

Avian breeding cycles

R. K. MURTON

AND

N. J. WESTWOOD

Institute of Terrestrial Ecology
Natural Environment Research Council
Monks Wood Experimental Station
Huntingdon

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Preface

We aim in this book to stimulate research and so have addressed ourselves to post-graduate workers and senior undergraduates. Notwithstanding this objective, we hope that the book will appeal to ornithologists in general. Our aims have to some extent delimited the style. It would certainly have been easier to draw general broad conclusions, which may as a result have been oversimplifications, than to summarize other workers' results accurately and we hope that we have adopted the most useful course. We have not neglected the early literature, for many of the experiments and observations made in the past remain valid, even if they have been repeated with the greater sophistication that comes with hindsight. Some topics are particularly difficult to present in a readable manner and we are very conscious of the technical jargon referring to the so-called 'pituitary gland'. There are no simple names for the structural components of the neuro-hypophyseal system, yet knowledge of its structure is essential if the problems of understanding avian photoperiodism are to be resolved. We hope that the liberal use of text-figures will help the reader.

When Lofts and Murton (1968) reviewed photoperiodic and physiological adaptations regulating avian breeding cycles they pleaded for a greater synthesis of ecological and physiological research, rather than a multiplicity of photoperiodic manipulations of a few north-temperate species; at the same time they suggested that ecologists had neglected the field consequences that may follow from a primarily physiological adaptation. It is still true, in spite of the increasing use of such terms as eco-physiology in the biological vocabulary, that research on avian biology is too polarized between ecology or physiology. Our thesis is that this represents an out-moded approach and that the exciting advances will be made only by those prepared to adopt a much more integrated and multidisciplinary viewpoint. The text concentrates on avian breeding cycles but the viewpoint is applicable to other aspects of avian biology. This is particularly true for some of the topics which today are important in an applied context.

Environmental pollution in general and, in particular, the subtle effects of organochlorine insecticides on the reproductive performance of individuals and populations of raptorial birds, has highlighted our lack of knowledge of avian eco-physiology. Often one observes a marked inter-specific variation in response to a given pollutant, presumably partly reflecting differences in biochemical make-up of the species and partly ecological differences in exposure risk. Why are raptorial species so sensitive to organo-chlorine compounds? Dieldrin has been responsible for the direct death of adult birds, DDT and its metabolites cause egg-shell thinning and a reduced breeding success, while PCBs (polychlorinated biphenyls) cause egg infertility as well as other harmful effects. Each organohalide compound interferes

with a particular range of physiological mechanisms. Normally population processes operate on wild animals in ways which allow a decrease in adult survival rate to be compensated for by a decrease in the mortality rate of the egg and nestling. However, when dieldrin and related compounds caused adult losses among raptorial birds, other chemicals were also in use which caused reductions in breeding success and productivity. Attacking an animal from different directions in this way is the object of integrated methods of pest control and it is not surprising that populations of many birds of prey declined drastically when the more persistent and toxic insecticides were introduced.

A multidisciplinary approach requires knowledge of a wide spectrum of subjects and is attended by the risk of becoming a 'jack of all trades and master of none'; we were conscious of this pitfall in writing this book. But there can be no real excuse for not trying. For example, much time would have been saved and research effort spared if those of us who were interested in the photoperiodic control of avian breeding seasons had appreciated the importance of a circadian rhythm of light sensitivity in animal photoperiodism. The relevant research was published as early as the late 1950s but it referred to plants and invertebrates. It required the pioneer efforts of Professor W. M. Hamner in the mid-1960s to show that birds measure daylength by essentially the same mechanism as that employed by invertebrates and plants. Now we realize that a multiplicity of physiological functions exhibit an endogenous circadian rhythmicity so that under appropriate experimental conditions a free-running periodicity close to, but not exactly equal to, a 24-hour duration can be demonstrated. These rhythms are entrained by the daily cycle of night and day, thereby assuming an exact 24-hour periodicity. However, entrainment also determines the phasing of rhythmic functions relative to the light-dark cycle and relative to each other. There is a need to measure how phasing effects alter with the seasonal daylength cycle and how species have evolved appropriate adaptations to suit their normal latitude range.

