

## THE INCUBATION PATTERNS OF BIRDS.

By ALEXANDER F. SKUTCH.

Received on 7 December 1955.

### CONTENTS.

Introduction.

Part 1. A classification of incubation patterns.

Synopsis of incubation patterns.

Notes and references.

Part 2. What determines the participation of the sexes in incubation ?

The evolutionary sequence.

Incubation and brood-patches in male passerines.

Incubation habits in relation to colouration and nidification.

Influence of the environment.

Incubation in relation to song and territory.

Incubation and the sex-ratio.

Conclusions.

Summary.

References.

### INTRODUCTION.

More than a decade ago, I began to collect material for a general survey of the modes of incubation of birds as a whole, giving special attention to the division of labour between the sexes, the rhythm of sitting, and the factors which determine the pattern adopted by each species or group. But the task proceeded slowly and meanwhile Kendeigh (1952) has performed a great service to all ornithologists by giving us in a single volume a summary of nearly all that is known of the modes of incubation and other aspects of parental care in birds. There would be no point in attempting to duplicate this vast and laborious undertaking. Yet I believe that a condensed synopsis of the known patterns of incubation, in the form of a "key", will be interesting and instructive to naturalists, as revealing at a glance the vast diversity of behaviour which birds have evolved in this single activity, and enabling them to place any observed pattern in the general scheme. Moreover, an analysis of the facts now available seems to permit the drawing of a few conclusions which appear to be new, or at least not sufficiently emphasized by earlier writers.

### PART 1.

#### A CLASSIFICATION OF INCUBATION PATTERNS.

The following classification is logical rather than phylogenetic. It does not pretend to trace the course of evolution of incubation patterns, but offers an arrangement based upon differences actually observable. The primary



divisions are determined by the number of adults incubating, whether one, two, or as in a few exceptional groups, more than two at a single nest. When the two parents incubate, we obtain a further division by considering whether they sit alternately or (as rarely occurs) simultaneously. Alternate care of the eggs by male and female is the method most widespread among birds; and in this great division obvious subdivisions are suggested by the occupancy of the nest by night. Whether the male or female is in charge during the hours of darkness seems more significant in strictly diurnal birds than in those which are active both day and night. But in a number of families, especially among seabirds, either sex may cover the nest through the night. Whether this alternation occurs, or whether the same sex is always in charge by night, seems to be determined primarily by the length of the sessions or the frequency of changes in occupancy; for obviously when the sexes replace each other at intervals consistently longer than twelve hours, it will fall now to one, now to the other, to sit at night. Hence the frequency of change-overs forms the basis of further subdivisions in the great group of birds of which the sexes alternate on the eggs.

In the section in which a single parent takes charge of the eggs, the major subdivisions are determined by the sex to which this duty falls. In each of the two resulting classes, further subdivisions are determined by the length of the sessions, or the frequency of coming and going. Since there is a graded series from birds which sit for only a few minutes at a stretch to those which remain continuously on the nest for all or nearly all of the incubation period, further divisions must be somewhat arbitrary. A parent which sits continuously for many days may either fast or be fed by its mate, and this suggests a final dichotomy in the key (IIA3).

When more than two birds take charge of the eggs, we wish to know how many of the coöperating partners are parents and how many are voluntary assistants. Among the anis *Crotophaga* several females lay their eggs in a common heap and the parents of both sexes take turns in covering them. In Bush-tits *Psaltiriparus minimus* three birds sometimes incubate in one nest. In Black-eared Bush-tits *P. melanotis*, of which the sexes are more readily distinguishable, supernumerary males help the mated pair to attend their nest and young and many take tufts of down into the pouch while incubation is in progress; but I could not make sure that any of these assistants actually warmed the eggs. Simultaneous incubation by two females of the same or even different species in a nest where both have laid has from time to time been reported as an abnormality, but our classification is concerned only with more constant behaviour.

Finally, to complete our conspectus of the modes of incubation, we have included certain expedients whereby the parents avoid the possibly tedious occupation of applying to their eggs the heat of their own bodies. They may either drop their eggs into the nests of other birds, as with a number of

cowbirds, cuckoos, and a few ducks and others; or they may utilize the heat of the sun, decaying vegetation, or volcanoes, as with the megapodes.

