Photoperiodism and the control of breeding season

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Introduction

Control of the timing of breeding season in birds is accomplished by a wide variety of internal and external factors. These mechanisms allow birds to breed in the most favourable period of the year and modify their breeding in response to seasonal fluctuations in resources.[1,2,3,4,8,9,10,11]

There are two main reasons why it is important for avian veterinarians to understand the factors that control breeding season.

To aid in the successful breeding of species that are held in locations and conditions vastly different to those they evolved in.

To allow the modification or cessation of breeding in birds with reproductive problems.

I will discuss the underlying mechanisms of the control of breeding season with particular emphasis on photoperiod. The current model of the factors affecting breeding season is described and there is a discussion of the implications and possible uses of this information in the therapy of reproductive problems of companion and aviary birds.

Why do birds breed seasonally?

Most bird species align both behavioural and physiological mechanisms with periodic changes in their environment. In particular, breeding season is timed to coincide with environmental conditions that maximise the survival of both the young and the parents. Gonadal activity is never continuous. Both endogenous annual rhythms and exogenous conditions (eg. photoperiod, rainfall, and humidity) influence the synchronisation of the events that constitute breeding. [1,2,3,4,8,9,10]

Species in widely differing habitats have evolved a bewildering variety of reproductive strategies. The factors that influence the onset and duration of the breeding season have been shown to vary greatly in the few species studied to date.[1,2,8,11] No simplistic model has been able to explain the control of breeding season in all birds but there are thought to be common underlying mechanisms that are used to differing extents by different species.[2,8,11] It is important to note that most of the studies carried out have been on passerines, and in particular, migratory passerines [2,3,4,7,8,9,10] which may have different control mechanisms to psittacines.

Mechanisms controlling breeding season

Endogenous reproductive rhythms

The evidence for an underlying internal cycle of reproductive rhythm comes from three sources:

(i) Captive birds, from all latitudes, which are held in constant environmental conditions (including daylength), have demonstrated continued gonadal cycling and breeding.[3,4,9,11] That is, environmental changes are not required for these birds to go through complete and successful reproductive cycles. Interestingly, these birds have shown varying duration of their reproductive cycle between individuals of the same species, although the cycles were constant for an individual from year to year. Most of the cycles deviate from the natural year, eg. African stone chats cycle on average every nine months.[3,4]

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(ii) Long distance migratory species are exposed in the course of a year to very complex photoperiods yet can maintain highly synchronised breeding, moulting and migratory rhythms.[3,8,11]

(iii) Tropical species, which are exposed to little variation in photoperiod, still maintain an annual cycle. It has been assumed that factors associated with the alternation between dry and rainy seasons were responsible for synchronising breeding. However, these factors vary much more between years than the birds' seasonal activities, suggesting the involvement of endogenous rhythms.[4,5,8]

Exogenous (environmental) factors

Environmental factors influencing the onset of breeding season are generally distinguished into two broad groups, 1. Ultimate and 2. Proximate factors.[2,8,11]

1. Ultimate factors

Ultimate factors are those factors that select individuals that produce young at the optimum time for survival. The most important ultimate factor for most species is the availability of food for feeding the young and for post-fledging survival.[1,2,7,8,11]

2. Proximate factors

Proximate factors directly regulate the timing of breeding from year to year.[2,8,11] They have been subdivided into four main types of information:

i. Initial predictive

These factors initiate gonadal development in anticipation of the ensuing breeding season. They bring the bird into the physiological state for breeding and maintain it throughout the breeding season. On their own these factors are not enough to initiate the nesting phase. The main factor in most species is photoperiod and I will elaborate most on this factor.

ii. Essential supplementary

These factors supplement the initial predictive information and initiate the final stages of gonadal development up to nesting. These are expanded upon later but include social cues, territorial behaviour, climate and nutrition.

iii. Synchronising and integrating

These factors regulate the sequence of breeding events including nest building, copulation, oviposition, incubation and rearing. They include the important social interactions between the bonded pair. This type of information falls outside the scope of this review and will not be discussed further.

iv. Modifying

These are factors that can disrupt the reproductive cycle. This includes adverse weather, loss or disturbance of nest site, predation and loss of mate.

