Photoperiodism in waterfowl: phasing of breeding cycles and zoogeography

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(Accepted 17 January 1978)

(With 1 plate and 16 figures in the text)

The egg-laying seasons of various captive waterfowl in the Wildfowl Trust collections at Slimbridge and Peakirk are compared with the situation in the wild. Special attention is focussed on the shelduck and sheldgeese (Tadornini), perching duck (Cairinini), diving duck (Aythyini), sea duck (Mergini), eiders (Somateriini) and stifftails (Oxyurini).

Two kinds of response could be distinguished at Slimbridge. In one, egg-laying began sometime in spring, when daylengths reached a stimulatory level, and continued until the corresponding daylengths in summer or autumn were reached, that is, the egg-laying season extended symmetrically on either side of the summer solstice. This is regarded as a "primitive-type" response and is characteristic of phylogenetic lines which are thought to have evolved in, and radiated from, the tropics; the comb duck, muscovy duck, ringed teal and southern pochard are examples. The second kind of response was characterized by the cessation of egg-laying when daylengths still remained stimulatory, that is, a characteristic photorefractoriness to long days developed, and egg-laying occurred during the first half of the year at Slimbridge. We term this a "temperate-type" response, and examples are provided by nearly all the sheldgeese and shelduck, by the mandarin, Carolina, white-winged wood duck and all Aythya and the sea duck. Only a few examples of apparently intermediate breeding response were noted and these transitional species are discussed, for example the Andean goose, Abyssinian blue-winged goose and Radjah shelduck.

The egg-laying cycles can be described as entrained rhythms and their phase angles measured in relation to seasonal daylength changes at Slimbridge. In Aythya, the onset of reproductive activity was strongly correlated with the latitude of origin whereas the end of breeding was not. This was because refractoriness developed at about the same time in all species, even though they began breeding in response to different photoperiods. For this reason, the length of breeding season expressed at Slimbridge was correlated with the mid-latitude of the breeding range in the wild but even more strongly with the photoperiod under which egg-laying was initiated. The onset of breeding in the sheldgeese and perching duck was not related to latitude, perhaps because species have had time to modify their ranges. However, the end of breeding in perching duck was related to latitude. Cessation of breeding corresponds to the onset of moult and the secretion of thyroid hormones.

We suggest that as waterfowl radiated to higher latitudes their "biological clocks" became entrained to the new light regimes and a host of physiological functions were ordered in an adaptive rather than competitive sequence. It is because so many biological functions are liable to compete for scarce environmental energy supplies that some kind of endogenous partitioning is necessary. This endogenous component is seen when different species are kept under standard lighting conditions. It follows that the photo-response of a species reflects its evolutionary history and so the discussion broaches zoogeographical and taxonomic topics. For example, it seems unlikely that the white-winged wood duck evolved in the tropics, and likely that the sheldgeese and shelduck radiated from a post-
Gondwanaland land mass. There are physiological grounds for putting the red-crested pochard and rosybill into separate genera and these are supported by morphological characters.

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Introduction

The dates, and hence photoperiods, on which different waterfowl species (swans, geese and ducks of the family Anatidae) begin laying in the collection of the Wildfowl Trust at Slimbridge, Gloucestershire (52°N) are fairly consistent from year to year. For many species, records go back 20 years or more and implicate many females; however, the standard errors for mean laying date are small despite annual temperature variations (Murton & Kear, 1973a, 1976; Kear & Murton, 1976). When the mean daylength at egg-laying is plotted against the mid-latitude of the natural breeding range for a group of closely related waterfowl (usually members of the same genus) straight line regressions sometimes emerge whose slopes and constant terms vary from genus to genus. This is true for *Cygnus, Anser, Branta, Tadorna* (Murton & Kear, 1973a), *Aythya* (Murton & Kear, 1973b) and *Anas* (Murton & Kear, 1976). The principle is likely to apply to other avian taxa when appropriate data are accumulated, for example, see Mallinson & Mallet (1975) for Phasianidae. Thus far, with the exception of *Anas* and *Dendrocygna* (Murton & Kear, 1976) and *Cygnus* (Kear & Murton, 1976), only the onset of breeding has been considered. In this paper we define the whole egg-laying cycle under controlled conditions and in the wild of the tribes: Tadornini (shelduck and sheldgeese), Cairinini (wood duck or perching duck and geese), Aythyini (scaup and pochard), Mergini (scoters, goldeneyes and mergansers), Somaterini (eiders) and Oxyurini (stifftails).

Our aim in this paper is to demonstrate the existence of an important endogenous component (cf. Gwinner & Dorka, 1976) in avian reproductive periodicity which imposes more constraints on ecological adaptation and species distribution than is often assumed.
This thesis in no way denies that environmental food supplies are of prime importance nor that the female may provide the final proximate timing of the cycle (cf. Jones & Ward, 1976). The crucial issue is the extent to which birds are able to predict when breeding is likely to be possible and to order their physiological state accordingly. Breeding seasons, like cycles of moult, fat deposition, protein synthesis, are physiologically controlled by the periodic secretion of appropriate hormones, and the endocrine basis of the breeding and moult cycles of domestic strains of the mallard *Anas platyrhynchos* is becoming defined (Assenmacher, 1974; Haase, Sharp & Paulke, 1975). Endocrine secretions are regulated by appropriate seasonal photoperiodic stimuli and this is well established in the mallard (Assenmacher, 1974). In turn, photoperiodic phenomena resolve into problems of time measurement and involve the "biological clock" and circadian rhythm mechanisms (Pittendrigh & Minis, 1964; Lofts, Follett & Murton, 1970; Daan & Aschoff, 1975; Pittendrigh & Daan, 1976). Interspecific differences in breeding periodicity have to be explained in these terms, while Assenmacher (1974) suggests grounds for implicating circannual rhythms of reproductive function. These topics will be pursued separately (Kear & Murton, in prep.) in relation to the evolution of dimorphism and to this end we shall refer again to *Anas* species.

The entrainment of endogenous physiological rhythms by photoperiodic mechanisms is likely to prove of fundamental importance in understanding ecological adaptation. For example, Würdinger (1975) has shown how the rate of growth and development of various goose species, kept under identical rearing conditions, is species-specific and correlated with the latitude of origin, in the same way as are egg-laying cycles of these same geese (Murton & Kear, 1973a). In northern species the maximum weight increase of goslings occurs early in the development period but later in those species originating from lower latitudes. The response is adapted to the duration for which vegetation suitable for grazing is generally available. The important point is that an approximately appropriate physiological response to ecological conditions is built into the species and is manifested as a photo-entrained endogenous response when the species is studied in captivity.

The study of long term rhythms ideally necessitates holding subjects for at least two cycles under constant, non-entraining, photoperiods which allow any underlying endogenous free-running periodicities to be expressed. To do this for a large number of closely related bird species, in a manner that allows comparative information to be derived, is clearly expensive in terms of cage facilities. However, at Slimbridge a unique and representative collection of swans, geese and ducks is kept and breeds under reasonably standard conditions so that the mode of entrainment to the same light regime or *zeitgeber* (this being the seasonal daylength cycle at 52°N) can be compared between subjects. In a few cases it has been necessary to supplement Slimbridge records with data from Peakirk, Cambridgeshire (53°N), where a smaller collection is maintained by the Wildfowl Trust, or occasionally from other zoological collections.

**Methods**

At Slimbridge and Peakirk, the waterfowl considered here are kept in outdoor enclosures supplied with a pond and vegetation that constitute a reasonable approximation of natural conditions. In the wild, food supplies often vary markedly in quantity and nutritive quality throughout the year, while changes in the endogenous physiological condition of the bird may result in highly seasonal demands for particular nutrients (Jones & Ward, 1976). Nevertheless,
at Slimbridge the birds receive a regular balanced diet and are exposed to more or less the same seasonal changes in daylength, temperature and state of vegetation. The birds are either kept as pairs, or else, depending on the behaviour of the species, in larger enclosures containing several kinds where conspecific pair-bonds are soon formed. Most females produce normal clutches of eggs in nests sited under the cover of vegetation or in specially provided boxes and burrows.

In the Anatidae, as with avian species in general, the production of a clutch of eggs in a properly constructed nest means that the female has received appropriate courtship stimuli from a male at the peak of his reproductive cycle, and so egg-laying marks a precise stage in the breeding cycle. Records have been kept of the date of first egg-laying of every species and, as mentioned, in some cases these embrace more than 20 seasons. It has not been feasible to keep individual records where several females of one species are present and, adding to the complexity, some species normally produce repeat clutches which, in others, is encouraged since the first ones are removed to be incubated artificially. Thus, the history of all clutches produced is not known, and we cannot define the mean egg-laying season for any one year. However, the mean date of production of first eggs over the years for which records are available gives a good indication of the normal start to the egg-laying season and difficulties arise only in the case of species that have seldom laid in captivity. The date of laying of the last clutch can be calculated because records are kept of many hatching dates.

For this paper, the egg-laying season is defined as the period extending from the date on which the earliest clutch ever recorded at the Wildfowl Trust was begun, that is, a datum from only one year, to the date on which the latest recorded clutch was started, irrespective of the year, this usually being calculated by subtracting the incubation period and time to produce the whole clutch from the latest recorded hatching date. The median date for first egg-laying was also calculated from the first egg records for all years that were available. Dates and equivalent photoperiods (sunrise to sunset plus civil twilight at 52°N) are detailed in the Appendix and they have been presented in a series of figures in relation to the seasonal daylength cycle at Slimbridge. The results compare the breeding seasons at Slimbridge and Peakirk with those in the natural range when information exists.

For descriptions of plumage colour and pattern the reader is recommended to consult Delacour (1954–1964) or Scott (1957). Figure 1 presents a hypothetical evolutionary tree from Kear (1970), to illustrate relationships within the Anatidae. This is based largely on Johnsgard’s (1965, 1967) taxonomy.

### Results

The most “primitive” living members of the waterfowl family are the Magpie goose *Anseranas semipalmata* (tribe Anseranatini) and the Whistling duck of the genus *Dendrocygna* (included with the swans and geese in the sub-family Anserinae). The Anserinae are monomorphic with generally white, black or brown plumage, a single annual moult, and long pair bonds. In contrast, the “higher” ducks (tribes Cairinini, Anatini, Mergini, Somaterini, Oxyurini and Aythyini) have two body moults a year, and are often brightly coloured with iridescent plumage, may show marked dimorphism and have short pair bonds. The Tadornini (shelduck and sheldgeese) appear to be modern representatives of the evolutionary stage between anserines and ducks; they provide examples of both sexual dimorphism and plumage variation between moults (Kear, 1970), and are often

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**Fig. 1.** A hypothetical evolutionary tree of the waterfowl and screamers (Anseriformes), and the flamingos. At the foot of the picture is a pair of monomorphic mute swans, both of which care for their young, while above is a pair of dimorphic mallard, in which only the cryptic brown female tends the brood. Based on Johnsgard (1965–67) and after Kear (1970).
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FIG. 1.

- **Mergini**
  - Sea ducks 18 sp.
  - (including Eiders)

- **Oxyurini**
  - Stifftails 8 sp.

- **Anatini**
  - Dabbling ducks 39 sp.

- **Aythyini**
  - Diving ducks 16 sp.

- **Cairinini** (including *Merganetta*)
  - Perching ducks 14 sp.

- **Tadornini**
  - Shelducks 6 sp.
  - Sheldgeese 8 sp.

- **Aythyini**
  - Diving ducks 16 sp.

