THE INTERNAL RHYTHM OF REPRODUCTION IN XEROPHILOUS BIRDS UNDER CONDITIONS OF ILLUMINATION AND DARKNESS

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(With Plate 10)

INTRODUCTION

Vaugien (1952, 1953) took young male Australian budgerygahs (*Melopsittacus undulatus*) shortly after they left the nest and divided them into three batches which were respectively placed: (1) under natural European daylengths; (2) in continuous light; and (3) in complete darkness. Samples of each group were killed for examination after 52 and 84 days. Spermatozoa had appeared within 52 days in all birds killed in each group (a total of 14 individuals). After 84 days the four survivors under continuous light contained only primary spermatocytes. Of the five birds under natural daylengths four held spermatozoa and the remaining individual only primary spermatocytes. Yet the six survivors in total darkness all contained spermatozoa.

These results have been widely quoted (e.g. Benoit & Assenmacher, 1953; Aschoff, 1955; Farner & Mewaldt, 1955). Vaugien concluded that total darkness seems to favour spermatogenesis in *Melopsittacus*, and that continuous light, on the contrary, appears to retard it. He was of the opinion that such results might find 'une interprétation dans les origines exotiques de cet oiseau' (Vaugien, 1953).

The budgerygah is a xerophilous form that in many areas breeds only after rainfall and irrespective of the season (Marshall, 1955). Therefore, although one could readily imagine that it might fail to respond to light, there is no factor in its environment to suggest that its sexual development could be enhanced by darkness.

Close examination of Vaugien's illustrations has provided an answer to the problem. The testes of birds kept in continuous light (primary spermatocytes only) are seen to have reached the 'regressed' condition that follows natural reproduction or gross laboratory photostimulation. In short, far from being less developed than the birds under natural illumination and total darkness, the constantly illuminated birds had far outstripped them. They had been driven right through one sexual cycle and had entered another. The organs with spermatocytes illustrated by Vaugien

remarkably resemble those of xerophilous species that have been reactivated by unseasonal rainfall after a normal breeding season (Serventy & Marshall, 1957).

At the same time there is no suggestion of misinterpretation in regard to the rapid development of spermatozoa by *Melopsittacus* in total darkness. It was thought worthwhile therefore, to investigate the sexual reactions of a second, and unrelated, Australian xerophilous species to darkness and to varying degrees of illumination.

MATERIALS AND METHODS

The zebra (or chestnut-eared) finch (*Poephila castenotis* syn. *Taeniopygia castanotis*) resembles the budgerygah in occurring in extensive nomadic flocks that reproduce after rainfall irrespective of the annual cycle of the sun. When the young leave the nest the sexes are externally indistinguishable. The present study is based on forty-seven young birds of both sexes which were obtained while still in juvenile plumage. At this period the testes measure about 1 mm. in diameter (Pl. 10, fig. 1) and the largest ovarian oocytes are only about 360 μ in diameter. Beak-colour and plumage provide external indications of age. Juveniles of both sexes are drab, with almost black beaks. The beaks of both sexes, and the plumage of males, become progressively coloured until fully adult males possess a bright orange-red beak, chestnut ear-patches and white-spotted flanks. Adult females, too, possess an orange beak which is, however, slightly paler than that of the male. The female plumage remains comparatively drab.

The birds used were obtained from aviary suppliers and laboratory stocks. There is evidence (D. Morris, pers. comm.) that in general behaviour at least, such birds do not materially differ from those recently caught in the wild. The forty-seven experimental birds were kept in identical dietary, and almost identical housing, conditions at laboratory temperature, i.e. at an average 24 hr. temperature of 19° C. with negligible fluctuations. Nesting boxes and material were provided.

Experimental conditions were as follows:

I. Fifteen birds kept for 60 days in near darkness. (Faint indirect light was necessary to enable them to locate food, water and perches.)

II. Eight birds were kept under 6 hr. light per day for a period of 60 days. (This amount is of course far less than that which could be possibly experienced in their natural environment; see Table 1.)

III. Eight birds were kept under naturally decreasing photoperiods in London from 21 September to 21 November, i.e. from 12 hr. 19 min. to 8 hr. 33 min.

Table 1. *Daylengths to which* Poephila castenotis *is naturally subjected in the wild*

Geographical range	21 June	23 December
15° S.	11 hr. 7 min.	12 hr. 53 min.
35° S.	9 hr. 39 min.	14 hr. 21 min.

IV. Eight birds were kept during the same period as group III but under artificially increasing photoperiods equalling those of the corresponding period of spring.

V. Eight birds were kept under 15 hr. of light per day for 1 week, 17 hr. per day for a further week, and thereafter continuous light for a further 54 days, making a total of 68 days illumination.