In examining the following classification, a certain symmetry is evident. In division I (incubation by both parents) B2a, in which the female covers the eggs by night and the male takes one long session each day, has its counterpart in B3a, in which the male incubates by night and the female takes one long session each day. Similarly B2b, in which the female sits by night and the sexes alternate several times a day, has its counterpart in B3b, where the situation is reversed. In division II (incubation by a single parent), the three subclasses under A (incubation by the female) are almost exactly mirrored by the three subclasses under B (incubation by the male). But there seems to be no known instance of a female bird feeding her continuously incubating partner, to match the nourishing of the immured female hornbill by her mate.

Many birds whose method of incubation is known in a general way, as whether one or both parents sit on the eggs and even which is in charge through the night, have not been studied in sufficient detail to permit their allocation to the finer subdivisions of our table. It is to be hoped that this lack will little by little be remedied. The examples cited under each ultimate division are intended to be illustrative rather than exhaustive; and I have in most instances limited their number to four, even when scores of examples might have been given. Also in order to keep the "key" compact, I have relegated all comments and citations of literature to the notes which follow immediately after it. When no authority is given, either the mode of incubation was learned by my own observations, or it is generally known and recorded in works of reference. An extensive bibliography of pertinent studies, with brief summaries and analyses, is to be found in Kendeigh's monograph (indicated by K in these notes).

#### SYNOPSIS OF INCUBATION PATTERNS.

##### PARENTAL INCUBATION.

#### I. Incubation by two parents.

##### A. By both sexes simultaneously.

Red-legged Partridge *Alectoris rufa*.

##### B. By both sexes, alternately.

##### 1. Either sex may cover eggs by night.

(a) Change-overs at intervals of about 24 hours, so that the same parent does not often sit for the whole of successive nights.

Diving Petrel *Pelecanoides urinatrix*, Sooty Tern *Sterna fuscata*, Bridled Tern *S. anaethetus*, Ringed Kingfisher *Ceryle torquata*.

(b) Change-overs at intervals of much more than 24 hours, so that the same parent may sit for several nights in succession.



Adélie Penguin *Pucheranphus adeliae*, Manx Shearwater *Puffinus puffinus*, Royal Albatross *Diomedea epomophora*, and many other Procellariiformes.

- (c) Change-overs at intervals of less than one day (sometimes by both daylight and dark).

Semipalmated Plover *Charadrius hiaticula*, Herring Gull *Larus argentatus*, Cape Wagtail *Motacilla capensis*.

2. Female covers eggs by night.

- (a) Male takes one long session each day.

Pigeons and doves, Citreoline Trogon *Trogon citreolus*, Black-throated Trogon *T. rufus*.

- (b) Sexes alternate on nest several times a day, the diurnal sessions therefore usually shorter than in 2a.

Amazon Kingfisher *Chloroceryle amazona*, Rufous-tailed Jacamar *Galbula ruficauda*, antbirds (Formicariidae), many warblers (Sylviidae).

3. Male covers eggs by night.

- (a) Female takes one long session each day.

Ostrich *Struthio camelus*, Pale-billed Woodpecker *Phloe-oceastes guatemalensis*.

- (b) Sexes alternate on nest several times a day, the diurnal sessions therefore usually shorter than in 3a.

Many woodpeckers, anis *Crotophaga*, American Coot *Fulica americana*.

## II. Incubation by one parent only.

### A. Incubation by female.

1. One recess each day, usually long.

Bobwhite Quail *Colinus virginianus*, Marbled Wood Quail *Odontophorus gujanensis*, Guan *Pauxi pauxi*.

2. Several or many recesses each day, sometimes also by night.

Red-head Duck *Nyroca americana*, most hummingbirds, manakins (Pipridae), American flycatchers (Tyrannidae), most song-birds.

3. Female sits continuously for many days.

- (a) She fasts while incubating.

Golden pheasant *Chrysolophus pictus*, Great Argus Pheasant *Argusianus argus*, Eider Duck *Somateria mollissima*, Blue Goose *Chen caerulescens*.

- (b) She is fed by male.

Hornbills.

### B. Incubation by male.

1. One long recess each day.

Little Tinamou *Crypturellus soui*, Bonaparte's Tinamou *Nothocercus bonapartei*.