- **Tachyeres**
  - Steamer ducks 3 sp.

- **ANATINAe**

- **ANATIDAE**

- **ANHIMIDAE** (*Chauna*)
  - Screamers 3 sp.

- **ANSERIDAE**

- **ANSERINAe**

- **ANATIDAE**

- **CERIDAE**

- **ANSERIFORMES**

- **PHOENICOPTERIDAE**
  - Flamingos 4-6 sp.

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**Stictonetta**
- Freckled duck 1 sp.

**Anser and Branta**
- True geese 15 sp.

**Cereopsis** 1 sp.

**Coscoroba** 1 sp.

**Cygnus**
- Swans 5 sp.

**Thalassornis**
- White-backed duck 1 sp.

**Dendrocygna**
- Tree ducks 8 sp.
Fig. 2. Distribution of the tribe Cairinini (perching duck).
Photoperiodism in waterfowl

brightly coloured. The Cairinini (perching duck) are the group most closely related to the shelduck; indeed, Johnsgard (1965) makes it clear that evidence, from hybridization and the pattern of the downy young, places the perching duck between the shelduck and dabbling duck, although closely adjacent to the latter. Male shelduck, sheldgeese and perching duck have very similar tracheae, with bullae that are usually osseous and rounded, and lack enlargements of the tracheal tube. The perching duck are today represented by a mixture of morphologically generalized and highly specialized forms which in various respects are thought to typify the “primitive” anatine condition. But, no one species does so exactly, and they also exhibit a puzzling mixture of characters so far as their breeding seasons, plumage dimorphism and expression of parental care are concerned. Certain features of the photoperiodic responses shown by some members of the perching duck group give a better indication of the evolutionary pathway between Dendrocygna-like ancestors and the true duck (Anas, Aythya and “higher” forms) than do the responses of the Tadornini and, for this reason, the perching duck are discussed first.

Perching duck (Cairinini)

Figure 2 shows that the modern Cairinini are mostly tropical species with some supposedly relict distributions; it is likely that the evolutionary centre of the group was in equatorial and tropical regions, as with Dendrocygna (Murton & Kear, 1976) but not with the swans and true geese (Murton & Kear, 1973a; Kear & Murton, 1976).

The egg-laying seasons of the Cairinini are plotted in Fig. 3 (raw data given in Appendix 1) in relation to the light cycle at 52°N. Two groups can be distinguished: the first characterized by long breeding seasons (1) and the second by relatively short breeding seasons with egg-laying terminating in mid-summer (2). All the group 1 species have breeding seasons that extend almost symmetrically on either side of the summer solstice. This group is typified by the African comb duck Sarkidiornis m. melanotos, the western race of Hartlaub’s duck Cairina (Pteronetta) h. hartlaubi and the wild muscovy duck C. moschata. We have not previously considered the Ringed teal Anas leucophyrys and it is convenient to include details here since it is thought by some authorities to be a perching duck and is placed by them in the genus Callonetta (see below). There are too few breeding records at Slimbridge for the South American race of the Comb duck S. m. carunculatus to warrant much comment; the earliest egg-laying was recorded on 15 June and the latest recorded hatching was early in August. It is very likely, as explained below, that the Spur-winged goose Plectropterus g. gambensis belongs in this first group. Unfortunately, the records from Slimbridge are unsatisfactory because the species has never hatched eggs there. Finally, the Australian wood duck Chenonetta jubata should be included in this group for, since Kear & Murton (1976) first broached the likelihood that the species potentially has an extended egg-laying season in Britain, further records have accumulated to confirm this suspicion.

Long, almost symmetrical, breeding seasons are characteristic of Dendrocygna and of primitive members of the genus Anas (Murton & Kear, 1976) and, similarly, we suggest that they represent a primitive condition among perching duck. Indeed, Johnsgard (1965) considered Plectropterus, Cairina and Sarkidiornis to be generalized or “primitive” forms within the Cairinini. They are large species with extensive metallic plumage that lacks specialized patterns; vocalizations are simple and there is little sexual dimorphism in plumage or display, although there is much dimorphism in size. These genera have
FIG. 3. Egg-laying season of Cairinini species at Slimbridge or Peakirk in relation to local changes in daylength. The earliest recorded date of egg-laying is plotted against the appropriate photoperiod and date and then extended as a line to the date of laying of the latest recorded clutch. The median date of laying for all recorded clutches is indicated by the arrow. Solid lines are used for species with "primitive-type" cycles and dashed lines for those defined as showing "temperate-type" responses; the dotted line for the Spur-wing goose demarcates an area where records are unavailable from Slimbridge (see text). Numbers refer to species and the key to these is given in the Appendix.

equatorial distributions and probably extended breeding seasons in the wild. Osteological evidence (Woolfenden, 1961) indicates that the Spur-winged goose is probably representative of the connecting link between the shelduck group and the perching duck.

Species with "primitive-type" breeding rhythms

Spur-winged goose. There are two races of Spur-wing which intergrade. The sexes are similar although the male is larger and has a knob on the base of the upper mandible. The pair-bond is short, the male does not help in rearing the brood (Seth-Smith, 1933; Prozesky, 1959) and for much of the year the birds live in flocks. Captive Spur-wings hatched on 28 May at Olney, Buckinghamshire (Marler, 1973), laid in June at Whipsnade, Bedfordshire (Seth-Smith, 1933), laid in mid-October at Lisbon Zoo (39°N) (Frade & Pinho, 1971), and in mid-September near Pretoria (26°S) (Prozesky, 1959). Praed & Grant (1952) gave breeding season details for parts of Africa: Nigeria—August to January; Uganda and Kenya—July and September, although it seems to lay in almost any month. In South Africa, the dark-flanked race *P. g. niger* breeds mainly from August to May with peaks of activity in September and January (McLachlan & Liversidge, 1957). Benson, Brooke, Dowsett & Irwin (1971) gave rather better details for Zambia (Fig. 16) which indicate peak breeding in January but a laying season extending throughout the year.

Comb duck. The pair-bond is brief in this species also, the sexes are nearly alike in plumage though the male is considerably larger with a prominent caruncle on the upper mandible, and polygamy is suspected (Pitman, 1965). It is evident that the breeding season must be initiated under a shorter photoperiod in equatorial Africa or South America than the
17.3 hour day noted in Fig. 3 for first breeding at Slimbridge. An apparently similar need for a long photoperiod to initiate breeding at Slimbridge has been noted for some equatorial *Dendrocygna* species and we previously attributed this to the inhibitory effects of a cool climate on these small, tropical forms (Murton & Kear, 1976; Kear & Murton, 1976). In fact, it appears that several species exhibit this pattern and we were wrong to dismiss it as an artifact. Rather, it seems that the phasing of the breeding rhythm, relative to the annual photoperiodic cycle, is of a form where the mid-point of the egg-laying season is almost in phase with the summer solstice, in both Africa and Slimbridge (see Fig. 16 and p. 267). In Zambia, the Comb duck begins breeding in November and peak nesting occurs soon after the longest day in January, there being little activity after March (Benson, Brooke, Dowsett & Irwin, 1971).

In India, the Comb duck in the north-west provinces breeds in July, August and September, and in January and March in Ceylon (Hume & Marshall, 1880), while Whistler (1941) gave the breeding season as June to September, depending on the rainy season. Little appears to be known about the breeding season in South America.

*Muscovy duck.* Again the sexes are alike, except that the male is twice the size of the female, possesses a more brightly coloured bill equipped with a basal caruncle, and has head feathers that are more conspicuous and erectile than those of the female. The pair-bond is short or non-existent and the males are promiscuous, which means that the female cares for the brood alone. Virtually nothing is known about the species in its native haunts, although Fig. 3 and the ability of the domesticated form to produce eggs over a long season indicate that breeding is also extended in the wild.

*Hartlaub’s duck.* The sexes are similar except that the male is a little larger than the female and has more white on the front and top of the head. In contrast with the preceding three species, Hartlaub’s duck has a strong pair-bond (Jones, 1972) and the male defends his brood (Johnstone, 1960)—a feature suggested by Kear (1970) to be “primitive”. Wing moult in birds in England can occur as late as the end of October following breeding. Hartlaub’s duck differs from other members of the genus *Cairina* in structure (Woollfenden, 1961) and behaviour, and Johnsgard (1965) has suggested naming it *Pteronetta.* Unfortunately, there is virtually no information on the breeding season in the wild—it is probably extended—and the only record seems to be of a nestling seen in September in the Sudan (Praed & Grant, 1952).

*Ringed teal.* The exact taxonomic status of the Ringed teal has been debated. Delacour (1956) initially placed it in the genus *Callonetta* but later considered it an *Anas,* subsequently, Johnsgard (1965) believed the species to be a perching duck and he and Woollfenden (1961) replaced it in *Callonetta.* Recently, and on the basis of feather proteins, Brush (1976) has unequivocally promoted it to the Anatini. It shows permanent sexual dimorphism, the male being bright and the female brown. This is in contrast to nearly all *Anas* (where any dimorphism is seasonal and apparently mediated by endocrine factors (Kear & Murton, in prep.)) but like *Chenonetta* (see below). In fact, only three *Anas* species show permanent sexual dimorphism and two of these have long “primitive type” breeding seasons at Slimbridge. There is, perhaps, a case for regarding the Ringed teal as representing a link between the Cairinini and the primitive members of *Anas.* The pair-bond is long term and, as in Hartlaub’s duck, the male stays with the brood taking a major part in the defence of his young.

*Maned goose.* The Australian Wood duck or Maned goose is thought to be close to *Aix*
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(discussed with the group 2 species below). This species is permanently dimorphic, the female having a brown plumage like that of the juvenile (Delacour, 1959). The pair-bond is long term and the male stays with the brood. The breeding season of Chenonetta, judged by Peakirk as well as Slimbridge records, could be representative of the transition stage towards the short temperate-type condition found in group 2 (Fig. 3). However, at Martin Mere, Lancashire (54ºN), the earliest egg was laid on 4 March and the last hatch occurred on 1 September; and at Copthorne, Sussex (51ºN) a female laid five clutches in a season, the first being started on 15 March and the last on 8 September (Betty Locker Lampson, pers. comm.). At Tallahassee, Florida (31ºN) captive Maned geese have two breeding seasons, eggs being laid both in early February and early July (de Kloet, 1977). These records show that the species really does have a long egg-laying season. In north-east New South Wales it breeds throughout the year and ducklings may be seen at any time, although most nesting occurs in January, February and March following the rains (Frith, 1967).

Species with “temperate-type” breeding rhythms

White-winged wood duck. The rare White-winged wood duck Cairina scutulata is almost monomorphic, although the female is somewhat smaller than the male. Little is known about the nature of the pair bond, although the male does not seem to involve himself in the care of the young. The species has the kind of breeding season at Slimbridge that is typically found in temperate birds and, in this respect, it contrasts with the other Cairina species (Fig. 3). Again, it has been suggested that the species might not be so close to the Muscovy duck as its present taxonomic allocation would indicate (Mackenzie & Kear, 1976). Wing moult among Slimbridge adults occurs during July following breeding. Consistent observations apply to birds held at Rotterdam, Holland, and also at Gauhati Zoo, Assam—which, at 26ºN, is close to the natural breeding range—where clutches are started between 18 March and 21 May. This suggests that the White-winged wood duck evolved at more temperate latitudes and has only secondarily invaded the tropics. In the wild in Assam, the bird lays from May, at the start of the rains, and apparently mouls in September; for the tropical part of its range, Hoogerwerf (1950) recorded December breeding in southern Sumatra and February breeding in Java.