At the conclusion of each experiment the birds were killed with coal gas. Descriptions were made of plumage and beak, and the gonads were dissected out and fixed in formol-calcium. One testis and half of each ovary were wax-embedded and stained with iron haemotoxylin for the identification of gametogenetic stages. Corresponding material was embedded in gelatine and coloured with Sudan black for the retention of interstitial and tubule lipids.

RESULTS

Group I (continuous near-darkness). Four males had the larger testis measuring 4×3 mm. Two others had testes enlarged to $3 \times 2{\cdot}5$ mm. and 2·5 mm. in diameter. All these possessed bunched spermatozoa (Pl. 10, fig. 2). The oocytes of nine females had increased to only about 1 mm. in diameter. All birds had come into adult colour.

Group II. (6 hr. light daily). The larger testis of each of the three males measured between 4 mm. in diameter and 6×3 mm. long. All contained bunched spermatozoa. The five females possessed some oocytes that had enlarged to between 2 and 3 mm. in diameter. All birds in adult colour.

Group III (decreasing daylengths). The larger testis of each of the five males ranged between 4·5 mm. in diameter and 7×4 mm. long and contained bunched spermatozoa. The largest oocytes of the three females varied between 2 and 3 mm. in diameter. All birds in adult colour.

Group IV (increasing photoperiods). The larger testis of four males ranged between 4 mm. in diameter and 5.5×3 mm. long. All contained bunched spermatozoa. The largest oocytes in all four females had increased to between 2 and 3 mm. in diameter. All birds in adult colour.

Group V (almost continuous daylight). The four birds of each sex possessed gonads of the same average dimensions as those of group IV. The seminiferous tubules of each male contained bunched spermatozoa (Pl. 10, fig. 3). In one bird a tubule was seen already to be undergoing 'post-nuptial' steatogenesis (Pl. 10, fig. 4). All birds were in adult colour.

DISCUSSION

Vaugien's more striking assumption, i.e. that spermatogenesis is advanced more considerably in darkness than in light, has been examined and rejected on p. 666. His second remarkable conclusion appears to be confirmed. Certainly in the young of another xerophilous species, the zebra finch, complete spermatogenesis can take place within 60 days in the almost total absence of photostimulation.

At the same time, the zebra finch, like the budgerygah, is probably susceptible to photostimulation. Birds given 6 hr. daily illumination and those subjected both to increasing and decreasing photoperiods showed slightly greater testis development and strikingly greater ovarian development than the birds in the dark cage. All illuminated groups showed some interest in nesting materials. No nesting material was taken to the nest boxes in the dark cage.

The explanation of the above-described phenomena may be as follows:

Both the budgerygah and zebra finch are opportunist breeders, reproducing only when their generally dry environment irregularly offers conditions propitious for them to do so. If their cycles were rigidly controlled by photoperiodicity they would be eliminated by natural selection. If food and water remain plentiful, an internal rhythm of reproduction goes forward unchecked and the males produce spermatozoa even in darkness. The females require illumination before oocytes enlarge even to a limited extent. At the same time it is by no means sure that illumination has a direct effect on the reproductive processes of females. It may be that the light encourages behavioural reactions, including manipulation of nesting material, that affect the neuro-endocrine mechanisms and lead to gonad modification. It will be recalled that in all species yet investigated the male cycle far outstrips that of the female in the wild (Marshall, 1955).

Susceptibility to artificial illumination has already been proved in males but not females of the similarly xerophilous (even equatorial) weaver-finch (*Quelea quelea*) (Marshall & Disney, 1956). The cage experiments described above make it appear that the males at least of both zebra finch and budgerygah retain an ancestral capacity to respond to photostimulation. But under natural conditions any such tendency would be often over-ridden by external inhibitors that are significant to reproductive success.

The rapid production (within 60 days) of spermatozoa in the young of both parrot and finch is no doubt a physiological aspect of drought adaptation, i.e. it enables birds to reproduce quickly when the external environment is advantageous. Such speedy spermatogenesis occurred in warm cages well supplied with food and water. Under drought conditions external inhibitory factors would prevent rapid gametogenesis (Keast & Marshall, 1954; Serventy & Marshall, 1957).

SUMMARY

1. A report that total darkness is more effective than illumination in the production of spermatogenesis in young of the xerophilous budgerygah is shown to be due to a misinterpretation of results.

2. An internal rhythm of reproduction allows young male zebra finches (like young budgerygahs) to produce spermatozoa within 60 days in almost total darkness when provided with plenty of food and water at laboratory temperatures. Oocytes enlarge only slightly. Both sexes come into breeding dress in the dark.

3. Various conditions of illumination (including decreasing photoperiods) cause in both sexes greater gametogenetic activity than occurs in darkness.

4. Both budgerygah and zebra finch are xerophilous. They are opportunist breeders after rainfall, irrespective of season. Although they retain an ancestral capacity to respond to photostimulation, any such tendency under natural conditions could be over-ridden by external inhibitors.