2. Several or many recesses each day.

Pheasant-tailed Jacana *Hydrophasianus chirurgus*, Ornate Tinamou *Nothoprocta ornata*.

3. Male incubates continuously for a number of days, fasting.

Emperor Penguin *Aptenodytes forsteri*, Kiwi *Apteryx*, Emu *Dromiceius n. hollandiae*.

## III. Incubation by more than two birds at a single nest.

### A. Eggs laid by one female.

1. Several adults assist the female.

Bush-tit *Psaltiriparus minimus*.

### B. Eggs laid by two or more females.

1. Several birds of both sexes participate in incubation.

Anis *Crotophaga*, ?Acorn Woodpecker *Melanerpes formicivorus*.

## SUBSTITUTE INCUBATION.

## IV. Eggs incubated by birds of other species.

Many cuckoos, cowbirds (Icteridae), honey guides (Indicatoridae), Black-headed Duck *Heteronetta atricapilla*.

## V. Eggs incubated without animal heat.

Megapodes, Egyptian Plover *Pluvianus aegyptius*.

## NOTES AND REFERENCES.

- IA. I have placed first this extraordinary mode of incubation to emphasize by juxtaposition its contrast with the following heading—incubation by both sexes alternately. The Red-legged Partridge is the only example I know. The female lays in close succession two sets of eggs in separate nests; she incubates one set while her mate takes charge of the other (Goodwin 1953). In the Bobwhite Quail, according to Stoddard (1946), either the cock or the hen may take exclusive charge of the nest, and more rarely the two take turns on the same set of eggs, or in captivity sit side by side in the same nest. Apparently there is no record of the male and female of a pair incubating simultaneously separate sets laid by the latter; but it seems that this custom might easily develop from the situation found in the Bobwhite. In *Lophortyx* the male may take full charge of incubation if the female deserts or is killed (K.).

In a number of rails, motmots, barbets, woodpeckers, swifts, titmice, etc. both sexes sleep in the nest cavity; but we have no evidence that they divide the eggs between them and incubate simultaneously, by night if not by day.

- IB 1a. Diving Petrel—Richdale (1943); Terns—K.

- IB 1b. Male Adélie Penguins may fast up to 40 days, females 21—Sladen (1953). Albatrosses fast up to 32 days—K. Manx Shearwater—Lockley (1942).

- IB 1c. Semipalmated Plover—Spingarn (1934); Herring Gull—K. The only instance of a passerine in which either sex may incubate by night known to me is the Cape Wagtail, in which Skead (1954) found sometimes the male, sometimes the female sleeping on the nest. This irregularity becomes more understandable in the light of the statement by Moreau (1949) that in the African Mountain Wagtail *Motacilla clara* both parents slept on or



alongside the nest. In cases like this, it is usually scarcely possible to tell which actually sits upon the eggs, and whether there is constancy in this detail. A similar uncertainty exists with all those birds, mentioned above, in which both parents sleep with the eggs in well closed nests. When this happens with passerines, such as some titmice and swallows, it is more likely to be the female who maintains close contact with the eggs, since in the Passeres males usually lack brood patches for the efficient transfer of heat.