At present interest centres on the manifestation of circannual rhythms of body function, for example, of seasonal body moult, fat deposition, the waxing and waning of the reproductive system. These circannual rhythms appear to be entrained by the amplitude produced by the seasonal variations in daylength throughout the year. It is not yet fully established whether these circannual rhythms are controlled by endogenous circannual oscillators, in the way that circadian rhythms appear to be controlled by circadian oscillators. We incline to the view that they are compounded from a diversity of circadian rhythms which alter in phasing throughout the year, thereby producing new rhythms. However, the essential point is to define the manner in which rhythms are entrained. In the tropics—where twilight effects can be very important—there are many species whose rhythms are entrained by the daylength oscillations of very low amplitude, but entrainment is weak so that different individuals within a population are not well synchronized, one with another; special adaptations are needed to ensure synchrony. In other species entrainment may not occur so that rhythmic functions run free to result in breeding activity intervals of less than 12 months. The assertion of some field workers

that the slight change in daylength near the equator cannot affect the timing of breeding cycles therefore results from a misunderstanding of the mechanisms involved.

The above does not deny that other factors are also important in timing seasonal events. Males, whether of tropical or temperate species, are brought into full reproductive condition by appropriate responses to the light cycles under which they have evolved adaptive responses. On the other hand, in females the ovarian follicles can be stimulated only to a point at which limited quantities of yolk are added and some other factor is needed for the final expression of ovarian development. (Lofts and Murton 1968). The final growth phase during which much yolk is added, resulting in a ten-fold increase in weight prior to ovulation, occurs over the 6–12-day period of pre-incubation courtship from the male. It now seems from the work of Jones and Ward (1976) that a labile protein reserve is accumulated in the flight muscle of the female before egg-laying—in *Quelea* the reserve increases by 80% in females prior to breeding but by only 14 per cent in males—and this is rapidly transferred to the developing follicles during the period of courtship; the amount available could have a direct effect in determining clutch size. The achievement of an appropriate nutritional state obviously provides the final proximate regulation for the onset of egg-laying, that is, the critical day-to-day adjustment within the broad time spectrum of reproductive activity which is dependent on the photoperiod and on male courtship. But it would be wrong to conclude with Jones and Ward that no other environmental releasers are required for birds to breed at the appropriate time of year.

The extent to which photoperiodic responses serve to control breeding, or other seasonally occurring events in the bird's calendar, in a permissive or obligatory fashion broadly changes with increase in latitude and the intensity of the selective disadvantages of any imprecision. In short, the seasonal cycle of a wild bird implicates an extremely complex interaction between endogenous, autonomous components, which are expressed as self-sustaining diurnal and annual rhythms, and environmental stimuli. A considerable species-specific variability in adaptive response is discerned, although the degree of adaptiveness is necessarily open to subjective assessment. One of the points we wish to stress is that evolutionary changes are constrained by the complexity of the physiological mechanisms involved so that closely related species can be shown to have photoperiodic responses which conform to a common pattern. The food and feeding ecology of ducks of the genus *Anas* differ quite considerably between species yet all have reproductive cycles which are determined by a photoperiodic mechanism which is relatively constrained within the genus (Chapter 14). To what extent such physiological restraints inhibit the full ecological exploitation of a niche it is impossible to say, when competition from better adapted phylogenetic lines is absent. It is not easy to identify biological compromise. There are many indications that species may evolve physiological adaptations at a particular latitude that effectively pre-adapt them for niches in a totally different range and we provide some examples referring to montane species and those which have adapted to drastically man-altered environments.

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 N.J.W.