Photoperiod effects

The primary source of initial predictive information for many bird species is the annual cycle of daylength. Almost all species studied experimentally have been shown to respond to changes in daylength although the way in which this information is used varies considerably.[1,2,3]

Photosensitivity is the readiness of the birds to be reproductively stimulated by increasing daylength. There is dramatic stimulation of gonadotrophin secretion and gonadal growth in some species.(6,8,10)

Photorefractoriness is the loss of response of the reproductive system to photoperiod and the regression of the gonads. There are two main types of photorefractoriness, absolute and relative.(2,6,8,10)

2. Absolute photorefractoriness

This is a complete regression of the gonads and the reproductive system cannot be stimulated, even by very long photoperiods.(2,6,8,10) In these birds there is a complete loss of the neural activity that controls GnRH in the hypothalamus.(6) In these birds increasing photoperiod (long days), the same factor that stimulates gonadal development in the first place, terminates breeding.

3. Relative photorefractoriness.

This is said to have occurred in species whose gonads regress but are readily stimulated again by exposure to long day lengths.(2,6,8,10) These birds have a reduced level of neural activity controlling GnRH.(6) In these birds decreasing photoperiod (short days) terminates breeding.

Photosensitivity is gradually recovered after photorefractoriness, usually as a result of exposure to short daylengths. In natural conditions most species become photosensitive in autumn. This is manifested in some species as a brief resurgence of autumnal sexuality that usually does not lead to breeding.(2,8)

For birds that normally breed in high latitudes (further from the equator) long daylengths are needed to induce photorefractoriness and very short daylengths are required to regain photosensitivity in absolute photorefractory species.(2,8) In contrast the reproductive system of species that normally breed in low latitudes (tropical regions) can be altered by changes in photoperiod of less than one hour.(5)

That most birds do not go on to breed immediately in autumn has been explained by the endogenous control of the hypothalamo-pituitary-gonadal axis.(8) In spring-breeders there is a high resistance of the pituitary to gonadal steroid feed back that inhibits the onset of reproduction. Gradually the ‘photoperiodic drive’ overcomes this inhibition as daylength increases after winter. There may also be a gradual increase in the ‘hypothalamic drive’, that is a gradual lowering of the pituitary’s resistance to gonadal steroids and a progressive increase in the level of GnRH produced by the hypothalamus.(8)

In species that breed in autumn, such as house sparrows, the grey partridge and the great tit, there is a low resistance of the pituitary to gonadal steroid feedback and GnRH levels begin to rise immediately.(8)

Other factors

There are species in which photoperiod has little or no obvious effect in the wild, usually due to their migratory patterns encompassing vast changes in latitude and photoperiods. In these species other theoretical sources of initial predictive information include annual cycles of rainfall and humidity, especially in some tropical and arid zone species.(2,11)

Zebra finches have been shown to maintain their reproductive system in a near functional state so that breeding can commence as soon as conditions allow.(9) The mechanism underlying this stimulation is not certain but postulated theories include the sight of rain or a change in humidity.

Essential supplementary information [8,11]

This includes:

- Establishment and defence of a breeding territory, which is linked to peaks in plasma testosterone levels in both males and females
- Social cues like breeding plumage in sexually dimorphic birds, mate presence and pair courtship behaviours. This can be visual, auditory and tactile information
- Interactions between rival males can significantly alter plasma androgen levels, either stimulatory or inhibitory depending on the outcome of the interactions
- Nutritional levels influence the timing of the first clutch by the limits of available food for the formation of eggs. A dependable supply of energy, protein (including essential amino acids) essential fatty acids, vitamins and minerals must be available[1,7]
- In some species, constituents of the diet may be directly stimulatory or inhibitory to gonadal development. Phytoestrogens can be present in new herbage growth and have been shown to inhibit the gonadal growth of the Californian quail *Lophortyx californicus.* Stimulation of gonadal growth by a compound or compounds unknown, in the new growth of herbaceous plants, has been documented in rodents but not in birds[11]
- Temperature. Low temperatures tend to depress testis growth and disrupt ovulatory cycles in some species. These conditions were accompanied by increases in circulating corticosterone levels and may be indicative of a general stress effect on reproduction
- Rainfall may be supplementary as well as predictive in arid zone species

Implications for veterinarians

It is important that biologists consider food to be the ultimate factor in determining the onset of breeding seasons [1,2,7,8,9,11] and hence nutrition should be the first thing addressed when dealing with modifying breeding in companion and aviary birds.