- IB 2b. In addition to many certain examples of this class, there are many more that are probable; but the similarity of the sexes makes it difficult to determine which is in charge of the nest by night. It is likely that many toucans, motmots, woodhewers (*Dendrocolaptidae*), and ovenbirds (*Furnariidae*) belong here; but the sex which incubates through the night is not definitely known.
- IB 3a. Ostrich—K. The Pale-billed Woodpecker is included here provisionally on the strength of a single day's observation at a nest which was prematurely lost.
- IB 3b. Anis often nest communally, but nests of single pairs fall here. American Coot—Gullion (1954).
- IIA 1. Bobwhite—Stoddard (1946); *Pauzi*—Schäfer (1953, 1954a).
- IIA 2. The Red-head Duck takes recesses by night as well as by day (Low 1945).
- IIA 3a. Golden Pheasant and Eider—Goodwin (1948); Argus—Delacour (1951); Blue Goose—Manning (1942).
- IIA 3b. As is well known, the female hornbill encloses herself in the nest cavity by walling up the doorway, leaving only a small aperture through which her mate passes food for her and later for the nestlings as well (Moreau 1936, 1937; Moreau & Moreau 1940, 1941). Although no other instance of uninterrupted incubation by a female sustained by her mate is known to me, more or less close approach to it is made by a number of other species, in which the sitting female is so well nourished by her partner that her absences are infrequent or short, or both. Among these are owls and parrots (K), and such passerines as the Cedar Waxwing *Bombycilla cedrorum* (Putnam 1949) White-throated Magpie-Jay *Calocitta formosa* (Skutch 1953), and numerous cardueline finches, such as the Goldfinch *Carduelis carduelis* (Conder 1948).
- IIB 1. Bonaparte's Tinamou—Schäfer (1954 b).
- IIB 2. Pheasant-tailed Jacana—Hoffmann (1949); Ornate Tinamou—Pearson and Pearson (1955).
- IIB 3. Emperor Penguin—Stonehouse (1953); Emu and Kiwi—K.
- IIIA 1. Bush-tit—Addicott (1938); (compare Skutch 1935).
- IIIB 1. Anis—Bent (1940), Davis (1940). Four or five Acorn Woodpeckers may attend one nest, but the number of layers is uncertain.
- IV. Cowbirds—Friedmann (1929); parasitic ducks—Friedmann (1932).
- V. Megapodes—Wallace (1872), Sibley (1946), K; Egyptian Plover—K.

## PART 2.

### WHAT DETERMINES THE PARTICIPATION OF THE SEXES IN INCUBATION ?

The type of the incubation pattern is determined largely by innate factors, so that it persists through fairly wide fluctuations in weather, although it may break down in extreme conditions. Hence the position of a species in the foregoing classification is rarely changed by the normal, day to day variations in temperature, rainfall, and the like, which, however, may markedly affect the length of the birds' periods on and off the nest. An exhaustive study of incubation patterns would include these variable features along with the more constant features. At present, however, we shall confine our attention to the latter, especially the role of the sexes, reserving the former for future discussion.

*The evolutionary sequence.* In a number of families placed lowest in current schemes of classification, as the rheas, emus, and kiwis, the male takes care of the eggs and chicks with little if any help from the female, and in a great many families considered to be more advanced he has a share in incubation equal to, if not greater than, that of his mate, while in the highest group, the Passeriformes, the female is largely and in many species wholly responsible for keeping the eggs warm. When one recalls these facts, it is tempting to postulate that incubation by the male alone is the primitive condition in the avian stock. The fact that in a number of fishes, including Stickle-backs, Fighting Fish, and Pipe Fish, and in such batrachians as the Nurse-frog of Europe, the male alone takes charge of the eggs and young, makes this hypothesis more attractive. One might suppose that, with the psychic development of birds, as the affective bonds between the sexes grew stronger, the female's closer association with her mate led her to share increasingly in his parental duties, until the participation of both parents in all phases of the nesting operations became widespread among birds. Finally, with the evolution of song, territorial defence, or ornamental plumage along with elaborate courtship displays, the male came to neglect domestic pursuits for these more exciting occupations, until he quite ceased to incubate or, as in many pheasants, hummingbirds, cotingas, manakins, and birds of paradise, he lost all interest in the nest and young.

Weighing against this attractive speculation is the fact that in a number of orders of birds, especially those occupying intermediate positions in current taxonomic systems, are families in which the female takes the sole or at least the leading role in incubation, along with families in which the male is largely or wholly responsible for the eggs. Thus in the Gruiformes, in the majority of whose families the sexes share parental duties rather equally, the female alone is said to incubate in the bustards, whereas in the hemipodes it is chiefly if not solely the male who attends the eggs. In the Charadriiformes, where again incubation by both sexes is the prevailing mode, the male takes charge of the eggs in the painted snipes, the jacanas, and some of the phalaropes and sandpipers; while the female does most of the incubation in a number of other species of Scolopacidae, so that in this single family both trends are evident. When we recall how, through much of the avian class, the weight of incubation shifts now to the female, now to the male sex, we must agree with Kendeigh (1952) that incubation by both sexes is most probably the primitive, as it is the prevailing, method among birds, and from this basic arrangement various stocks have diverged in the direction of greater male or greater female participation. For this, too, we can find analogies among the cold-blooded vertebrates from which the warm-blooded birds and mammals have descended. In some of the cichlid fishes the sexes alternate in the care of the eggs and newly hatched young in a manner that reminds one strongly of birds (Lorenz 1952).