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Introduction to avian reproductive strategies

Summary

Successful reproduction demands the temporal organization of gamete preparation in relation to the mate and environmental resources of energy. Photoperiodism is the process whereby endogenous circadian and circannual rhythms of body function are synchronized with external daily and seasonal rhythms. Latitudinal gradients in the adaptive phasing of a wide range of these body functions, involving also breeding seasons, can be identified. Since rhythmic processes also control rates of development and attainment of maturity a host of physiological parameters, including body size and metabolic rates, are correlated, although it is difficult to identify causality. For example, body size increases with increase in latitude in closely related species (Bergmann's rule) while the metabolic rate declines. The body weight of *Anser* and *Branta* goose species is inversely correlated with mid-latitude of the breeding range (positively with the mid-latitude of the winter range) but is more closely correlated with the photoperiodic response which itself is related to the latitude. This photoperiodic response is in turn very closely related to the survival rate of various species, suggesting that the 'biological clock' is the fundamental mechanism controlling a wide range of co-adapted physiological and ecological responses.

In very predictable environments, such as equatorial evergreen forests, the survival rate and life span of birds increases, although their reproductive rate declines. The evolution of species-specific survival rates, conversely mortality rates, is mentioned in the context of the increased risks consequent on reproduction, particularly in the tropics. Age of attainment of reproductive maturity and the reproductive rate will depend on a balance of survival probabilities between breeding and increasing the risk of adult death, or of not breeding and leaving no progeny. These species-specific survival rates are not to be confused with the factors which regulate animal numbers (see Chapter 16).

Breeding seasons

In the past, most studies of avian reproduction have been divided between two major disciplines, the domain of ecologists and physiologists respectively. Ecologists have been interested in the evolutionary significance of clutch size, productivity rates, nesting dispersion, and other parameters of reproduction that can be related to the external environment. They have concerned themselves with the so-called *ultimate* factors (see below) which determine breeding adaptations, whereas physiologists have studied the mechanism of reproduction and the internal environment of the individual. Whereas all workers recognize the existence of a co-adapted system, some ecologists have tended to make the tacit assumption that given sufficient environ-

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mental pressure physiological adjustment is relatively easy. In attempting to synthesize some of our physiological and ecological understanding of avian reproduction, one object of this book will be to illuminate some of the patterns of ecological adaptation that result from the restraints imposed by complex physiological mechanisms. Another aim is to persuade physiologists to relate their experiments to the natural conditions under which their subjects live. We believe that future advances will involve a multi-disciplinary approach and we hope our book will provide a starting-point and stimulus.

Mention above of *ultimate* factors introduces a clarification brought to the subject many years ago by J. R. Baker (1938a). Baker was concerned with the determination of breeding seasons but his ideas apply to clutch size, nest construction, migration, and a host of other topics. He distinguished *ultimate* factors as being those which essentially have survival value and not much causal function, from the *proximate* factors, which provide the actual mechanisms whereby breeding adaptations are achieved; both factors are of course determined by natural selection. Most bird species breed around the time when food supplies for themselves and their young are most readily available (Thomson 1950). This follows because natural selection favours those genotypes whose progeny are reared at the most appropriate times. Attempts to raise young at less advantageous seasons are nullified by a wasteful and disproportionate nestling mortality; indeed, parental survival may even be endangered as well. A differential survival rate in relation to food resources can define the spread and characteristic pattern of the breeding season, thereby constituting an ultimate regulator of breeding periodicity. Similarly, egg size must ultimately be set in relation to the needs of the young chick and resource availability. Ultimate factors affecting reproduction have provided the subject-matter of three masterly books by David Lack (1954, 1966, 1968a).

To achieve breeding condition and anticipate an approaching season of good food supplies and the availability of nesting cover, etc., birds have evolved response mechanisms to a host of environmental stimuli which function as signals heralding the approach of suitable times. The most important proximate factor is the seasonal change in length of day which stimulates, via neurohypothalamic pathways, endocrine secretions that allow the gonads to assume a functional state. However, many other proximate factors, including temperature, population density, appropriate behavioural stimuli from the mate, and availability of nesting sites, influence the birds' capacity to reproduce. The study of proximate factors has primarily been the prerogative of the physiologist and experimental studies of photoperiodism have featured prominently in their repertoire (major reviews by Burger 1949; Farner 1959, 1964; Marshall 1959; Wolfson 1959; Benoit 1961; Lofts and Murton 1968; Farner and Lewis 1971).