Brazilian teal. The Brazilian teal Amazonetta brasiliensis is nearly monomorphic, but the male has brightly coloured feet and bill compared with the female while her head pattern is more brown and white than that of the male. The pair-bond is long-term. The male helps rear the young; indeed in one captive pair, he reared the first brood while the female laid and incubated a second (Phillips, 1923). Like the Ringed teal, the species may be close to the link between the Cairinini and Anas, but whereas the Ringed teal has a “primitive-type” breeding rhythm, that of the Brazilian teal tends to be of the “temperate-type”, and presumably evolved in the southern hemisphere. In the wild in north Brazil, the nominate form is said to lay irregularly from August to January (Phillips, 1923), while the larger, more temperate sub-species, A. b. ipecuti, produces eggs from November until January. Thus, seasonal breeding seems to be the rule in the wild.

Aix species. The mandarin duck Aix galericulata (Fig. 4) and Carolina or North American Wood duck A. sponsa are clearly relicts (Fig. 2) of an early radiation of perching duck into the north-temperate zone, a radiation which has been replaced by the more recent evolution of the Anas dabbling duck. Both species are dimorphic with a dull
coloured female and brightly coloured male, and the male has a post-breeding eclipse plumage in which he resembles the female and juveniles. The pair-bond is short and, as with all species of waterfowl in which the male has an eclipse (with the single exception of the Brown teal *Anas aucklandica*), he does not remain with the brood.

The breeding season of the Carolina in the wild is well known, nests with eggs being found within the period February to early June, according to latitude (Bent, 1925). At the Mingo Wildlife Refuge, Missouri, nesting began between 16 February and 7 March but not until 10–22 April in central Minnesota—about 600 miles further north. In collating these records for North America, Bellrose (1976) pointed out that, over a span of about 1000 miles of latitude, there is an approximate 80-day difference in the date on which nesting first begins; nevertheless, last nests (presumably corresponding with onset of refractoriness, see p. 268) were always started in late June, irrespective of latitude. In this way, the breeding season varies in length between about 140 days in the south of the range to 60 days in the north.
The Mandarin has a fairly long egg-laying season, compared with the majority of temperature zone Anas ducks living at the same latitude, and records extend from the last third of April to mid-June in southern USSR (Dementiev & Gladkov, 1952).

**Summary of perching duck breeding patterns**

The Cairinini can be divided into two broad categories. In one group the species are characterized by the possession of long, deemed “primitive”, egg-laying seasons at Slimbridge and they comprise the Spur-winged goose (for which more records are needed), Comb duck, Muscovy duck, Hartlaub’s duck, Ringed teal and Maned goose. The first three exhibit a marked sexual dimorphism in size which appears to be associated with promiscuity, presumably a secondary trait. In contrast, the pair bond is long in Hartlaub’s duck, the sexes are very similar, and the male cares for the brood. The Maned goose and Ringed teal are unusual in having a permanent sexual dimorphism, long pair bonds and male involvement in brood care.

The second group of species possesses a temperate-type egg-laying cycle at Slimbridge and comprises the White-winged wood duck, Brazilian teal, and Aix. Although the first two species have evolved temperate-type egg-laying cycles, presumably an “advanced” condition, they retain the primitive feature of plumage monomorphism, while the Brazilian teal has a long pair bond and male involvement in brood care. Aix exhibits an advanced condition which parallels that found in the temperate Anas species. The trend has been towards a bright plumage colouration, but this is suppressed in the female (who consequently resembles the juvenile) and in the male during eclipse. Only in Aix do the breeding seasons at Slimbridge give a good guide to the situation pertaining in the wild.

**Sheldgeese and shelduck (Tadornini)**

The sheldgeese, Cyanochen and Chloephaga, are considered to represent an earlier radiation of the tribe than the shelduck Tadorna (Johnsgard, 1965). The sheldgeese are today almost all confined to South America (Fig. 5) but at one time were more widely distributed. Fossil remains in North America have been attributed to the group (Howard, 1964; Short, 1970) and, even more significant, is the existence in Africa of the monotypic, monomorphic and relatively dull-coloured Abyssinian blue-winged goose Cyanochen cyanopterus, which has a relict population in the highlands of Ethiopia above 2400 m (Fig. 5). This last is regarded by Johnsgard (1965) as being near to the phylogenetic origins of the sheldgeese. At Slimbridge the Blue-winged goose exhibits a longer, and presumably more primitive, breeding season than the other sheldgeese (Fig. 6). In the wild, the breeding season is also long, extending from May until December (Praed & Grant, 1952).

**Sheldgeese**

Two species are dimorphic (Plate I) and three monomorphic. All Chloephaga species have breeding seasons at Slimbridge that are of the temperate type. In the main, breeding begins in the spring and ends before the summer solstice, whereupon a characteristic temperate-type refractoriness develops to long photoperiods (Fig. 6). Only the high altitude Andean goose lays beyond the summer solstice at Slimbridge, but up to a month after the other Chloephaga species have stopped nesting. In this respect it appears to be rather distinct from other members of the genus and its taxonomic status may deserve further examination (see p. 272).
PHOTOPERIODISM IN WATERFOWL

FIG. 5. Distribution of the tribe Tadornini (shelducks and sheldgeese). The genus *Chloéphaga* is demarcated by black shading while *Tadorna* is shown by stipple shading. Hatched areas demarcate three monotypic genera: (1) *Alopochen*, (2) *Neochan* and (3) *Cyanochen*.

FIG. 6. Egg-laying season of Tadornini species at Slimbridge and Peakirk in relation to local changes in day-length. Dotted lines refer to Abyssinian blue-winged goose (1), Falkland flightless steamer duck (6), Orinoco goose (8) and Egyptian goose (7). Other numbers on left refer to genus *Tadorna* plotted as solid lines while those on right refer to *Chloéphaga* plotted as dashed lines. For key to numbers see Appendix. Other conventions as for Fig. 3.
Plate I. Pair of Greater Magellan geese (Tadornini) to show sexual dimorphism between white male and cryptic female.

Shelduck

The shelduck of the genus *Tadorna* are generally agreed to derive from sheldgoose-like ancestors. There is only one South American shelduck-like species, the Orinoco goose *Neochen jubatus*. It and the Egyptian goose *Alopochen aegyptiacus* of Africa are thought to be close to the base line of the shelduck, although they are not necessarily the lines from which the present day shelduck radiated. Both these species are monomorphic with long pair bonds, and they possess only a small amount of the iridescent plumage that becomes such a feature of the “higher” duck. Like the true shelduck, they lay one egg per day whereas the sheldgeese resemble the swans and true geese in laying a little more frequently than once every 48 hours.

The remaining shelduck are grouped in the genus *Tadorna* and most are only slightly dimorphic, although in the majority both sexes are brightly coloured. Male and female help rear the brood. The Radjah shelduck *T. radjah*, of which there are two subspecies, is the only completely monomorphic member of the genus. Its duckling pattern with chestnut coloured head, and the trachea of the male, are distinctive within *Tadorna* (Johnsgard, 1965). Though specialized, it may be more representative of the ancestral shelduck condition than the other *Tadorna* species and there may be grounds for allocating it to a separate genus.
The South African *T. cana*, Paradise or New Zealand *T. variegata*, Ruddy *T. ferruginea* and Australian shelduck *T. tadornoides* are closely related; the South African could well derive from the Ruddy shelduck for these two species have approximately similar mid-latitude ranges on either side of the equator, suggesting that one is derived from the other (see Lofts & Murton, 1968 who discuss this phenomenon in other taxa and suggest that it is associated with a common photo-response mechanism).

All the shelduck have short temperate-type breeding seasons at Slimbridge but those of the Egyptian goose and the supposedly “primitive” Radjah shelduck are distinctly longer than is the case with the other species. Slimbridge records refer to the Red-backed Radjah *T. r. rufitergum* from Australia (Kear & Murton, 1976). The Black-backed Radjah *T. r. Radjah* from New Guinea and the Moluccas has never produced eggs at Slimbridge. Captive birds of this race in Berlin laid eggs in mid-May (hatched 18 June), while at Crandon Park, Miami, clutches were laid in mid-August in 1969 and again in 1970, when local daylengths were around 13-25 hours (sunrise–sunset). In the wild in tropical Australia the Red-backed Radjah produces clutches between February and July in the Northern Territory (Frith, 1967) and from December to February in north-east Queensland (North, 1901–14). There is little information for the Australian shelduck, though Campbell (1901) wrote that it is an early breeder laying during July, August and September and on Rottnest Island, the egg-laying period extends from the first week in June until mid-September (Riggert, 1977). The breeding season of the New Zealand shelduck in the wild is rather longer, nests with eggs having been found between 10 August and 23 December (Kear, unpubl.), but it clearly approximates to a north-temperate pattern with a start in early spring and a cessation around mid-summer. The same holds for the Cape shelduck, with egg-laying occurring in South Africa from July to November (McLachlan & Liversidge, 1957). Variations on the above theme are also to be seen in the Ruddy shelduck (Dementiev & Gladkov, 1952) and the Common shelduck *T. tadorna*, and Fig. 6 gives a good indication of their natural seasons. Thus, in the Common shelduck egg-laying begins in Mid-April in Britain but does not reach a peak until about the second week of May.

**Steamer duck**

Species of the genus *Tachyeres* of South America are regarded as aberrant members of the Tadornini. They show only a slight size and colour sexual dimorphism and the juvenile resembles the adult in plumage. They are territorial and structurally bear a convergent resemblance to the eiders (*Somateria*) of the northern hemisphere, occupying a similar niche in that they are marine duck that dive for their food. Yet, unlike the eiders, the pair-bond seems to last for life in the steamers, and, in typical Tadornine manner, the male defends his offspring. At Slimbridge, the Falkland Island flightless steamer *Tachyeres brachypterus* has laid clutches in six years, the dates spanning the period 15 March to 27 April but there has been only one repeat laying and so insufficient records to define the length of the season. Captive birds at Duisberg Zoo, Germany (51°N) also bred in March and April, while at Zurich Zoo (47°N), first eggs were laid on 16 February and 4 March (Schmidt, 1969). In the wild (at 52°S), laying occurs in October according to Pettingill (1965) and specifically between 12 October and 9 November (Vallentin, 1904).

**Summary of shelduck and sheldgoose breeding patterns**

The Tadornini exhibit a primitive condition in the Anatinae in terms of an extended
pair bond with both sexes sharing in rearing the brood: in this respect they resemble the Anserinae. The supposedly most primitive sheldgeese (Abyssinian goose and Andean goose) and most primitive shelduck (Orinoco goose, Egyptian goose and Radjah shelduck) are monomorphic and the juvenile plumage is similar to that of the adult but duller. All these species have noticeably longer egg-laying seasons at Slimbridge than the remaining Chloéphaga or Tadorna species, but all Tadornini, except possibly the Radjah shelduck, have temperate-type breeding seasons. Two of the five Chloéphaga species are markedly dimorphic, and all the Tadorna species, again excepting the Radjah shelduck, show a degree of dimorphism, but this is only really marked in the New Zealand shelduck and the recently extinct crested shelduck T. cristata, and to a lesser extent in the common shelduck. This trend to dimorphism is correlated with an increase in the mid-latitude of the natural breeding range. The breeding seasons of the Tadornini at Slimbridge give a good indication of the situation in the wild, where known, except in the case of the species possessing more extended cycles such as the Egyptian goose and Radjah shelduck.

