND METHODS

In the present study, we used wild birds caught and kept in an outdoor aviary at Meerut. At Meerut (29 °N), seasonal variations in official daylength (measured from the onset of official dawn to the end of official dusk) occur between the shortest daylength of 11 h 05 min (22nd December) and the longest daylength of 14 h 57 min (23 June); this includes 24–28 min of morning and evening official twilight periods. The birds were acclimatized to indoor laboratory conditions for 15 d before experimentation. During artificial photostimulation in the different photoperiods of series I–III, the birds were held in lightproof chambers lit by fluorescent tubes at an intensity of ≈ 300 lux.

All birds were provided food and water *ad libitum*. Periodic observations of the gonads were made by laparotomy. In males, the dimensions of the left testis and in females, the diameter of the largest ovarian follicle were recorded. Testicular volume was calculated from $4/3\ \pi\ ab^2$ where a and b denoted half the long and short axes, respectively. In females, an unstimulated ovarian follicle was rated as 0.3 mm in diameter to make the observations statistically comparable. In this study, we chose the testicular volume (TV) in males and the diameter of the largest ovarian follicle (FD) in females as indexes of the photoperiodic effects on reproductive activity since increase in the size of the gonads over a period of time, as a function of photoperiodic stimulation, reflects the summation of the gametogenetic changes involving at least LH, FSH and androgens (Lofts and Murton, 1973; Lofts *et al*, 1973; Lofts, 1975). Further, ovarian follicles develop in 2 phases (an initial slow growth phase followed by a phase of rapid or exponential growth) and so the measurement of the largest follicle indicated the response of the ovarian follicle of the prospective clutch which was ready to mature (Farner and Lewis, 1971).

Experimental design

Series I

This series determined the relationship between the onset of photorefractoriness and daylength. Two experiments were performed. In experiment I, which began on 4 May, 1989, a group ($n = 6$) of male and female birds were placed in continuous light (LL, 24 L:0 D), long photoperiods (LDL, 16 L:8 D) and normal daylengths (NDL) for 120 d: the latter served as controls. Monthly observations on TV and FD were carried out.

Experiment II commenced on 6 August 1989 when gonadal regression had begun (fig 2). It thus differed from the above experiment regarding reproductive status of the birds. We examined simultaneous changes at 10-d intervals in the gonads of groups (n=6 each) of male birds, held in NDL and LDL for 30 d to ensure the effect of LDL on the onset and progress of gonadal regression.

Series II

This experiment, begun on 23 July 1989, determined whether the development of photorefractoriness and/or spontaneous gonadal regression in NDL birds could be delayed or deferred by shifting to the artificial photoperiods. At this time, the birds in nature were experiencing a daylength of ≈ 13.7 h (measured from sunrise to sunset and excluding twilight periods). Four groups, each consisting of 6 males and 6 females, were studied for 60 d. In group 1 (12 L → LL), birds first experienced 12 L/12 D for 30 d and then LL for an equal period to determine if the shift to a lower photoperiod (12 L/ 12 D) at that time would postpone eventual development of photorefractoriness. The birds in groups 2 and 3 (14 L or 16 L → LL) were exposed to 14 L/10 D or 16 L/8 D on d 0–30, respectively, and then to LL on d 31–60; this procedure determined whether an additional increase in daylength would prolong the breeding season and prevent the onset of refractoriness. Group 4 was continuously maintained in LL to confirm the development of photorefractoriness in the brahminy myna. The change in gonad size measured at 30-d intervals was considered as an index of the development of refractoriness in the present study.