The information on other factors has been collected from two extremes. Much of the photoperiod information comes from either domestic fowl [1], which have been intensively bred to minimise seasonal breeding, or from wild caught birds kept in temporary captivity. [2,3,4,6,7]

The patients a veterinarian sees will fall somewhere between the two. Domestication tends to dampen the external controls on breeding season. Pet birds are often exposed to the same erratic daylengths as their owners. Avicultural birds may be kept in conditions that in no way resemble their wild habitats.

It is frustrating that very little of this research has been carried out on commonly kept species. I have been unable to find any photoperiod studies carried out on psittacines. There has been some work on other factors controlling breeding season published on cockatiels [12,14] and orange-winged amazons [13] recently. Hopefully in the near future there will be more information available to base recommendations on.

There are two main situations where this information would be of use to avian veterinary science; 1.Improving breeding success and 2. Terminating breeding behaviour.

1. Improving breeding success

In the first place it is important to ensure that the specialised dietary requirements of the species are met and that nutrition is capable of sustaining reproduction. The use of protein and energy ‘flushes’ just prior to breeding season to improve fertility is an important tool. Some species, in the wild, have diets that change during the breeding season from their standard ration eg. Swift parrots [16,17] and toucans. [14,15] Other factors that influence the breeding season should then be addressed.

Birds maintained in outdoor aviaries with no supplementary lighting may not be getting the reproductive triggers they need for successful breeding or their response to these triggers may be dampened. For example low latitude species kept closer to the tropics may not receive enough short days to terminate photorefractoriness. [8] In the reverse situation the high latitude species may terminate the breeding season early due to excessive photostimulation. [3,10,11]

Matching photoperiod to the species normal light to dark cycles would be the ideal solution. It may be possible to provide longer light hours with supplementary lights but unless using a completely indoor facility it is difficult to simulate short days. Problems also arise in mixed aviaries where birds from many different habitats are managed in a similar fashion.

Many birds that are short to long distance migrants can be exposed to a bewildering schedule of photoperiod. For example the swift parrot, the orange-bellied parrot and the blue winged parrot breed in Tasmania in the spring but winter on the mainland. [18] Swift parrots can migrate from Tasmania to Victoria, South Australia and as far north as southeast Queensland.[16,17] It has been speculated that photoperiod is of less importance in migratory species than the endogenous reproductive rhythms. [3,11]

There is the interesting question of the effect of night-lights on breeding success. It is possible that these lights may be interfering with the natural photoperiodic cycles. I have been recommending that the lowest intensity lights that will prevent "night frights" be used. I think further research is needed on this issue. Most of the breeders that use night-lights do so for cockatiels. Being an arid zone species it is possible that these birds are similar to zebra finches in the constant readiness of their reproductive cycle, or at least photoperiod may be of lesser importance. If this is the case then the night-lights will have little impact.

Aviculturists should provide the essential supplementary information required for breeding. The main problem that occurs here is the lack of available information on each species' specialised requirements. Aviary design and management have their most appreciable impact at this point. In particular, the pairs' need to establish and defend a territory has a profound impact on breeding success. This has also to be balanced against the stimulatory effect on territorial defence and interactions. [2,8,13]

In summary, the aviculturist and the clinician faced with the task of improving breeding success may be overwhelmed by the variables that can be involved. It should be emphasised that most species have a degree of flexibility to the controls that drive breeding (eg. ostriches). Getting birds to breed is only half the challenge. The next step, and the hardest, is to gain optimum breeding success from the birds.

- **The termination of breeding behaviour**

There are a number of situations where clinicians find it necessary to switch off breeding behaviour. This can range from the simple nuisance value of masturbation and aggression in a companion bird to life threatening disorders of the reproductive tract in hen birds (including calcium deficiency, egg binding, egg peritonitis, metritis, cloacal impaction or obstruction and chronic egg laying). [14,15]

2a. Hormonal therapies

Suppression or termination of breeding by hormonal therapy is an option. Progesterone has an unacceptably high level of side effects including hepatic lipidosis, diabetes mellitus and immunosuppression. Sudden death following progestagen administration is another recognised side effect. [14]

Human chorionic gonadotrophin (hCG) is being increasingly used for treatment of egg peritonitis in birds.[20] It should act to inhibit GnRH release from the hypothalamus and so switch off reproduction. The duration of treatment effectiveness is at this stage unreported.