Fig. 7. Distribution of the tribe Aythyini (pochards). The genus Netta is demarcated by stipple and Aythya by diagonal-hatching.

Diving duck—scaup and pochard (Aythyini)

Aythya has almost certainly arisen from Netta and both genera probably derive from an Anas-like stock, perhaps via a form similar to the Marbled teal Anas (Marmaronetta) angustirostris. Netta is distinguishable from Aythya on anatomical grounds, being structurally less well equipped for diving; in turn Netta is biochemically and physiologically less well adapted to diving than is Oxyura (Cook, Siegfried & Frost, 1977). The distribution of the pochards is shown in Fig. 7.

Netta

The African race of the Southern pochard Netta erythrophthalma brunnea is close to the South American sub-species N. e. erythrophthalma. The distribution of these two forms
could be indicative of a previously wider distribution in the southern hemisphere or reflect the dispersal powers of wildfowl, since ringing recoveries indicate the capacity of the African pochard to cover long distances (Moreau, 1966) (compare the similar distribution of the Comb duck and Fulvous whistling duck *Dendrocygna bicolor*).

Jones (1972) reported that an African pochard laid fertile eggs throughout the year at Leckford, Hampshire, and the breeding season is clearly also extended at Slimbridge (Fig. 8). In the wild, breeding is recorded between August and December and during May in the Cape; from February until July and August in the Transvaal (McLachlan & Liversidge, 1957); in May, July and November in Kenya; in December in Tanganyika; and from August to May in Nyasaland (Praed & Grant, 1952); for Zambia see Fig. 16. Breeding can presumably occur throughout the year in Africa, the actual season being determined by ecological factors (see “Discussion”). The Rosy-bill *Netta peposaca* also has a long breeding season at Slimbridge but the photosensitive threshold appears to be higher than that of the southern pochard, consistent with a centre of distribution at 30°S. In the wild at General Lavalle, Argentina (c. 37°S), eggs and broods were found between late September and mid-November (Weller, 1968a) which compares with an egg-laying season extending from mid-April to early July at Slimbridge.

The breeding cycle of the Red-crested pochard *N. rufina* differs from that of the other species in having a lowish photo-threshold with refractoriness developing to long days; 35 seasonal records exist for Peakirk and Slimbridge combined and eggs have never hatched later than 13 July. There seem, therefore, to be physiological grounds, including the possession of an eclipse plumage phase in the male mentioned above, for separating the Red-crested pochard from the other *Netta* species, a view supported by the skeletal differences outlined by Woolfenden (1961). The species may represent a stage between *Netta* and *Aythya*. In the wild, breeding occurs from May (perhaps earlier in the Mediterranean) through to July (young ducklings recorded on 27 August) in southern Russia (Dementiev & Gladkov, 1952).

![Fig. 8. Egg-laying season of Aythini species at Slimbridge and Peakirk in relation to local changes in daylength. *Netta* species shown by dashed lines and *Aythya* by solid lines. Key to numbers in Appendix and other conventions as for Fig. 3.](image-url)
Aythya

The breeding seasons of Aythya at Slimbridge are of temperate type with photorefractoriness developing in June (Fig. 8). Figure 8 probably also gives a fair indication of the situation pertaining in the wild. Thus, the Tufted duck Aythya fuligula has laid over the period 30 April to 19 June at Slimbridge, the median date of first eggs being 2 June, while in the wild in Britain laying begins in mid-May, although the peak is not reached until the first half of June. In contrast Baer's pochard A. baeri has laid at Slimbridge between 1 June to 27 June, (median 13 June) which appears to fit records from Transbaikal in East Siberia (Dementiev & Gladkov, 1952). Bent’s (1925) dates for 25 Ring-necked duck A. collaris clutches in the wild span the period 31 May to 6 July; the Peakirk clutch completed on 3 June hatched on 1 July which is not much different from Bent’s record.

In captivity at Delmar, N.Y. (c. 43°N), first clutches of the Redhead A. americana were started on 2 April and the last on 15 July; peak production was during the second week of June (Holm & Bauer, 1959). In the wild in Columbia Plateau, Washington (45–48°N), the first hatches were noted in the first week of May and the last in the second week of August, the peak occurring during the third and fourth weeks of June (Yocom, 1950). Captive Canvasback A. vallisneria observed at Delmar over three years produced the first egg on 18 April and the last on 27 June with the peak in the last week of May (Holm & Bauer, 1959). With more records, the latest date of egg-laying at Slimbridge is likely to be extended to June. Weller (1959) made a detailed study of the parasitic tendencies of the Redhead, for a proportion of females lay their eggs in the nests of other ducks. He pointed out that at the Delta Marsh in southern Manitoba (c. lat. 50°N), during the years 1952–4, egg-laying by the Redhead extended from mid-May to around 23 June with peak laying concentrated in the first half of June. The breeding season of the Canvasback at the same locality was from early May to mid-June, with peak activity around 10–15 May. Hence, although both species showed a similar spread in laying dates, the Canvasback population bred, on average, rather earlier than the Redhead, and a parallel situation is noted at Slimbridge (Fig. 8). In the wild the Lesser scaup A. affinis begins courtship and nesting later than either of these two species (Weller, 1965) and the same chronology is noted at Slimbridge.

The radiation of Aythya has almost certainly occurred in the northern hemisphere so that the Australian white-eye A. australis derives from Northern white-eye stock, while the New Zealand scaup A. novaeseelandiae is likely to be descended from the Northern scaup (see also Bull & Whitaker, 1975). This kind of colonization has occurred in several northern Anas species which may migrate to islands as remote as Tahiti and Polynesia during the contra-nuptial season (Voous, 1960); examples are seen in various derived races of Mallard Anas p. platyrhynchos, including the Hawaiian duck A. p. wyvilliana, and other examples are given in Kear & Murton (in prep.). Adaptation to Australian conditions has necessitated a drop in the photo-sensitive threshold in the native white-eye so that it is among the first of the diving duck to begin breeding at Slimbridge. The onset of breeding by the New Zealand scaup (mid lat. 41°S) is only a few days earlier than in the Common white-eye Aythya nyroca (mid lat. 45°N) and there is little doubt that either species could readily adapt to conditions in the opposite hemisphere. In the wild, the Australian white-eye has a regular breeding season in October and November which Frith (1967) considered to be mainly timed by the seasonal photoperiod. In New Zealand, 14
nests with eggs of the New Zealand scaup were found between 4 November (photoperiod 14.8 hours) and 22 December and the last hatching recorded in the wild was on 2 February (Kear, unpubl.).

There is a general trend for the breeding seasons of birds to shorten from the equator to the poles (Baker, 1939) and this is hardly surprising in view of the variation in ecological conditions. The pochard are a convenient group in which to demonstrate the relationship between length of breeding season at Slimbridge and latitude of origin (Fig. 9(a)). Obviously, differences in the length of breeding seasons must depend to a large extent on endogenous factors, otherwise the relationship should not be manifested at Slimbridge. Figure 9(b) is instructive in this respect in demonstrating that the length of the breeding season is more closely related to photoperiodic response than it is to latitude: latitude accounts for 55% of the inter-specific variability in length of breeding season whereas the photoperiod effect accounts for 72% of the variation (see Fig. 9).

Fig. 9. Relationship between length of egg-laying season in days of 11 Aythya species at Slimbridge (ordinate) and: (a) mid-latitude of the natural breeding range of each species; (b) median photoperiod under which each species begins egg-laying at Slimbridge.

Summary of diving duck breeding patterns

The most primitive species, N. erythrophthalma, with a tropical distribution, is almost monomorphic, and has a long, “primitive-type”, egg-laying cycle at Slimbridge; it is uncertain whether the pair bond in the wild is extended. The other Netta species have fairly long egg-laying seasons but they are of a temperate-type, as they are in all Aythya. Throughout the diving duck tribe there is a noticeable trend towards sexual dimorphism with increase in the latitude of the breeding range, and towards a decrease in length of the egg-laying season. In all cases but one, the dimorphism is seasonal for the male has an eclipse phase during which he resembles the female; the Rosybill is exceptional in exhibiting a permanent sexual dimorphism. Although there is a negative correlation between the length of the egg-laying season of different Aythya species at Slimbridge and the latitude of origin, there is an even stronger correlation between the length of breeding season and the photoperiod under which breeding is initiated. There are grounds for separating the Red-crested pochard from the genus Netta.
Sea duck

This provides a convenient heading under which to group the Somateriini (eiders) and the Mergini (scoters, goldeneyes and mergansers). The Mergini are considered to have emerged from the Somateriini by Woolfenden (1961) and Johnsgard (1965), but whether the eiders arose from Anas as Humphrey (1958) argued, from Aythya-like stock, or from perching duck ancestors, remains uncertain. Feather proteins make it clear that the eiders are distinct from the mergansers and their allies, and that the sea duck are not immediately related to the Anatini but instead show more affinity with Oxyurini and Aythyini, with whom they may have had a common ancestor (Brush, 1976). The Bufflehead Bucephala albeola provides a link between the Goldeneyes on the one hand and the Smew Mergus albellus and mergansers on the other. All the living sea duck but one are inhabitants of the north-temperate region, exhibiting marked sexual dimorphism, seasonal pair bonds and a male eclipse. The Brazilian merganser M. octosetaceus from South America is exceptional in being monomorphic with an apparently long pair-bond.

The breeding seasons of the sea duck are of the temperate spring type, the median dates for first eggs of all that have laid at Slimbridge being separated by only six weeks (Fig. 10). In the wild, the old world Smew breeds later than the Hooded merganser Mergus cucullatus which replaces it ecologically in North America but which has the centre of its breeding range 7° further south. Both these species are limited in range to the tree zone and the availability of woodpecker holes which they use for nesting. At comparable latitudes and locations in Europe, the Goosander M. merganser merganser breeds before the Smew; the Goosander takes bigger fish than its congener and is probably less dependent on the availability of young fish and invertebrates. The Red-breasted merganser M. serrator breeds later than either the smew or the goosander (Witherby et al., 1939). A similar temporal relationship is seen between the American merganser M. m. americanus (a subspecies of the Goosander) and Red-breasted merganser in North America, while the
Bufflehead *Bucephala albeola*, another duck that depends on woodpecker holes for nesting sites, breeds early like the Goosander and at about the same as Barrow’s goldeneye *B. islandica*. Hence, the breeding seasons depicted in Fig. 10 tend to be a true reflection of the natural seasons, except that the wild Barrow’s goldeneye nests much later than the European goldeneye *B. c. clangula*, even though the centre of its breeding range is 10° further south. This may depend upon the fact that Barrow’s goldeneye nests at higher altitudes, especially in the southern part of the range, and is mainly non-migratory.

The breeding season of the King eider *Somateria spectabilis* at Slimbridge is virtually the same as that of the European eider *S. m. mollissima* even though, in the wild, it frequents very high latitudes and breeds on the arctic coastal tundras. Here egg-laying does not occur until mid-late June (Dementiev & Gladkov, 1952). The answer to this anomaly may be that, unlike other high latitude breeders, the King eider mostly remains within the arctic circle during the contra-nuptial season, where it can survive the presence of winter ice, and so the annual daylength cycle to which it is exposed is rather unlike that to which it is exposed at Slimbridge and entrainment may be different (see p. 266). According to Palmer (1977) it migrates earlier and travels further than the eider.