Series III

These experiments were carried out to determine whether exposure to short daylengths (8 L/16 D) for 9 wk (a period of exposure which otherwise enabled regressed brahminy myna to regain photosensitivity at a time when the birds had attained full growth and gonad development) could prevent the development of photorefractoriness. In other words, would a short-day treatment enable reproductively mature birds to remain responsive to stimulatory photoperiods. On 20 May 1989, 4 groups (*n*=6) of male and 3 groups (*n*=6) of female birds were transferred to 8 L:16 D for 63 d and examined at monthly intervals; at that time they had fully developed gonads (TV = ≈240.00 mm^3; FD = ≈ 1.50 mm). At the end of short-day exposure all the birds had fully regressed gonads (average TV = 0.49–0.80 mm^3; average FD = 0.35 mm). Subsequently, the males were transferred to 12 L, 14 L, 16 L and LL and males the females to 12 L, 16 L and LL for a total duration of 90 d. However, after 60 d the birds in 12 L and 14 L were shifted to LL to determine photosensitivity. A control group (*n*=6) was kept on NDL to demonstrate the rate of natural gonadal regression during the time of year covered by the experiment.

A few birds (one bird in each series II group, and 2 birds in series III) died during the course of investigation, and their data were excluded from the statistical analysis. The mean and standard errors of the data were computed. The data were subjected to analysis of variance, ANOVA (Sokal and Rohlf, 1973), followed by Duncan's multiple range test, DMRT (Duncan, 1955), at 5% and 1% levels.

RESULTS

Series I

When exposed to LL and LDL during the early reproductive phase (first week of May) stimulated males regressed in LL ($P < 0.001$), but not in LDL within 30 d; in fact, LDL birds maintained enlarged testes until d 30 (fig 1A). The females responded in a similar manner but no significant regression was found in ovarian follicles of LL birds on d 30 (fig 1B). However, fully regressed gonads ($P < 0.001$, ANOVA; $P < 0.01$, DMRT) were found in all birds in both treatment-groups by d 60 (fig 1); the birds remained gonadally regressed until the end of the experiment. In NDL, the birds had active gonads until d 60 (early July) after which they underwent regression. Fully regressed ($P < 0.001$, ANOVA) testes and ovaries were found in NDL birds on d 120, in early September (fig 1A, B).

The data from the second experiment (fig 2) reveal that transfer to LDL at the time when the gonads had begun to regress had no effect on the rate of gonadal

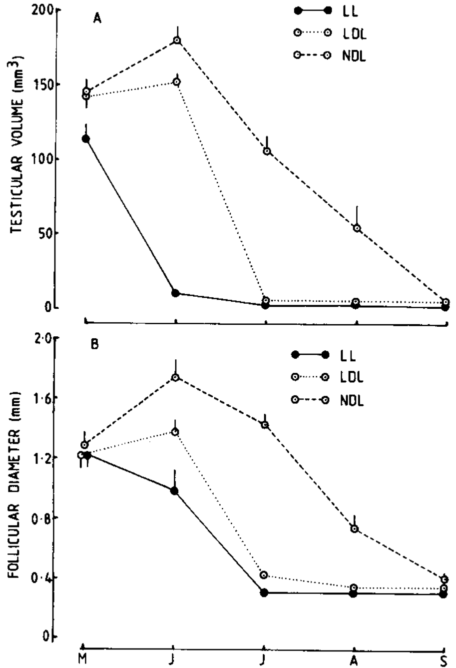

Fig 1. Gonadal response in brahminy myna transferred from NDL to continuous light (LL) and long daily photoperiods, LDL (16:8 D) in the first week of May and maintained for 4 months on this schedule. Each circle represents the mean for data on a group of birds; the vertical bar indicates limits of the standard error.