The constancy of the incubation pattern in each species and even in whole families of birds, leaves little doubt that it is genetically determined; and it is highly probable that its physical basis lies in the structure of the nervous system and the functioning of the endocrine glands. It will help us to understand the evolution of incubation patterns if we bear in mind that the habit of incubation is a secondary sexual, if not a sex-linked, character, like song and ornamental plumage in birds, horns and manes or beards in mammals. As a result of genetic "accidents", sometimes no doubt the crossing-over of genes from one to another of the sex chromosomes, these secondary sexual characters often pass from male to female, or vice versa, in a way for which no good reason in the form of a recognized utility can be assigned. The fact that in some deer and cattle the females as well as the males bear horns, in others the male alone, seems to be largely unrelated to the usefulness of these weapons to the females. In many families of birds, there are species in which both sexes are brightly coloured along with those in which the male alone is brilliant; and in many instances it seems impossible to correlate these differences with the habits and needs of the birds. Similarly, song is on the whole a male character which may or may not pass to the female, and it is often difficult to find a reason for the singing of the female in one species and her failure to do so in a related species. Many of the fluctuations in incubation habits seem to be of the same irrational or non-adaptive character, the result of genetic accidents uncontrolled by the needs of the birds.

In certain families or wider groups, incubation habits are in a particularly unstable condition, so that we find species in which the male incubates along with those in which he rarely does so. For example, in the vireos the male's part in incubation is most irregular. The most careful studies of the Red-eyed Vireo *Vireo olivacea* (Lawrence 1953) and the closely related or possibly conspecific Yellow-green Vireo *V. flavoviridis* (Bent 1950) revealed incubation by the female alone; but statements that the male of the former sits on the eggs are not lacking (e.g. Forbush 1929), and in view of the variability of this feature in the genus as a whole are not to be lightly brushed aside as unreliable. On the other hand, in the Philadelphia Vireo *V. philadelphicus* (Lewis 1921), Warbling Vireo *V. gilvus* (Rust 1920), Hutton's Vireo *V. huttoni* (Van Fleet 1919), and Bell's Vireo *V. bellii* (Nice 1929), the males seem regularly to incubate, often singing freely while they sit in the nest. So, too, in the warblers (Sylviidae) there are a number of species in both the Old and New World in which the male incubates, along with many, at least in the Old World, where the family is best represented, in which he fails to do so (Witherby *et al.*, 1938). The swallows show the same inexplicable mixture of species in which both sexes incubate and those in which only the female does so (Allen & Nice 1952).

The great suborder of the Tyranni is generally held to contain some of the more primitive families of the order Passeriformes, although many of its

members exhibit amazing specializations in various directions; and in view of its taxonomic position the study of the wide fluctuations in incubation habits and other aspects of parental care to be found within it should be particularly instructive. Although in the antbirds incubation by both sexes seems general, the ovenbirds and woodhewers exhibit cases of non-participation by the male which are difficult to explain. In the American flycatchers and cotingas the male is not known to incubate and may or may not feed the young; in the manakins he is not known to attend the nest at any stage in any species. The failure to incubate, or even to feed the young, probably preceded rather than followed the amazing developments in plumage and courtship habits in many manakins and cotingas, and in less conspicuous degree in some of the American flycatchers. It is far more likely that a genetically determined release from attendance upon the eggs left the males free to acquire colours, ornamentation, and modes of life which make them unfit for parental duties, than that the acquisition of these peculiarities was followed by a growing aloofness from the nest. So, too, in the suborder Passeres, or song-birds proper, elaborate song and great preoccupation with territory by the males may have followed upon rather than preceded abstinence from incubation.