Other high latitude species that winter at lower latitudes, e.g. the Brent goose *Branta bernicla*, have a high photo-threshold and tend not to breed readily in captivity at lower latitudes, where daylengths hardly reach the stimulatory threshold (Murton & Kear, 1973a). An advantage of late breeding in the related Red-breasted goose *B. ruficollis* is that it is able to nest at the same time as, and close to, the Peregrine falcon *Falco peregrinus* on which it depends for protection from the Arctic fox *Alopex lagopus*. The Spectacled eider *Somateria fischeri* also breeds on a narrow coastal strip of northeast Arctic Siberia and Alaska (replacing the European eider) but winters further south than the King eider, for example, on the southern edge of the ice in the Bering Seas. The only three laying records for Slimbridge, on 21 May 1975, 24 May 1976, 11 May 1977, might be indicative of a higher photo-threshold than that of the European eider.

**Summary of sea duck breeding patterns**

All the living sea duck, but one, are markedly dimorphic, north temperate species, that have temperate-type breeding cycles at Slimbridge. The exceptional Brazilian merganser is monomorphic but its breeding cycle is not known.

**Thalassornis**

At one time, the monomorphic African White-backed duck *Thalassornis l. leuconotus* was thought to be an aberrant stifftail (*Oxyurini*) (discussed below) but Johnsgard (1967), Kear (1967) and Raikow (1971) considered it to be closer to the whistling ducks (*Dendrocygnini*), and their view is supported by its feather proteins (Brush, 1976). The pair-bond is long term and there is dual parental care, even to the extent that the male shares in incubation—a noticeable “primitive” feature of *Dendrocygna*. Whether there is any evolutionary link between the whistling duck and the stifftails is uncertain, but it is convenient to treat the White-backed duck at this point and Fig. 11 details its egg-laying season and allows comparisons to be drawn with those *Oxyura* species for which information is available.

*Thalassornis* and *Oxyura* have in common the fact that they are summer breeders, their egg-laying seasons at Slimbridge being rather different from the other groups so far
discussed. Long photoperiods seem necessary to evoke egg-laying but refractoriness does not develop until after the summer solstice when daylengths have started to become appreciably shorter again. The Madagascar sub-species of the White-backed duck *T. l. insularis* laid at Foxwarren Park, Surrey in June 1931. In 1933, the female produced her first eggs in April, and, having reared the ducklings, then laid again and hatched a second clutch of eggs on 12 July (Ezra, 1934). Breeding dates for the White-backed duck given by Praed & Grant (1952) are: Kenya—April to July and also October to November; Pemba island—June to August; Nyasaland—April to August; Natal—November to February; see also Fig. 17.

![Fig. 11. Egg-laying seasons of Thalassornis (dashed line) and Oxyura (solid lines) at Slimbridge in relation to local changes in daylength. Key to species in Appendix and conventions as for Fig. 3.](image)

**Stifftails (Oxyurini)**

The stifftails comprise a low latitude (Fig. 12) group of very aquatic, mainly freshwater duck that are highly specialized for diving; the tail retrices are long and stiff and presumably serve in controlling movement underwater. All, except the Musk duck *Biziura lobata* of Australia, are markedly dimorphic in plumage with a male eclipse; *Biziura* is markedly dimorphic in size. In general the pair-bond is short or non-existent.

The Black-headed duck *Heteronetta atricapilla* is a monotypic species which has been considered to be an aberrant member of the tribe Oxyurini, providing a link with the *Anas* dabbling duck group (Johnsgard, 1965; Woolfenden, 1961). Brush (1976) thought that feather protein analysis clearly indicated that it is a member of the Anatini and not the Oxyurini. This viewpoint seems to us to be too extreme, for feather protein analysis does not nullify the observations which indicate a relationship to *Oxyura*. The Black-headed duck is native to South America and is unique in being an obligate brood parasite of other birds, including rails, duck, and herons. Breeding records are available only from Slimbridge where eggs were laid between 27 April and 9 June 1977. Weller (1968b) has described the species' biology in the wild.
As mentioned, the stifftails are summer breeders at Slimbridge. Indeed, the White-headed duck *Oxyura leucocephala* may not enter a true refractory phase, for breeding ceases after the solstice, at the point when daylengths fall to the same length at which breeding was initiated; thus the egg-laying season is aligned symmetrically on either side of the longest day as in *Dendrocygna* (Murton & Kear, 1976) and some other "primitive" species shown in Fig. 3. This argues against the group coming from *Aythya*-like ancestors or any other group with an advanced temperate-type breeding rhythm, but it could derive from tropical *Anas*-like stock near to *Heteronetta*. At Slimbridge the earliest egg date for the North American Ruddy duck *Oxyura j. jamaicensis* is 17 April while last clutches have been started around 26 July. At Slimbridge, both the Ruddy duck and White-headed duck frequently produce a second clutch if the first is removed for artificial incubation; they may produce a third but, as it is not easy to tell the females apart, this is not confirmed. A captive pair in Sussex laid four clutches in one season beginning on 27 April, 7 May, 3 June while the fourth hatched on 5 August (D. Mulholland, pers. comm.). Captive Ruddy ducks in Louisiana (30°N) mostly lay three clutches a year but some lay four (McClore, 1970).

In the wild, all *Oxyura* species tend to be late breeders. The young are probably dependent on gnat larvae for food and these become more abundant in the late summer. For the Maccoa duck *O. maccoca* Praed & Grant (1952) gave the following dates: Abyssinia—June onwards; Kenya—May to July and also October to January; Tanganika—May and June. Figure 16 gives details for the S. W. Cape based on records from Siegfried (1969) who commented that the Maccoa breeds about two months after sympatric Dabbling duck, and noted a similar relationship between the Australian blue-bill *O. australis* and Australian dabblers.
The North American Ruddy duck may only recently have extended its breeding range beyond 50°N and rarely breeds north of 60° (Siegfried, 1973) so probably it should be allocated a lower mid-latitude point than the 48°N given in the Appendix. According to Bent's (1925) records, nests with eggs have been found between 26 April and 11 August in California, the peak being from 22 May to 10 June; in North Dakota, records span the period 8 June to 19 July and from December to March in Puerto Rico. Yocom (1950) thought that first hatches occurred in the first week of June in Washington State, and the last were noted in the second week of August. In N. W. Iowa, Ruddy duck nest initiation occurs in May, peak nesting is in June and the last clutch was begun on 11 July; in Manitoba nest initiation extends from late May to late July and from mid-May until early July in California (Bellrose, 1976). Evidently, throughout a wide latitude range in North America, the period of nest initiation in the Ruddy duck stays around the same length at 53–63 days. In contrast, it is pointed out on page 268 that the length of the Carolina’s nesting season in N. America decreased the further north it bred.

Feral populations of the Ruddy duck are now established in Avon and Staffordshire, England. According to Hudson (1976), an exceptionally early brood was reported in April in Leicestershire, following a mild winter, and broods are sometimes seen in May and June; however, it is more usual for ducklings to appear in July, August and early September, and a small duckling was even seen at Chew Valley, Avon on 31 October.

Stifftails differ from other waterfowl (and most birds) in moulting their wing feathers twice annually (Siegfried, 1970, 1973; Palmer, 1976). Siegfried (1970) speculated on the selective advantages of this remarkable double wing-moult, and could find none. He noted that stifftails do not use their wings under water so that extra wear on these feathers could not be the reason for their twice yearly renewal. However, as Palmer (1976) pointed out (for the Ruddy duck at least), that same moult includes not only the body plumage but also the tail, which in other waterfowl is moulted once only, with the wings. It seems to us that the phenomenon may occur primarily in order to renew the tail which, in these aquatic duck, is long and stiff to serve in underwater control and is presumably subject to considerable feather wear. If the mechanism by which the tail retrices and the wing remiges are moulted is physiologically linked—that is, one group cannot be shed without the other—then this fact could account for the stifftails’ complete double moult. The habit could not have evolved if two annual periods of flightlessness were an enormous disadvantage but, presumably, in these highly aquatic divers, any loss of flying ability is unimportant in comparison with the possibility of having an inefficient underwater “rudder”. The moult cycle is also unusual, compared with that of the Mallard and other dabbling ducks, in that the display plume (alternate plumage) is acquired during the spring moult and it is lost during the second moult in late summer/early autumn, that is, eclipse or basic plumage is worn throughout the winter (Palmer, 1972). In the Mallard the display plume is acquired at the autumn moult and this is then carried until the following early spring in the female and summer in the male so that the eclipse phase persists for only a few months during the summer.

These observations on breeding season and moult suggest that the photoperiodic control of the annual cycle is somewhat unusual in Oxyura. In particular, the onset of breeding cannot be advanced by early exposure to stimulatory photoperiods and in this respect the Ruddy duck bears resemblance to Dendrocygna (Murton & Kear, 1976), Thalassornis (Fig. 11) and to the Comb duck (Fig. 3). If the period during which basic
plumage is worn corresponds to the photo-refractory phase then photorefractoriness does not end until the spring in *Oxyura*, whereas it ends in October in the Mallard. Perhaps this is the reason why the breeding season cannot be advanced in the spring.

**Summary of stiltail breeding patterns**

All species of *Oxyura* are seasonally dimorphic in plumage colour and pattern; the sexes of the Musk duck more closely resemble each other in this respect but during the breeding season the male acquires a prominent lobe which protrudes from the chin and lower mandible. Egg-laying seasons at Slimbridge tend towards the symmetrical pattern observed in *Dendrocygna* so that breeding occurs in summer rather than spring.

**Phase relationships of breeding seasons**

Some workers favour the view that birds possess ultradian endogenous periodicities in body function, including their seasonal gonad and moult cycles, which are entrained by the annual cycle of night and day acting as a *zeitgeber* (Gwinner, 1973, 1975); evidence has accrued to suggest that a circannual rhythm mechanism controls antler growth in deer (Goss, 1969a, b; Goss & Rosen, 1973). There is no argument about the existence of circannual rhythms and the critical question is whether these are regulated by circannual oscillators or instead are compounded from the interaction of different circadian oscillators. The topic is raised here because it is desirable, as Aschoff (1965) long ago emphasized, to measure the phase relationships of rhythms by reference to their mid-points (see also Daan & Aschoff, 1975). For convenience we shall for the moment assume that the egg-laying seasons of waterfowl at Slimbridge represent entrained circannual rhythms of gonadotrophin activity. The x-axes of Figs 1, 2, 3, 6, and 8 comprise 365 days which can be transformed to 360° without appreciable loss of accuracy. In this way it is easy to measure the phase angle difference between the mid-points of the egg-laying season and of the seasonal daylength cycle (that is, the longest day is the reference point).