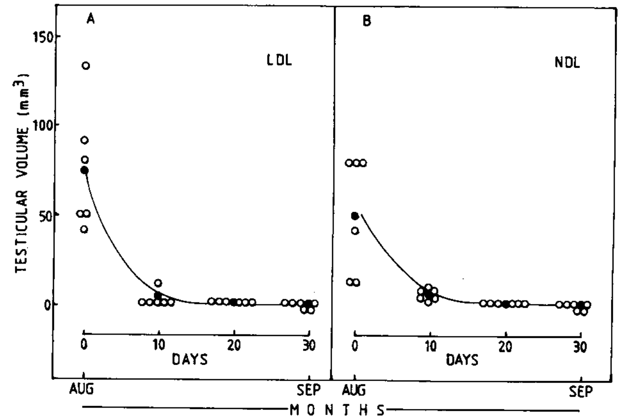

Fig 2. The changes in testicular volume at 10-d-intervals in groups of brahminy myna kept in LDL, 16 L:8 D (A) and NDL (B) for 30 d from the first week of August. Open circles represents individual data; solid circles indicate the mean for the group. Gonadal regression trend is shown by a curved line which eventually becomes horizontal between the last 3 mean points.

regression (*cf* figs 1A, 2A). Fully regressed testes were found in LDL birds by d 10 (fig 2A). The following observations (d 20 and 30) revealed fully involuted testes in NDL as well as in LDL groups.

Series II

The results from this series (fig 3) confirm that the change in daylength had no effect on the reproductive cycle of brahminy myna at the onset of gonadal regression. The gonads collapse ($P < 0.001$, ANOVA; $P < 0.01$, DMRT) within 30 d of exposure to 12 L, 14 L, 16 L and LL. These birds remained gonadally regressed until the end of the experiment. A transfer of 12 L, 14 L and 16 L birds to 24 h light caused no renewed gonadal growth, indicating that the birds had become absolutely photorefractory.

Series III

The results are summarized in figure 4. As expected, short days caused complete gonadal regression ($P < 0.001$, ANOVA; $P < 0.01$, DMRT) at the time when birds experiencing natural daylengths had enlarged gonads (fig 4). Gonads of the short-day group of birds did not recrudesce on subsequent transfer for 60 d to 12 L or 14 L (fig 4A), except for a slight initiation in a few females in the 12 L (fig 4B). The transfer of these birds to LL for 30 d also failed to cause gonadal growth (fig 4). On the other hand, the testes of a few birds in the group were slightly stimulated in 16 L and LL, although the average TV for the group was never statistically different (fig 4A). However, the females in these treatment groups exhibited ovarian development ($P < 0.01$, DMRT; fig 4B). These partially stimulated birds became fully regressed after the next 30 d (fig 4).

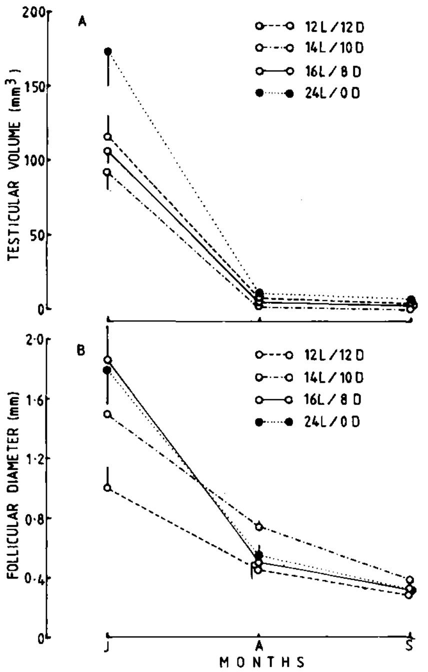

Fig 3. Gonadal regression in brahminy myna exposed for 60 d to different photoperiods (12 L, 14 L, 16 L and LL) from 23rd of July. The birds were examined at 30-d intervals. The first measurement was made 1 day prior to experimentation. A higher 24 L group in males and lower 12 L group in females was found incidentally due to random grouping and the inclusion of a few birds with large or small gonads. Note that this was the time of onset of gonadal regression. Circles and vertical bars represent mean data and standard error respectively for a group of birds. Note that 12 L, 14 L and 16 L groups were transferred to LL on d 30.