*Incubation and brood-patches in male passerines.* The apparently non-adaptive character of many variations in incubation habits, at least within the passerines, is further attested by the lack of correlation between incubation and the presence of a brood-patch in the males. While it is true that even without an incubation patch a bird can retard the cooling of already warmed eggs by sitting on them as a sort of heated blanket, it is through the area of highly vascularized bare skin which most incubating birds apply directly to the eggs that heat is most effectively transferred to them. Although the males regularly take turns on the nest in such oscinine groups as bush-tits *Psaltiriparus*, wren-tits *Chamaea*, and grosbeaks *Pheucticus* or *Hedymeles*, they fail to develop highly vascularized incubation-patches, and it is doubtful if these are present in typical form in any males of the suborder Passeres (Bailey 1952). Yet Smith (1950) saw the male Yellow Wagtail *Motacilla flava* apply bare ventral skin to the eggs as he settled down for his regular turns at incubation, and found the eggs warm after he had been sitting. Mewaldt (1952) found incubation patches on a number of male Clark Nutcrackers *Nucifraga columbiana*, and in some cases they seemed as well developed as in nesting females. Likewise Amadon and Eckelberry (1955) collected in Mexico a male Magpie-Jay *Calocitta formosa* with a well developed brood-patch; although at a Guatemalan nest of this species that I watched carefully I failed to find evidence that the male covered the eggs, and incubation by males is unusual in the Corvidae.

In the Tyranni or non-oscinine passerines the situation is equally confusing; for incubation patches are sometimes present even in families and genera



in which males do not incubate, at least in the species which have been watched at the nest (e.g. *Tityra* and *Myiodynastes*—Davis 1945). In American flycatchers of the genus *Empidonax* the males of some species do show an incubation patch while those of other species lack it (Parkes 1953); yet in no member of this genus or even family is the male known to incubate. Except in the tropical antbirds, it is not easy to find a nest of a passerine at which the male incubates and which is at the same time favourably situated for observing whether he applies a patch of bare skin to the eggs, in the manner of Smith's Yellow Wagtail; but anyone who has an opportunity to determine this point may without any sacrifice of life make an important contribution to ornithology.

It appears, then, that the pattern of incubation, and especially its major feature the participation of the sexes, is genetically controlled, and like other heritable characters may be altered by mutations which are not called forth by the needs or mode of life of the race in which they occur. So long as these changes do not seriously detract from reproductive efficiency, they may persist even if they are no improvement over the earlier mode of incubation; but where they result in a marked decrease in hatching success they will be eliminated by selection. Thus there is no reason to suppose that every modification in incubation patterns is adaptive. The only condition for its persistence is that it is not detrimental. Can we detect definite trends in the evolution of incubation patterns in relation to the structure, coloration, or mode of life of birds?

*Incubation habits in relation to colouration and nidification.* It was long supposed that there is a close correlation between the colouration of a bird and its part in incubation. Thus Wallace (1871) wrote: "when both sexes are of strikingly gay and conspicuous colours, the nest is . . . such as to conceal the sitting bird; while, wherever there is a striking contrast of colours, the male being gay and conspicuous, the female dull and obscure, the nest is open and the sitting bird exposed to view". Since colouration is so variable a character in animals, and birds are on the whole conservative in their habits and architecture, Wallace supposed that colouration was determined by the form of the nest, rather than the reverse. If a species nested in a hole or burrow, both sexes could don brilliant plumage without jeopardizing eggs and young by their conspicuousness; if it used an open cup, the sitting female was kept dull by natural selection and the male alone was free to become colourful. Wallace appeared to be ignorant of the prevalence of incubation by males in many avian orders.

In view of our vastly amplified—although still far from adequate—knowledge of the life histories of birds, it may be worth our while to re-examine the facts and try to discover some correlation between the three variables, colouration, nidification, and incubation pattern. In some of the most colourful of the non-passerine families, as kingfishers, motmots,

jacamars, bee-eaters, toucans, and woodpeckers, male and female are nearly or quite equal in brilliance and share fairly equally all the labours of the nest, which is nearly always in a cavity of some sort, so that the colour of the incubating bird is not likely to catch the eye of a predator. But in some families in which the females of North American species are far duller than the males the Central American representatives have the sexes alike. In my early years in Central America, I was eager to learn whether, when the sexes were similar in appearance, they would take more equal parts in the nesting duties than in the north where they are strikingly different. But as the years passed I became convinced that, among the passerines at least, colouration has little to do with the participation of the male in incubation, and shows almost as little correlation with the form of the nest. No family displays a greater variety of bright colours than the tanagers, and in some of the most brilliant genera (e.g. *Tangara*) the sexes scarcely differ in appearance, yet only the female sits in the open nest. These are balanced by other genera (e.g. *Ramphocelus*), also with open nests, in which the male is far more brilliant than the female, which alone sits. When there is a closed nest combined with striking sexual differences in colour, as in the euphonias and chlorophonias, the situation is the same, only the female incubates. In the Icteridae, some of the most brilliant of the tropical orioles exhibit slight sexual differences in their yellow and black attire; yet whether the nest is a shallow open cup or a deep closed pouch, the male, so far as known, fails to incubate. So, too, with the wood warblers, in some of the most colourful tropical species the females hardly differ from their mates; but the male is not known to incubate, even when the nest is roofed, as in *Myioborus* and *Ergaticus*.