Hudelson [12] in *Seminars in Avian and Exotic Pet Medicine 5 (4) 1996* reviewed other new therapies that show promise. While these drugs reviewed are experimental at this stage he found that prolactin showed great promise for safe and effective termination of reproduction.

2b. Surgical therapies

In some birds hysterectomy is a good solution to reproductive problems. In companion birds this may often be the preferred option for owners. It is recommended however that birds be stabilised prior to surgery to increase survival rates. [12,14,15]

There is a technique reported in which a single loop of suture is placed through the magnum of the oviduct. [12] In poultry this was enough to prevent egg laying in 75% of birds and reduce egg laying in the rest. It has not been used in companion birds to my knowledge. There is also no follow up data on complications in those birds that did continue to lay.

2c. Environment modification therapies

Modification of the birds' environment is used in the control of reproduction at least as an adjunct to other therapies but can be used on its own successfully. [12,20]

The effects of nutrition on the reproductive cycle can be used to advantage. Companion birds, and in particular, cockatiels and budgies are quite often maintained on high-energy seed diets.[19] If food is the main controller of breeding season in these birds it is no wonder that these birds are so frequently presented for sexual hyperactivity. Reducing the energy and protein base of these diets can dramatically alter behaviour linked to reproduction. Male cockatiels will often cease masturbatory behaviour and have reduced levels of aggression when switched to maintenance diets of pellets or low fat seeds.[19]

A change of photoperiod has been used to terminate breeding.[12] Previously I have been using a short day schedule of four hours light to twenty hours dark for four to five days. I suspect however that this has not been inducing the termination of breeding through the photoperiod effects but instead acting as part of the general environmental disruption I recommend concurrently. This schedule may induce photosensitivity in birds that were becoming photorefractory and have the opposite effect to what was desired. Hudelson [12] recommends a long day schedule of twenty hours light to four hours of dark.

The best recommendation for photoperiod change will ultimately depend on the main reproductive drives for the species. In some species in which photoperiod plays little role (eg. budgies and zebra finches) changing light to dark ratios will have minimal effect.

Decreasing light will aid in the termination of breeding of those species that do not develop photorefractoriness. Increasing light hours will terminate reproduction in those that do become photorefractory. I stress that at this point the information required is simply not available.

Using modifying factors to disrupt the breeding cycle is based on more reliable knowledge. Modifying factors include the loss of the nest, loss of the mate and predation of the eggs. [2,11]

Removing the bird from its usual cage and removing any nesting material and nestboxes can simulate the loss of the nest. Other techniques include moving the birds to a less secluded position in the house and changing around perches and cage furniture.

Removing a bird from the sight and sound of its mate is an effective technique for terminating breeding. In hand raised birds it is important to remember that the perceived "mate" may be a human or toy. Removing the toy or reducing the visual, auditory and tactile stimulation between a bonded owner and the bird may be effective in these situations.

Hudelson [12] questions the ethics of such a proposal, claiming that the loss of social interaction with a bonded pair should be considered as cruelty. I feel it is a justifiable technique to temporarily suppress the breeding cycle.

Predation of the eggs is another controversial technique. Some species (determinate layers) will only lay a set number of eggs regardless of what happens to the clutch. [1,2] In these species removing the eggs will not prolong egg laying. Other species (indeterminate egg layers) will respond to the loss of their clutch by production of another clutch.[1,2]

In these birds the clutch of eggs is necessary to stimulate the prolactin levels that terminate breeding. [1,12,14] In these birds the use of dummy eggs or "blowing" and replacing the eggs may be beneficial. [12,14] Some of these birds, especially if hand raised, will continue laying eggs above and beyond the normal clutch size. In these birds continued predation of the eggs when combined with other therapies may be needed to terminate breeding.

Summary

The control of breeding season in birds is a complex interaction between endogenous and exogenous factors. Where these factors are known, they can be used to enhance the captive breeding of birds kept in locations that vary considerably from their natural habitats. They can also be used to inhibit or terminate reproduction in companion or aviary birds with reproductive problems and so aid their recovery. Far more research is needed before sound recommendations can be made for all species.

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