**Relation to photoperiod**

Inspection of Figs 1, 2, 3, 6 and 8 shows that the shorter the daylength under which a species begins breeding is the more positive is the phase angle difference between the egg-laying rhythm and the *zeitgeber*. Obviously, this would be a truism if only the start of the egg-laying season were used as a reference point, for then calendar date would in effect be plotted against the movement of the sun: nevertheless, the relationship would disappear if some species did not begin breeding until after the summer solstice. The relationship would also disappear in considering the mid-point of the cycle if birds that started breeding on short daylengths compensated by remaining in breeding condition for proportionately longer than those that initially required long daylengths to respond. In fact, Fig. 13(a) illustrates that this tends to happen in those perching duck found to have “primitive” egg-laying patterns for, in these, there was relatively little phase shift related to the daylength under which breeding was initiated. The slope of the regression relating phase-shift to photoperiod is much steeper for the perching duck with temperate-type rhythms and for the other taxa detailed in Fig. 14 because refractoriness to long days develops and results in a marked positive phase shift in the egg-laying rhythm relative to the *zeitgeber*. 
FIG. 13. Phase difference between the mid-point of the egg-laying cycle of various Anatidae (key to numbers given in Appendix) and the daylength at which breeding begins at Slimbridge or Peakirk. (a) Cairinini with those species having "primitive-type" cycles (see Fig. 3) shown as open symbols and those with "temperate-type" cycles as solid dots; the correlation coefficients are not significant. (b) Tadornini with solid dots for *Tadorna*, open circles for *Chloéphaga* and open squares for *Cyamochen*, *Alopecoen* and *Neochen*. (c) Aythyini with open symbols for *Nettu* and solid symbols for *Athyra*. (d) Somateriini and Mergini shown as solid symbols, Oxyurini as open circles and *Thalassornis* as a cross. The regression line is for the first two tribes only.

Refractoriness does not develop under exactly the same photoperiod within any group of closely related species but there is less variability in the range of daylengths at which breeding stops than in the range under which it begins, as can be judged from Figs 6 and 8 in particular. In consequence, there is a negative correlation between the length of the breeding season ($y$) and the photoperiod needed to initiate breeding ($x$) as was demonstrated in Fig. 9.

Relation to latitude

If the phase-differences between the onset or end of the egg-laying cycle and the Slimbridge zeitgeber are plotted against the mid-latitude of the natural breeding range of each species, straight line relationships are sometimes noted between closely related species (Fig. 14). In these cases, similar results would be obtained by plotting the daylength under which breeding begins against the mid-latitude of the natural breeding range, as was done for *Cygnus*, *Branta*, *Anser* and *Tadorna* in Murton & Kear (1973a) and for *Netta* and
Aythya in Murton & Kear (1973b). A correlation between the phase shift of onset of egg-laying and latitude of origin is most evident in Aythya (Fig. 14(c)), as would be expected from the data referred to above (Murton & Kear, 1973b). No correlation was found in the phase shift of end of egg-laying with latitude, clearly because refractoriness develops in all Aythya species under approximately the same daylength. Presumably, this is also the reason why there is little variation in the date at which breeding ends in the Carolina throughout a wide range of latitudes (see p. 252). The sea duck would probably resemble Aythya but the data are more confused because several genera are involved, with few species in each (Fig. 14(d)). Previously, no significant relationship with day-length at egg-laying (number of days from winter solstice) and latitude of origin was found.

![Graphs showing phase difference between onset and end of egg-laying cycle for various waterfowl species.](image-url)
in the sheldgeese (Murton & Kear, 1973a) and likewise no correlation is found when the phase shift to onset or end is considered (Fig. 14(b)). Perhaps this is because the range of some species is different from their centres of origin (see p. 271).

In the perching duck the phase shift measured to the end of the breeding season is correlated with latitude, that is, the time of onset of moult. This is of interest because some while ago Snow & Snow (1964) suggested that a fixed timing of the moult in relation to varying environmental conditions synchronized the rest of the annual cycle, including the breeding cycle, in several Trinidad species (see also Snow, 1962). In a more recent study of the Cotingidae, Snow (1976) has also argued a case for implicating an endogenous circannual cycle of moult, without denying the importance of food availability. We agree with this viewpoint.

Discussion

In Kear & Murton (in prep.) we shall discuss the physiological control of breeding periodicity in the waterfowl. It will help the present discussion to recognize that two endocrine systems are involved; first, growth of the gonads leading to sperm and egg production and hence the onset of breeding is dependent on gonadotrophin secretion interacting with steroid secretions (androgen or oestrogen) from the developing gonad; second, the termination of breeding and the onset of photo-refractoriness is associated with thyroid activity that inhibits androgenic or oestrogenic function (see Assenmacher, 1974 for a useful review relevant to the Mallard). Gonadotrophin secretion (luteinizing hormone and follicle stimulating hormone) and thyroid stimulating hormone (TSH) secretion are photoperiodically regulated by light sensitive circadian rhythm mechanisms. For the present we shall simply refer to this complex system in terms of the factors initiating egg-laying and the factors responsible for terminating breeding, these last usually being associated with the onset of the post-nuptial moult.

Evolutionary aspects of photoperiodism

Effect of latitude

Why should closely related species within a genus such as Aythya exhibit photoresponses at Slimbridge that relate to the latitude of origin of each species in a systematic manner? Theoretically there need be no such relationship, and, for some taxa, none exists. The observations do make sense if is assumed that they reflect the adaptation of a basic photo-response mechanism that was possessed by an ancestral species, which subsequently speciated by radiating to higher latitudes. The systematic changes in photoresponse result because the seasonal light cycle likewise changes in a systematic manner with latitude.

Imagine some proto-Aythya living around latitude 45° N at the end of one of the earlier glaciations. As the ice retreated, new habitats became available further north into which the species could spread. Because summer arrives later closer to the poles, an adaptive response would be for the colonists to delay their migration north and to reach breeding condition later in the season. Equipped with ancestral photo-responses they would begin moving north too quickly; moreover, following the spring equinox, daylengths become longer with increase in latitude. Selection would evidently favour individuals possessing
higher photo-sensitive thresholds and, therefore, needing longer daylengths to stimulate
gonadotrophin secretion. In oscillator terminology, selection would favour a decrease in
the frequency of any light sensitive oscillators so that the breeding cycle was less positively
phased with regard to the light cycle. When returned to a common zeitgeber, a series of
species that had evolved such adaptative responses at different latitudes would be expected
to exhibit the pattern already noted in Figs 9, 13(c) and 14(c). It would be interesting to
know how "threshold" was determined genetically. Since sub-species (Lofts & Murton,
1968) and even morphs of the same species (Murton, Westwood & Thearle, 1973) can
vary in their photo-response threshold it is likely that relatively simple genetic changes
have been involved, perhaps a series of alleles.

It would also be interesting to discover how quickly a new phasing of the breeding
cycle could evolve if a species did not change its latitude but, for instance, altered its
feeding niche and this necessitated a different breeding pattern. The same light sensitive
pace-makers are possibly implicated in the control of several rhythmic functions so that a
change in breeding periodicity probably also alters the season of moult, migratory fat
deposition, etc. Figs 8, 13(c) and 14(c) suggest that, although the factors initiating the
egg-laying season (gonadotrophin secretion and steroid release) have been adjusted
within Aythya to give a series of photo-response thresholds, the factors timing the onset
of photo-refractoriness (thyroid feed-back) have been altered relatively little within the
genus. Perhaps this implies a more complex interacting system that cannot be easily
disrupted. Whatever the physiological explanation, the ecological implications are clear:
the ability of species to radiate and adapt to a given latitude is limited by the physiological
features of the ancestral species and the latitude to which this original species was adapted.

Suppose we postulate that the ancestral Aythya had a photo-mechanism similar to that
of the Common white-eye (mid lat. 45°N). Assume too, that the other Aythya species
radiated in the manner indicated in Fig. 14, that is, the extant species are indicators of the
maximum physiological flexibility of the Aythya ancestor. Photo-responses evolved at one
latitude might be preadapted for another. This could be the case when a species colonizes
the same latitude in the opposite hemisphere in a leap-frog manner. This is how the New
Zealand scaup (mid-lat. 41°S) probably arose, perhaps with selection occurring for a drop
in photosensitivity. A further drop in photosensitivity gives the breeding season observed
for the Australian white-eye (mid-lat. 28°S), which at Slimbridge lasts from 12 March to
1 July.

What would happen if a species living at lat. 45°N required to begin and finish breeding
earlier in the season than our ancestral Aythya? An earlier start might be achieved if the
Australian white-eye, having evolved an adaptive reduction in photo-response threshold
at lat. 28° (in this case S but it might have been N) could move to lat. 45° (arrows in Fig.
14 illustrate the concept we are trying to advance here). However, it would still remain in
breeding condition until too late in the year because at Slimbridge it begins breeding on a
photoperiod of around 12-7 hours and becomes refractory when the daylength reaches
18-1 hours. In fact, species having rather a different photoperiodic phylogeny would
probably be better candidates: for example, the Mandarin (from 47°N) has a breeding
season beginning on a 13-4 hour day and ending on 17-6 hour, while the Carolina (from
41°N) begins breeding on a 12-0 hour day but finishes at Slimbridge on a 17-3 hour
photoperiod; that is, both species are phased out of breeding condition before the
Australian white-eye. Actually, evolutionary pressures probably operated in the opposite
way to the example given above. That is, the breeding seasons of the Carolina and Mandarin were probably phased to begin and end too early in the year at 41° and 47° lat. N respectively, for them to be suitable ancestors for lines radiating to even higher latitudes (50°N and above); the species would need to begin breeding later than could be achieved by a drop in the response threshold of *Aix* and, unlike *Aix*, to have a capacity to continue breeding around the solstice. Presumably, the two *Aix* species are indicators of the limitations of the photo-response mechanism of a past radiation of the perching duck in temperate latitudes, a limitation that led to their replacement by the "higher" dabbling duck, leaving *Aix* as a relict genus.

Phylogenetically old groups would be expected to show a less clear cut relationship between the photo-mechanisms controlling breeding periodicity and latitude if there had been much opportunity for species to move to new latitudes or if, as in the perching duck, there had been time for differences at the generic level to evolve. In cases where the relationship between photo-response threshold and latitude is lost, as in the sheldgeese compared with the shelduck (Fig. 14), it can be imagined that adaptation in breeding schedule has not required an alteration in photo-response. Differences in photo-sensitivity threshold which affect the onset of breeding seem easily achieved within a genus, but differences in the timing of the end of the breeding season are usually not very marked unless inter-generic comparisons are made. There are exceptions, but these lead us to suspect that current taxonomy does not accurately reflect phylogeny. For example, Fig. 6 shows that all the *Chloéphaga* species have very similar photo-responses at Slimbridge with the exception of the Andean goose. This has a significantly longer laying season and in this respect it resembles the Abyssinian Blue-winged goose. In fact, the similarity of the pattern of the downy goslings of these two species already suggested a fairly close relationship (Blaauw, 1933; Johnsgard, 1965), which raises the question of whether the Andean goose should remain in the genus *Chloéphaga*. The need for a high photo-response threshold in the Andean goose is consistent with it being a high altitude breeder, like the Blue-winged goose.

**Zoogeographical aspects**

The Egyptian goose does have a long breeding season in the wild in Africa (see below) but, under a temperate daylength cycle, photo-refractoriness to long days develops in the manner characteristic of temperate species. Could this cycle, and others like it, have evolved under a tropical photoregime, or is it more likely that the Egyptian goose derives from ancestral stock, which developed an adaptive photo-refractory phase at high latitudes? Indeed, it is probable that the centre of evolution of the shelduck and sheldgeese was in the southern hemisphere, and the ancient land mass that remained after the break-up of Gondwanaland (which included Antarctica, Australia and South America) seems a likely evolutionary centre. The sheldgeese evidently had a wide distribution in both Old and New Worlds and the somewhat anomalous relationship of their photo-responses to latitude of origin (Fig. 14(b)) might be explicable in terms of a radiation from higher to lower latitudes.