Reproduction is essentially a matter of temporal organization in relation to the mate and environmental resources. Photoperiodism is the process whereby the animal adaptively synchronizes an internal rhythm of body function with the external chronology of day and night and the seasons. To understand avian reproductive strategy requires knowledge of the way in which the 'biological clock' functions. In reviewing

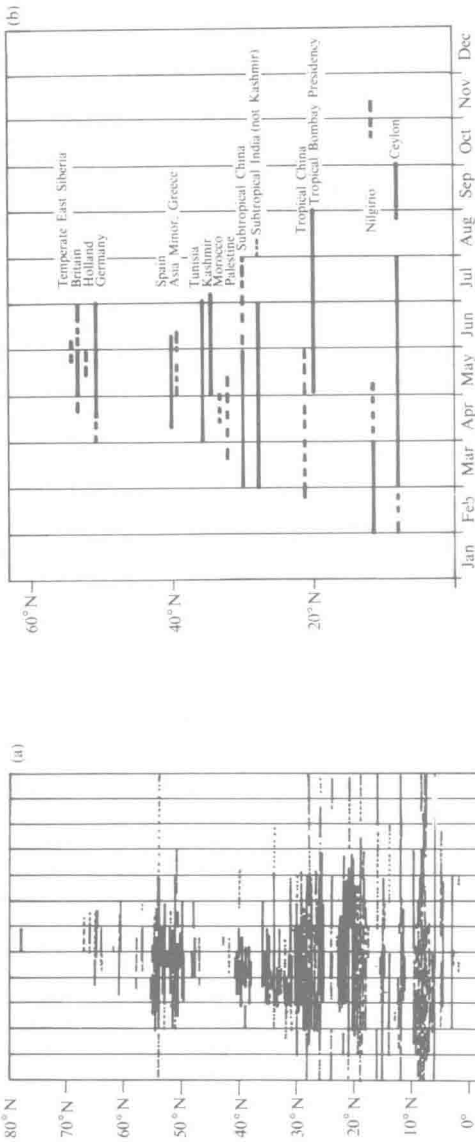


Fig. 1.1. Egg-laying seasons of passeriform birds at different latitudes: (a) passerines in general; (b) Great Tit *Parus major*. In (a) the line representing *Passer domesticus* in the original has been shortened since it was clearly inaccurate in the original and breeding is known to end in late July (see also p. 219), from Baker (1938a).

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avian breeding seasons (and also flowering seasons and periodic leaf-fall in plants), Baker long ago appreciated that he was dealing with an internal rhythm interacting with the external environment (Baker and Baker 1936) and he recognized patterns of change in breeding season with latitude (Baker 1938*a, b*). Much of what Baker wrote has been neglected or overlooked by later workers; for example the kind of data reproduced in Fig. 1.1, from which he concluded that 'neither a long day nor yet a rapidly increasing day are necessary concomitants of rapid reproduction by birds'. And

Despite all the intensively interesting experiments on the effects of light on the reproduction of birds, for which we are indebted mostly to the pioneer work of Rowan (1929 and earlier and later papers) and of Bissonnette (1930, etc.), yet clearly length of day stands in no direct and obvious relation to the breeding season of birds under natural conditions. One is forced to the conclusion that light is only one of the factors concerned. Why, otherwise, should birds breed later in the boreal zone than in the temperate? After the March equinox the days are longer the further one goes north.

It has taken nearly 30 years to resolve this topic, partly because the dichotomy of physiology and ecology failed to identify it as a problem. However, it has also been necessary to wait for the realization that circadian clocks are composed of systems of endogenous coupled oscillators entrained by the environmental 24-hour oscillation of day and night and, even more important, that circannual rhythms of animal function also exist, entrained by the yearly oscillation produced as the sun moves back and forth across the equator and the duration of day and night (and twilight) change accordingly (Chapters 11, 12, and 13). The significance of photoperiodism has been sadly misunderstood by many ecologists, Phillips (1971) exemplifying their quandary.