5. The rapid production of spermatozoa (within 60 days) is in both parrot and finch a physiological aspect of drought adaptation enabling very young birds to reproduce quickly whenever environmental conditions are propitious.

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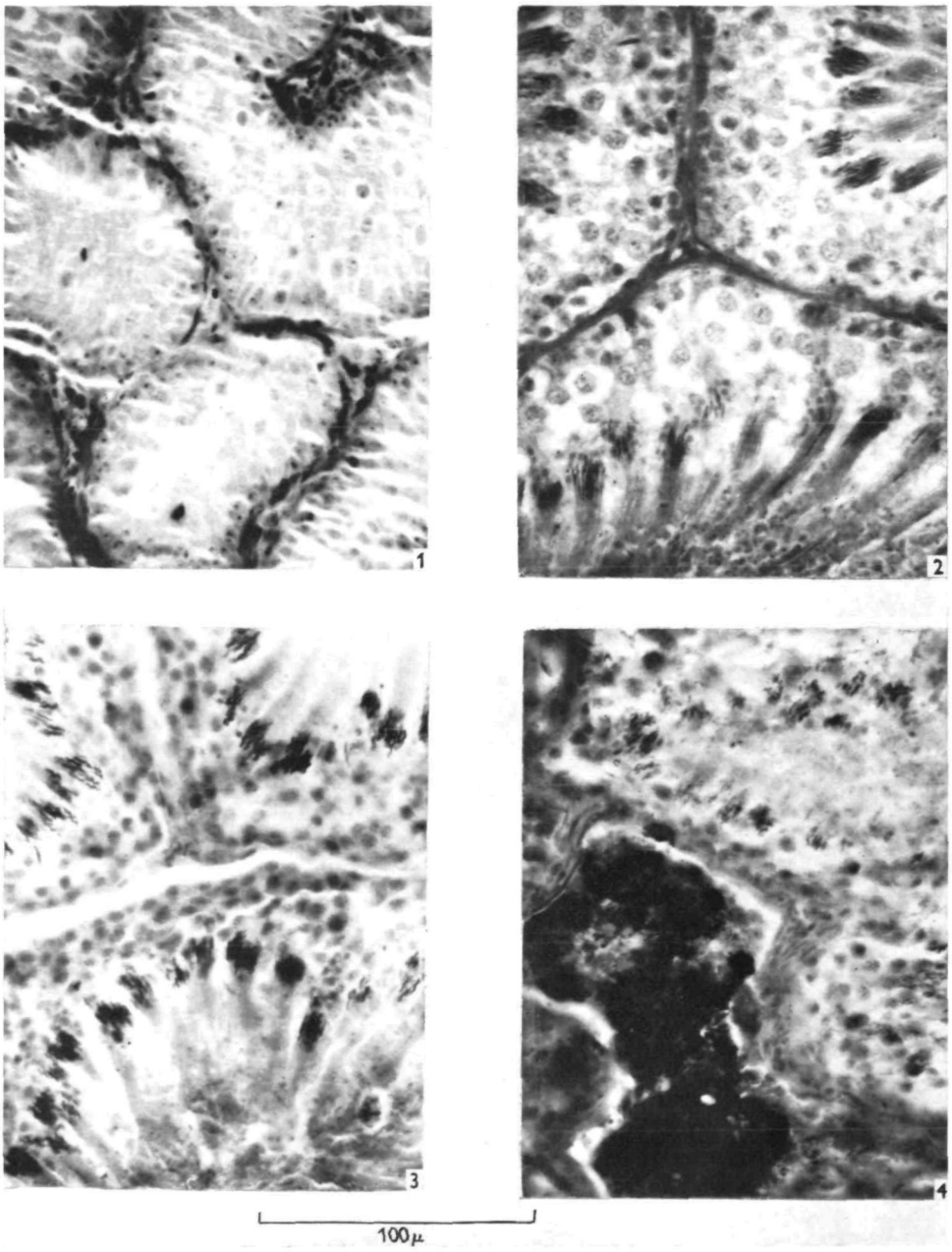
EXPLANATION OF PLATE

Fig. 1. Seminiferous tubules of young zebra finch at the age (40–45 days) used at the start of each experiment. There was in some birds already a minor spermatogenetic and colour development. Bouin fixation, wax embedding and iron haemotoxylin at 6μ.

Fig. 2. As fig. 1, but 100 days old after 60 days of almost total darkness. Technique as in fig. 1.

Fig. 3. As fig. 1, but 108 days old after 68 days of almost continuous illumination. Formalin fixation, gelatine embedding and Sudan black at 8μ.

Fig. 4. As Fig. 3; in this grossly over-stimulated bird one tubule has metamorphosed: 'post-nuptial' steatogenesis has begun. Shortly the whole organ would collapse. Technique as in fig. 3.



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(*Facing p.* 670)