The Andean goose—now an upland relict—represents the most "primitive" stage of a radiation of grazing birds in the Americas. Fossil evidence suggests that this radiation reached North America (Howard, 1964; Short, 1970) but that the group became extinct, conceivably in face of competition from the presumably better adapted grazing geese
The Blue-winged goose represents an upland relict of an early sheldgoose radiation in the Old World, probably an earlier radiation than that represented by the Andean goose since the Blue-winged goose exhibits more morphological and behavioural features that are considered "primitive" (Johnsgard, 1965). The shelduck too probably evolved in the southern land mass and radiated towards the equator.

The relict Orinoco goose and the aberrant steamer ducks are the only shelduck-like line in South America. Its origin in the ancient southern land mass could explain why the Orinoco goose has a temperate-type photo-response, in contrast to that displayed by the sympatric muscovy duck, whose origin is tropical if photo-responses provide a good guide.

Cygnus is obviously more "primitive" than the Tadornini. We have suggested that the Black swan Cygnus atratus, the swan species that today possesses most "primitive" features (Kear, 1970), evolved at a more southerly latitude than its present distribution suggests (Kear & Murton, 1976) and that, like the sheldgeese, the swans also radiated north towards the equator; some lines crossed into the north-temperate zone and from these, the "more modern" migratory northern swans are derived. Indeed, Short (1969) describes a fossil swan Paracygnus plattensis, from the Pliocene of Nebraska which most resembles of extant species the Mute swan Cygnus olor and Black swan and to a lesser extent the Black-necked swan C. melanocoryphus.

The Cape Barren goose Cereopsis novaehollandiae is evidently close to the swans (Kear & Murton, 1973) and perhaps evolved around the edge of the old southern land mass as a grazer of coastal grassland. It has a low photo-response threshold that causes it to breed between 19 November and 31 March in Britain (Kear & Murton, 1976). It could hardly have been ancestral to the northern geese which seem more likely to have arisen from northern swan-like stock and, moreover, to have evolved adaptive photo-responses at high latitudes. Cygnus falconeri of the Pleistocene is a fossil swan from Malta described as large, but having a relatively short femur, long tarsometatarsus and a short goose-like foot (Howard, 1964), which might represent the ancestor of the modern genera Anser and Branta.

The failure of the "true" geese to colonize a grazing niche in the southern hemisphere, thereby replacing Chloéphaga and Cereopsis, can possibly be explained by the changed position of the continents. There is no longer a grazing niche at a southern latitude for which the photo-response mechanisms of the true geese are pre-adapted, and the photo-responses of Chloéphaga and Cereopsis are presumably better adapted to the present day distribution of the groups. It must also be difficult for any animal whose young are reared on grass protein to cross the equatorial zones—although the sheldgeese apparently did so.

Tropical and temperate responses and entrainment

Egg-laying patterns of the kind displayed at Slimbridge by Hartlaub's duck and the Muscovy (Fig. 3) are considered to represent the original and simple tropical condition, since they are found among the most "primitive" representatives of the taxa considered here, as well as in flamingos (Duplaix-Hall & Kear, 1975), Anseranas, Dendrocygna and "primitive" species of Anas (Murton & Kear, 1976). At Slimbridge, breeding begins when daylengths are of approximately 12 hours duration and it continues until they fall below this level in the autumn; in consequence, the breeding season extends more or less symmetrically on either side of the summer solstice. The Southern pochard has a similar "primitive-type" cycle but the photo-threshold is lower so that breeding can begin under
daylengths of 9.4 hours; perhaps this indicates an evolutionary centre away from the equator.

In their natural ranges, species possessing the above kind of photo-response probably have the capacity to remain in breeding condition for much of the year; it is even possible that individuals free-run if the \textit{zeitgeber} at low latitudes is too weak for entrainment. It is well known that certain tropical oceanic sea birds have non-annual breeding seasons which appear to result from the free-running of endogenous "circannual" periodicities which are not entrained by the low amplitude tropical light–dark cycle (Chapin, 1954; Ashmole, 1963; Dorward, 1962), and it is becoming clear that some land birds also have non-annual breeding cycles (Lloyd, pers. comm.). Siegfried (1965a, b) gave evidence that the Red-billed pintail \textit{Anas erythrorhyncha} has a less than annual wing moult (see below). Even if the reproductive rhythm of these tropical duck is entrained by the low amplitude seasonal daylength cycle, it may be supposed that synchronization is weak so that individuals within a population are not closely in phase. This is commonly noted in tropical birds in which some individuals are occupied with incubation while others have large young and yet others may be undergoing a post-nuptial moult (Snow & Snow, 1964).

Egg-laying patterns of the kind displayed by the Comb duck at Slimbridge (Fig. 3) appear to be a modification of the "primitive" photoresponse just discussed in which the photo-threshold is set at a higher level. However, this cannot be the full explanation for, in the tropics, the birds would never experience the 17.3 hour daylengths apparently
needed at Slimbridge to initiate breeding. As with some *Dendrocygna* and *Oxyura*, the birds behave as if they are photo-refractory during the early spring. The data in Fig. 13 are consistent with a reduction in the frequency of some controlling oscillators, for the phase of entrainment to the Slimbridge daylength cycle has become more negative. If there were ecological pressure for the breeding cycle to become more easily entrainable by a weak *zeitgeber* this might be achieved by a reduction in the natural frequency of the animal’s endogenous oscillator system. Unfortunately, there is very little information to help answer this question, although a little circumstantial evidence is collated in Figs 15 and 16, based on various sources.

![Graph of daylength cycle at latitude 35°S with phasing of egg-laying cycle at Slimbridge at various points in the year.](image)

**Fig. 16.** Breeding seasons of various anatids in South Africa in terms of number of nests found with eggs. The daylength cycle at latitude 35°S is depicted and also the phasing of the egg-laying cycle at Slimbridge as a solid bar (adjusted for latitude as in Fig. 15). Data based on following sources: Hottentot teal (Clark, 1969); Cape teal (Winterbottom, 1974); Cape shoveler (Siegfried, 1965b); Southern pochard (Middlemiss, 1958); Yellowbill, solid for the S.W. Cape with winter rains and stipple for the Transvaal with summer rains (Rowan, 1963); Maccoa duck (Siegfried, 1969).

Four species which exhibit primitive-type egg-laying cycles in England (or Europe in the case of the Spur-winged goose) that are almost in phase with the solstice, and in which the photo-response threshold is set at a medium to high level, also breed around the solstice in Zambia; the four examples are the White-faced whistling duck *Dendrocygna viduata*, Comb duck, Spur-winged goose, and Red-billed pintail. (See Murton & Kear, 1976, for original records of the last, these having now been updated). Under a low amplitude tropical *zeitgeber*, the breeding seasons of these species slightly lag the season exhibited at Slimbridge, although the season of the Comb duck is virtually in phase with the light cycle at both localities. There is a suggestion in Fig. 15 that the Comb duck, which has a high photo-sensitive threshold at Slimbridge, has a much more synchronous breeding season in Africa than does the Spur-winged goose. Records for the White-back duck seem to be at variance with this interpretation and we must await the availability of more data to test the validity of this idea.
Figure 15 demonstrates that those species having temperate-type laying cycles at Slimbridge exhibit breeding seasons which are quite differently phased under an equatorial zeitgeber than the "primitive" group considered above. At Slimbridge the Egyptian goose (Fig. 6) and also the African Black duck Anas sparsa and Yellowbill Anas undulata (Murton & Kear, 1976) have breeding seasons which are positively phased relative to the zeitgeber. In Zambia, peak breeding similarly occurs during the season of short days (contrast the Comb duck discussed above). Presumably the difference in phasing of the breeding season of the Egyptian goose and Comb duck/Spur-winged goose in Africa is paralleled by similar differences between the sympatric Orinoco goose and Muscovy duck in South America, but unfortunately no data are available.

It would be quite wrong to assume from this discussion that breeding seasons in Africa are proximately controlled by seasonal changes in the photoperiod. Figure 16 immediately shows that this cannot be the case, especially if nest records for the Yellowbill are considered. Breeding occurs at different times of year in different parts of South Africa depending on when the seasonal rain occurs: in the winter rainfall area (S. W. Cape) most breeding is between July and October with none from February to May; in summer rainfall regions occasional birds breed at any time of year but about 70% of records are for the December–March period. Yet another variation in the breeding pattern is noted in Zambia (Fig. 15). We suspect that the final proximate stimulus enabling egg-laying to occur is the nutrient condition of the female and that the ideas of Jones & Ward (1976) are fully relevant in this context (see also Braithwaite, 1976, referring to Australian species). Nevertheless, for an animal to take advantage of favourable environmental food supplies, its own physiological condition must be suitably adjusted. This could be achieved slowly in response to the diet. But, obviously if the time of appearance of a protein rich source could be predicted, the bird could already be prepared to take immediate advantage of the situation, thereby breeding before its competitors.

Clearly predictive mechanisms operate in north-temperate species, for these live in environments where favourable seasons are reliably heralded by daylength changes; the individual can depend on photoperiodic stimuli to adjust its physiological condition in readiness for breeding. In males this means that full spermatogonetic development is achieved. In females the final growth of the follicle, after pairing, requires large energy reserves and if environmental resources are poor she may be unable to produce eggs. Thus, males broadly time the breeding cycle in response to photoperiodic changes whereas females provide the final timing in relation to food resources: the male response to photoperiod gives a timing to within two to three weeks, perhaps more precise, whereas the female times the cycle to within one day.

At lower latitudes, and in some southern hemisphere countries, photoperiodic changes are not reliable indicators of good ecological conditions. Even so, all birds are photoperiodic because entrainment to the daily light–dark cycle ensures that physiological and behavioural functions occur at appropriate times of day or night, and this is achieved via light sensitive oscillators. From these same oscillators are compounded mechanisms which control seasonal functions and they can be effectively entrained by low amplitude zeitgeber to ensure that, for example, moult and breeding schedules are discrete (flamingos do not appear to have a synchronized moult and do so before, during, and after breeding). At present we know virtually nothing about the mechanisms that order the priorities between moulting and breeding. Clearly one of the requirements is flexibility in the sense that the
response mechanisms of the bird must not be switched off too easily by the onset of a light induced photorefractoriness. Hence, we observe that although tropical waterfowl respond to temperate photo-regimes, they do manifest a potential for extending breeding. For example, the southern pochard evidently can breed at any time of year in Africa while at Slimbridge it has a very extended "primitive-type" cycle (cf. Figs 8 and 16), which is quite different from its European allies. On the other hand, tropical species which have evolved from temperate lines display their ancestry when exposed to a north-temperate light cycle for they now enter a typical photo-refractory phase; the Egyptian goose is a good example (cf. Figs 6 and 14). The photo-response threshold of the Egyptian goose is sufficiently low to ensure that under a tropical zeitgeber breeding can effectively occur at any season in response to environmental conditions.

There do appear to be differences in the ecological responses of species having "primitive-type" or low threshold "temperate-type" breeding rhythms in Africa and it will be valuable to have more data to investigate this question. The kind of breeding cycles shown by such species as the Comb duck and various _Dendrocygna_ at Slimbridge are evidently an artifact resulting from the unnatural daylength cycle. We need to measure plasma hormones in some of these species under a range of annual zeitgebers to try to understand the mechanisms involved.

We are grateful to Robert Gillmor and Nigel J. Westwood who drew the figures and to Brian Gadsby for the photograph in Plate I.