Baker recognized that the breeding seasons of birds varied in a systematic manner between the equator and poles but not in direct agreement with the way length of day alters with latitude. Other workers too have been impressed by latitudinal gradients in reproductive strategies, which appear to have some underlying fundamental basis rather than being a simple reflection of ecological changes from tropics to poles (see for example, Slagsvold 1975*a*). In the tropics clutch size is smaller (Lack 1948, 1968*a*; Lack and Moreau 1965; Cody 1966) the breeding season longer (Baker 1938*a, b*), and adult survival rates higher than in temperate zones but the change in these parameters with latitude is usually proportionately greater than the increase in day-length (but see Hussell 1972). This has led various workers to seek an alternative to a general explanation which is derived from Lack's specific explanation for an increase in clutch with latitude: that increase in the available hours of daylight enables birds to collect more food for their young. Ashmole (1963*a*) modified Lack's thesis by pointing out that stable tropical ecosystems would also be saturated with individuals, so that the real difference in resource availability could be between a saturated tropical habitat, and a temperate habitat, in which days are long and the pre-breeding population is much reduced by the mortality occurring during the contra-nuptial season.

The concept of stability is not easily quantified but it is widely accepted and Cody (1971) has justified it in a valuable review of ecological aspects of avian repro-

duction. The essential point is the extent to which ecological resources are predictable, and this is eventually dependent on the degree of seasonal fluctuation in climate. The Australian desert is frequently instanced as an unpredictable environment but in reality in many parts the rain arrives at a very regular time, even though the quantity may be very low and variable. Some plants are able to flower and fruit with extreme regularity and temporal precision in the same month each year, while others may be very irregular and bear variable crops. For this reason it is necessary to consider the actual resource which a bird demands in order to make generalizations about the predictability of the habitat. A really stable environment, such as equatorial evergreen forest, offers little stimulus for a change in well-adapted animals and once an individual becomes established the probability will be small that any offspring it produces will be better adapted than itself. In such conditions plants can resort to vegetative reproduction. In birds, the life-span in tropical species is on average higher than those of closely related temperate forms, whereas eggs and nestling success is lower. A relatively high survival rate is also noted in birds which inhabit the more stable habitats in temperate zones as does the Swift *Apus apus* (Lack 1954) and various oceanic birds (Wynne-Edwards 1962). Genetic variability is further reduced by the tendency for successful males and females to remain paired for life. Cody (1971) suggests that the relative stability of tropical ecosystems compared with those of temperate zones facilitates predators becoming specialists of eggs and young thereby reducing breeding success (e.g. Skutch 1966). On the other hand, adult losses are more likely to result from accidents, and these are perhaps more often provoked in fluctuating temperate systems compounded by inclement climates. In addition, competition from young must be increased in temperate areas as a result of the higher productivity rates. In unstable ecosystems there is more premium on realizing as much of the genetic variability that is potentially provided by random gene recombination, for this will offer a greater opportunity for a species to adapt to changing ecological conditions (but this might also result in a bigger wastage of genotypically unfit animals (Murton 1972)). In contrast to the long pair bonds and monomorphism characteristic of tropical birds, temperate species tend to dimorphism and short pair bonds.

Survival rates

As mentioned above, natural selection must favour those individuals which leave the largest number of surviving offspring, yet reproduction is attended by various risks which increase the probability of accidental death, for example, changes in metabolism occur, eggs must be attended, and the presence of young increase the pressure on food searching. This is clearly illustrated later in this book (Fig. 10.5, p. 257): juvenile mortality in the Rook *Corvus frugilegus* occurs during the summer droughts, when food supplies are restricted, whereas adult losses are concentrated in the breeding season (see also Tables 2 and 3 in Vowles and Harwood 1966). In the Starling *Sturnus vulgaris* it has been suggested that the parents are slightly less vigilant when busily collecting food for their chicks and that this enables them to be surprised more easily by cats and other predators (Coulson 1960). In this species the females