No family exhibits a more wonderful diversity of architecture than the Tyrannidae, yet whether the nest is open or well closed the male has never been seen to sit in it. On the other hand, the antbirds, without being brilliant, often exhibit pronounced sexual differences in colouration; yet male and female participate equally in incubation in their usually open nests. Among the passerine birds of tropical America, there is scarcely any correlation between colouration, nidification, and incubation pattern, which on the whole vary quite independently of each other. It is true that in some of the manakins and cotingas the ornate male leaves to the far duller female all the parental offices; but the same is true of some members of these families which exhibit little or no sexual dimorphism; and it is probable that the males relinquished incubation long before they acquired their colourful attire, their bizarre wattles, or their elaborate courtship antics.

In the most lavishly adorned of birds, as the peacocks, Argus pheasants, and the most ornate of the birds of paradise, the abundant, brightly coloured nuptial plumes of the males would not only jeopardize the nests by their conspicuousness, but by their size and unwieldiness might seriously impede



the birds in the performance of parental chores. It is quite understandable why in the more ornate species of these families the males remain aloof from the nest, although in the more plainly attired members, as the quail and the manucodes, the males not only take an interest in the young but sometimes incubate, or at least brood the nestlings (Rand 1938). But even in these families it is probable that the males ceased to sit in the nest before rather than after acquiring their splendid adornments. As Huxley (1938) pointed out, the evolution of exaggerated courtship characters is facilitated by the higher reproductive potential of males which do not pair but use all their arts to attract the greatest number of females. A strictly monogamous male can father only as many offspring as he and his single mate can adequately nourish; but a promiscuous male, who proves especially attractive to the females, can fecundate the eggs of many and so each season leave a numerous progeny. Such an outstanding advantage in reproduction accelerates the evolution of the bright colours, elaborate plumes, and striking postures which attract the females, bringing about results which could hardly be attained by monogamous birds. But the reproductive advantage which leads to these arresting products of sexual selection is enjoyed only *after* a male becomes polygamous and ceases to attend the nest; so that the most elaborate nuptial adornments are on the whole consequences rather than antecedents of the males' abstention from incubation. Yet in the Quetzal *Pharomachrus mocinno*, one of the most beautiful birds of the western hemisphere, the male takes his full share in incubating and attending the young, as in the less ornate trogons. The long, graceful plumes of his train are badly frayed or even broken off short by constant flexure and abrasion on his innumerable passages in and out of the doorway of the rough hole in a decaying trunk; but at the following moult he grows them afresh.

While on the subject of the influence of colouration on incubation patterns, we might consider the colours of eggs. The usually white, unmarked eggs of pigeons and doves are of a type common enough among birds which nest in holes or build covered structures but rare in such frail, open nests as most pigeons build. These birds sit on the first egg much of the time before the second is laid, after which male and female together keep the usually two eggs almost constantly covered, thereby reducing the probability that their gleaming whiteness will attract hostile eyes. If an enemy approaches the nest, the parent, as I have observed from concealment, crouches motionless and does not flee so long as there is a chance of escaping detection. Although it is not impossible that the conspicuousness of the eggs brought about the pigeons' habit of keeping them continuously covered, it is more probable that the birds' close sitting is responsible for their remaining unpigmented; for with them cryptic colouration lacks the selective advantage it enjoys in eggs more frequently exposed.