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**Appendix**

*Key to waterfowl species considered in the text and figures and their egg-laying seasons at Slimbridge or Peakirk (P)*

| Tribe Dendrocygini | Photoperiod* when earliest clutch laid | Photoperiod† when median laying date of first egg occurs beyond the summer solstice | Mid. latitude of natural breeding range | Number of years for which records available at Slimbridge and Peakirk |
|-------------------|---------------------------------------|-----------------------------------------------------------------------------------|----------------------------------------|---------------------------------------------------------------|
| 1. White-backed duck | 17.6 | 18.2 | 18.1 | 4 |
| *Thalassornis leuconotus* | | | | |

| Tribe Cairinini | Photoperiod* when earliest clutch laid | Photoperiod† when median laying date of first egg occurs beyond the summer solstice | Mid. latitude of natural breeding range | Number of years for which records available at Slimbridge and Peakirk |
|----------------|---------------------------------------|-----------------------------------------------------------------------------------|----------------------------------------|---------------------------------------------------------------|
| 1. Spur-winged goose | 12.6 | 14.5 | 15.9 | 8 |
| *Plectropterus gambensis gambensis* | | | | 
| 2. Comb duck | 17.3 | 18.3 | 13.2 | 15 |
| *Sarkidiornis melanotos melanotos* | | | | 
| 3. Muscovy duck | 11.7 | 15.2 | 13.5 | 10 |
| *Cairina moschata* | | | | 
| 4. Hartlaub's duck | 12.2 | 18.1 | 11.9 | 10 |
| *Cairina hartlaubi* | | | | 
| 5. White-winged wood duck | 13.9 | 15.0 | 18.0 | 8 |
| *Cairina scutulata* | | | | 
| 6. Ringed teal | 12.7 | 15.2 | 14.8 | 20 |
| *Anas leucophrys* | | | | 
| 7. Lesser Brazilian teal | 15.4 | 17.5 | 18.1 P | 18 |
| *Amazonetta brasiliensis brasiliensis* | | | | 
| 8. Maned goose | 11.7 P | 14.5 P | 17.9 P | 10 |
| *Chenonetta jubata* | | | | 


## PHOTOPERIODISM IN WATERFOWL

Key to waterfowl species considered in the text and figures and their egg-laying seasons at Slimbridge or Peakirk (P)

| Mid. latitude of natural breeding range | Photoperiod* when earliest clutch laid | Photoperiod† at median date of first egg laying | Photoperiod‡ when last eggs laid (italic figures mean that laying occurs beyond the summer solstice) | Number of years for which records available at Slimbridge and Peakirk |
|----------------------------------------|--------------------------------------|-----------------------------------------------|-------------------------------------------------|---------------------------------------------------------------------|
| 9. Mandarin duck, *Aix galericulata*    | 47°N                                 | 13:4                                          | 15:0                                            | 17:6 P                                                              | 33                                                                   |
| 10. Carolina, *Aix sponsa*              | 41°N                                 | 12:0                                          | 13:6                                            | 17:3                                                               | 36                                                                   |

**Tribe Tadornini**

**Sheldgeese**

1. Abyssinian blue-winged goose, *Cyanochen cyanopterus*
   - 10°N
   - 15:2
   - 17:1
   - 17:4
   - 20

2. Andean goose, *Chloéphaga melanoptera*
   - 24°S
   - 14:1
   - 15:2
   - 18:3
   - 18

3. Ashy-headed goose, *Chloéphaga poliocephala*
   - 45°S
   - 13:6
   - 15:0
   - 16:9
   - 27

4. Ruddy-headed goose, *Chloéphaga rubidiceps*
   - 55°S
   - 13:7
   - 15:1
   - 16:7
   - 21

5a. Greater magellan goose, *Chloéphaga picta leucoptera*
   - 55°S
   - 12:9
   - 14:2
   - 17:1 P
   - 28

5b. Lesser magellan goose, *Chloéphaga picta picta*
   - 45°S
   - 13:8
   - 14:5
   - 16:5
   - 24

**Steamer duck**

6. Falkland flightless steamer duck, *Tachyeres brachypterus*
   - 52°S
   - 13:7
   - 13:9
   - —
   - 7

**Shelduck**

7. Egyptian goose, *Alopochen aegyptiacus*
   - 32°N
   - 9:3
   - 12:6
   - 17:8
   - 22

8. Orinoco goose, *Neochen jubatus*
   - 7°S
   - 12:5
   - 13:5
   - 16:0
   - 9

9. Radjah shelduck, *Tadorna radjah*
   - 15°S
   - 12:0
   - 15:2
   - 17:0
   - 8

10. South African shelduck, *Tadorna cana*
    - 30°S
    - 11:9
    - 13:3
    - 14:7
    - 33

11. New Zealand shelduck, *Tadorna variegata*
    - 41°S
    - 11:9
    - 15:2
    - 17:0
    - 22

12. Ruddy shelduck, *Tadorna ferruginea*
    - 43°N
    - 13:8
    - 15:3
    - 16:8
    - 17

13. Australian shelduck, *Tadorna tadornoides*
    - 35°S
    - 10:7
    - 11:2
    - 13:5
    - 1 S

14. Common shelduck, *Tadorna tadorna*
    - 45°N
    - 14:6
    - 15:4
    - 16:8 P
    - 29
Key to waterfowl species considered in the text and figures and their egg-laying seasons at Slimbridge or Peakirk (P)

| Tribe Aythyini | Mid. latitude of natural breeding range | Photoperiod* when earliest clutch laid | Photoperiod† at median date of first egg laying | Photoperiod‡ when last eggs laid (italic figures mean that laying occurs beyond the summer solstice) | Number of years for which records available at Slimbridge and Peakirk |
|----------------|----------------------------------------|---------------------------------------|-----------------------------------------------|-----------------------------------------------------------------|------------------------------------------------------------------|
| Tribe Aythyini |                                       |                                       |                                               |                                                                 |                                                                 |
| 1(a). South American pochard | 5°S | — | 12·8 | — | 1 |
| 1(b). African pochard | 10°S | 9·4 | 12·8 | 12·8 P | 17 |
| 1. Rosy-bill | 30°S | 15·2 | 16·8 | 18·1 P | 30 |
| 2. Red-crested pochard | 43°N | 11·6 | 13·7 | 17·6 | 35 |
| 3. Ring-necked duck | 55°N | 17·2 | 17·8 | 17·9 P | 6 |
| 4. Australian white-eye | 28°S | 12·7 | 15·9 | 18·1 | 18 |
| 5. Common white-eye | 45°N | 15·0 | 16·9 | 18·1 P | 13 |
| 6. New Zealand scaup | 41°S | 14·0 | 16·2 | 18·0 | 20 |
| 7. Lesser scaup | 53°N | 16·6 | 17·8 | 18·3 P | 14 |
| 8. Greater scaup | 65°N | 16·5 | 17·8 | 18·3 | 22 |
| 9. Tufted duck | 60°N | 16·0 | 17·9 | 18·3 P | 23 |
| 10. Baer's pochard | 50°N | 17·8 | 18·2 | 18·2 | 12 |
| 11. Redhead | 45°N | 14·9 | 15·9 | 18·3 | 25 |
| 12. European pochard | 53°N | 14·6 P | 16·1 | 17·8 | 24 |
| 13. Canvasback | 50°N | 13·8 | 16·4 | 17·3 | 7 |

| Tribe Somateriini |                                       |                                       |                                               |                                                                 |                                                                 |
|-------------------|----------------------------------------|---------------------------------------|-----------------------------------------------|-----------------------------------------------------------------|------------------------------------------------------------------|
| 1. Eider | 65°N | 15·2 | 16·7 | 18·3 P | 33 |
| 2. King eider | 72°N | 15·2 | 16·7 | 18·2 | 13 |
| 3. Spectacled eider | 70°N | 16·7 | 17·3 | 17·5 | 3 |
**PHOTOPERIODISM IN WATERFOWL**

Key to waterfowl species considered in the text and figures and their egg-laying seasons at Slimbridge or Peakirk (P)

| Tribe Mergini       | Mid. latitude of natural breeding range | Photoperiod* when earliest clutch laid | Photoperiod† at median date of first egg laying | Photoperiod‡ when last eggs laid (italic figures mean that laying occurs beyond the summer solstice) | Number of years for which records available at Slimbridge and Peakirk |
|---------------------|----------------------------------------|----------------------------------------|-----------------------------------------------|-------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------|
| 4. Harlequin duck  | 60°N                                   | —                                      | 18:2                                          | 17:3                                                                                              | 1                                                                      |
| *Histrionicus histrionicus* |                                        |                                        |                                               |                                                                                                  |                                                                        |
| 5. European goldeneye | 60°N                                   | 13:8                                   | 15:5                                          | 17:3                                                                                              | 18                                                                     |
| *Bucephala clangula clangula* |                                          |                                        |                                               |                                                                                                  |                                                                        |
| 6. Barrow’s goldeneye | 50°N                                   | 16:0                                   | 16:8                                          | 18:1                                                                                              | 12                                                                     |
| *Bucephala islandica* |                                        |                                        |                                               |                                                                                                  |                                                                        |
| 7. Bufflehead       | 59°N                                   | 15:2                                   | 16:4                                          | 17:4                                                                                              | 4                                                                     |
| *Bucephala albeola* |                                        |                                        |                                               |                                                                                                  |                                                                        |
| 8. Smew             | 60°N                                   | 15:5                                   | 17:4                                          | 18:1                                                                                              | 15                                                                     |
| *Mergus albellus*   |                                        |                                        |                                               |                                                                                                  |                                                                        |
| 9. Hooded merganser | 53°N                                   | 14:0                                   | 15:0                                          | 16:7                                                                                              | 7                                                                     |
| *Mergus cucullatus* |                                        |                                        |                                               |                                                                                                  |                                                                        |
| 10. Goosander       | 55°N                                   | 15:0                                   | 16:8                                          | 17:5                                                                                              | 3                                                                     |
| *Mergus merganser merganser* |                                          |                                        |                                               |                                                                                                  |                                                                        |
| 11. Red-breasted merganser | 60°N                                   | 17:2                                   | 17:9                                          | 18:3                                                                                              | 16                                                                    |
| *Mergus serrator serrator* |                                          |                                        |                                               |                                                                                                  |                                                                        |
| Tribe Oxyurini      |                                        |                                        |                                               |                                                                                                  |                                                                        |
| 1. North American ruddy duck | 48°N                                   | 15:2                                   | 17:2                                          | 17:4                                                                                              | 30                                                                    |
| *Oxyura jamaicensis jamaicensis* |                                          |                                        |                                               |                                                                                                  |                                                                        |
| 2. Argentine ruddy duck | 37°S                                   | —                                      | 17:4                                          | —                                                                                                  | 1                                                                     |
| *Oxyura vittata*    |                                        |                                        |                                               |                                                                                                  |                                                                        |
| 3. African Maccoa duck | 14°S                                   | 15:4                                   | 17:6                                          | 17:7                                                                                              | 2                                                                     |
| *Oxyura maccoa*     |                                        |                                        |                                               |                                                                                                  |                                                                        |
| 4. White-headed stiff-tail duck | 45°N                                   | 16:5                                   | 17:6                                          | 16:4                                                                                              | 3                                                                     |
| *Oxyura leucocephala* |                                         |                                        |                                               |                                                                                                  |                                                                        |

* The daylength (plus civil twilight) on the date the earliest clutch was ever recorded, irrespective of year.
† For each year for which records were available the date of the first clutch was noted and the median date for all years was used to derive the photoperiod. Number of years (= clutches) contributing to the median is given in column 5.
‡ The latest date ever recorded, irrespective of year, on which clutches were laid.