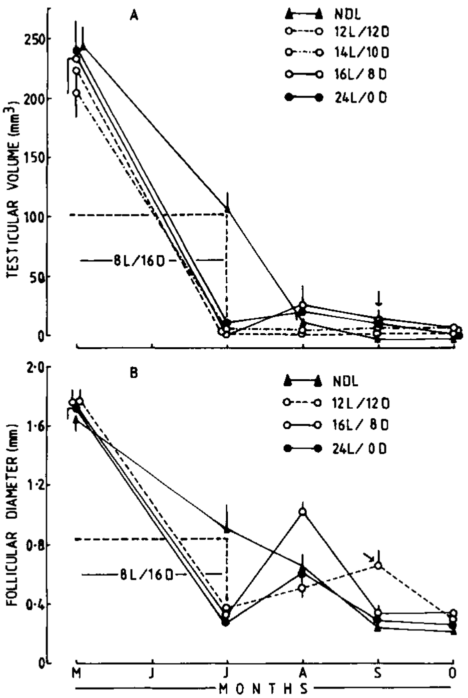

Fig 4. Photoresponse of male (A) and female (B) brahminy myna subjected to short days (8 L:16 D) for 60 d from the third week of May and subsequently transferred to different photoperiods (12 L, 14 L, 16 L and 24 L) for 90 d. Small arrows (↓) pointing towards September data indicate the transfer of 12 L and 14 L groups to LL. Each circle represents mean data for the groups examined and vertical bars denote standard error. The data for an NDL group of birds are is represented by solid triangles and indicate the gonadal regression trend in nature.

DISCUSSION

Results of the present study (figs 1–4) confirm that in brahminy myna the breeding season is terminated by a state of photorefractoriness which develops after attainment of full gonadal maturation. The data from the series I experiments provide evidence that the timing of the onset of refractoriness can be modified by exposure to longer daylengths; birds in LDL regressed later than those in LL, but earlier than NDL birds (fig 1). Also, as in other photoperiodic species exhibiting refractoriness (Wolfson, 1959; Storey and Nicholls, 1976; Harris and Turek, 1982; Dawson and Goldsmith, 1983), the time taken to undergo spontaneous gonadal regression in brahminy myna appeared to be an inverse function of the duration of the daylength experienced, once the period of minimum daily photoperiod inducing refractoriness was exceeded. In other words, the development of refractoriness was hastened by exposure to long photoperiods; the longer the photoperiods, the sooner the birds became photorefractory. However, this was true when the birds were exposed to long daylengths at the time of full gonadal maturation (*cf* figs 1A and 2). The data in experiment II (fig 2) indicate that exposure to LDL at the onset of gonadal regression had no effect whatever on the rate of gonadal regression.

Experiments in series II confirm that the loss of response to photoperiods during the late reproductive period was absolute, since exposure to any stimulatory photoperiods in late July did not extend the breeding season in this species. This is inconsistent with the findings on some photoperiodic birds and mammals (house sparrow: Vaugien, 1955; duck: Assenmacher and Tixier-Vidal, 1962; house finch: Hamner, 1968; quail: Robinson and Follett, 1982; ewe: Malpaux *et al,* 1988), showing that the natural breeding season can be prolonged by providing further photoperiodic stimulation shortly before regression or anestrus sets in.

Since exposure of gonadally-regressed birds to 24 h light caused no renewed growth (figs 1, 3 and 4), this species becomes, by definition, totally photorefractory. The refractoriness that developed in the brahminy myna thus resembles that described in white-crowned sparrows (Sansum and King, 1976), starlings (Bissonnette and Wadlund, 1932; Dawson *et al,* 1985, 1986; Nicholls *et al,* 1987), willow ptarmigan (Stokkan and Sharp, 1984) and Svalbard ptarmigan (Stokkan *et al,* 1986). It is also comparable to the loss of response under long photoperiods (15 L or LL) observed in a few palaeoarctic–Indian migrants overwintering in India (*Emberiza melanocephala;* Tewary and Kumar, 1982; Kumar and Tewary, 1983; *E bruniceps:* Prasad and Tewary, 1982; Tewary and Tripathi, 1983); however, the issue of absolute or relative refractory period has not been examined in these species.

Series III provides evidence for the involvement of the photoperiod in the development of photorefractoriness. It is known that short daylengths are used to terminate photorefractoriness and ensure photosensitivity in long daylength breeding species. In a separate study, we have observed that the gonads of brahminy myna exposed to 8 L or 9 L for 2–4 months from February/March were stimulated within 3 d of transfer to LDL, and that this treatment ensured photosensitivity in the post-reproductive regressed individuals (unpublished observations). In the present study, birds exposed to 8 L since the third wk of May failed to respond when subjected to 12 L or 14 L for 60 d and subsequently to LL for 30 d. Although a short subsequent gonadal cycle, like that in golden-crowned sparrows (Turek, 1975), was induced in females of 16 L and LL groups, only 1 or 2 birds of the 16 L and LL male groups showed slightly initiated testes. The difference between the 2 sexes in this experiment in response to photostimulation could be attributed to the reproductive status of the birds at the time when they were shifted to 8 L. Since the ovary matures after the testis, it is possible that the females were not fully reproductively mature when transferred to 8 L. Further, it is not possible to ascertain at present whether partial response in a few birds in some groups was because 8 L prevented the development of full photorefractoriness, or whether, having become photorefractory, the birds were then rendered partially photosensitive again as a result of 8 L treatment.

An interesting observation is that LDL maintained gonadal growth (at least for 30 d) in birds which were exposed to LDL in early May (fig 1), but not in late July (fig 3) or early August (fig 2). In addition, 8 L rendered full photosensitivity in February/March, but not in late May (fig 4). This suggests that birds will not enter a photorefractory state unless they have attained full gonadal maturation, and that the development of photorefractoriness becomes inevitable before gonadal regression. This raises the possibility that in brahminy myna in nature, spring/summer daylengths not only induce gonadal development, but also program for spontaneous gonadal regression in late summer. Whether photorefractoriness is fixed by daylengths experienced before the gonads have attained maximal growth (Moore *et al*, 1983), or whether it is fixed by the daylength available at the end of gonadal growth as in starlings (Falk and Gwinner, 1988), has to be further investigated. However, these observations indicate that brahminy myna has its own endogenous program for a gonadal growth-involution cycle which can be modified by environmental photoperiods. While longer photoperiods hasten gonadal growth and onset of refractoriness during early gonadal growth phase, the breeding season is not prolonged once the gonads have matured.

Our findings are not in agreement with those on the responses of some other tropical photoperiodic species. For instance, in low-latitude *Ploceus philippinus* (Thapliyal and Saxena, 1964; Singh and Chandola, 1981) and *Zonotrichia capensis* (Miller, 1965; Epple *et al*, 1972; Lewis *et al*, 1974) the transition from breeding to regression is not associated with loss of response to the inductive (≥ 15 h) daily photoperiods, which under laboratory conditions induce gonadal development during sexually quiescent periods and keep the gonads active for a long time or indefinitely. However, a seasonal decline in photosensitivity to LDL and loss of response to only natural daylengths have been suggested in *P philippinus* at 25 °N (Singh and Chandola, 1982; Chakravorty and Chandola-Saklani, 1985). Not withstanding, spontaneous gonadal regression under LDL has been observed in tropical *Acrilotheres tristis* (Thapliyal, 1981) and *Gymnorhis xanthocollis* (Tewary and Tripathi, 1985; Tewary and Dixit, 1986), but it is not known if the regressed individuals respond on subsequent transfer to longer photoperiods or LL. Further, a brief photorefractory period observed in low-atitude *Quelea* does not resemble the temperate type of photorefractoriness, for it is dissipated spontaneously irrespective of the photoperiods (Lofts, 1962). The present findings therefore establish that the termination of the breeding season by absolute photorefractoriness also occurs in birds breeding in the tropics.

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