With the Pauraque *Nyctidromus albigollis* of tropical America, I have repeatedly noticed that the eggs, although buffy and mottled, are more conspicuous against the browns of the ground litter on which they lie than is the plumage of the birds themselves. Since male and female together keep the eggs rather constantly covered, natural selection again has not produced that close resemblance to the substratum which might have resulted if they were exposed for longer periods. On the other hand, the anis and other cuckoos which only gradually work up to full constancy in incubation leave their chalky white eggs exposed for considerable periods. But the green leaves which anis and Squirrel Cuckoos *Piaya cayana* bring to their nests stain the eggs which lie upon them, and the scratches which soon disfigure the soft outer layer of anis' eggs allow the blue of the inner shell to show. Together the dark, irregular stains and scratches gradually reduce the conspicuousness of the originally white eggs.

*Influence of the environment.* When I began to study birds in the highlands of tropical America, I asked whether the more severe conditions there prevailing would not lead to incubation and brooding by the males, even in families of which the female alone sits on the nest in the warm lowlands. At high altitudes, low temperatures, chilling winds, cold rains, and frosts make it far more important to keep eggs and nestlings well covered; and male participation in these duties would seem to be highly advantageous. I found a number of nestlings which died apparently of cold and exposure. Many hummingbirds, and honeycreepers of the genus *Diglossa*, nested on the high mountains at a season when severe frosts were of almost nightly occurrence and penetrating winds sometimes blew by day. But I could find no instance of male incubation in hummingbirds, honeycreepers, wood warblers, wrens, thrushes, and other families in which the males fail to incubate in milder climates.

Although in spite of the cold the nests of the White-eared Humming birds *Hylocharis leucotis* which I watched in the high mountains of Guatemala were not attended by males, at least one member of the family which breeds at high altitudes has made the adjustment which the climate seems to demand. When Moore (1947) announced that in the highlands of Ecuador he had collected a male Gould's Violet-ear *Colibri coruscans* which had been sitting on eggs, ornithologists familiar with the habits of humming birds hesitated to conclude from this single observation that male incubation is customary even in this species. However, Schäfer (1954 c) found and photographed a male Gould's Violet-ear incubating eggs and feeding young in the mountains of Venezuela. In view of this confirmation of Moore's discovery, his observations on certain other Andean humming birds, whose males showed greater interest in the nest than one expects in this family, should stimulate further investigations. If a harsh environment is capable of radically altering the incubation pattern, one might expect this to occur



among the small birds of the high Andean páramos; and it is to be hoped that before long evidence will be accumulated on this point.

In the far north, severe conditions seem as little effective in inducing incubation by the male in passerine birds as on high tropical mountains. The male Snow Bunting *Plectrophenax nivalis* is as careless of incubation as most other male finches (Tinbergen 1939; Sutton & Parmelee 1954). Although Blair (1936) reported incubation by the male Lapland Longspur *Calcarius lapponicus* in arctic Norway, in arctic and subarctic America females alone were found on the eggs by Grinnell (1944), Wynne-Edwards (1952), and Sutton & Parmelee (1955). Similarly with the Greater Redpoll *Acanthis flammea*, Wynne-Edwards found only females incubating on Baffin Island.

In the Shetlands and other northern islands where food is relatively scarce, the Wren *Troglodytes troglodytes* is monogamous and the male takes a good share in feeding the nestlings, although under the milder conditions prevailing farther south polygyny is frequent in this species and the female often attends the young alone (Armstrong 1952, 1955). This climatically induced change in breeding behaviour might, if carried far enough, lead to incubation by the male; but except in the case of Gould's Humming bird, I am aware of no instance where such a departure from the system prevalent in the family has actually occurred, apparently in response to ecological conditions.

Our second example of a major change in an incubation pattern which we may with some confidence attribute to the environment is an instance of the loss rather than the acquisition of the habit of incubation by one of the sexes. In the penguins, rather equal participation by male and female appears to be general; but in the Emperor Penguin *Aptenodytes forsteri* the female goes off to the sea soon after laying her single egg on the Antarctic ice and leaves the male to take full charge of it through the cold and darkness of midwinter. This midwinter incubation brings the young out of the shell at such a time that the more favourable period of the year is available for caring for them through their five months of helpless dependency and they will be ready to go to sea while open water is close by. But during the coldest months, open water, where alone the penguins can find food, is so far distant from the breeding ground that change-overs on the egg, such as are practised by other penguins, could be effected, if at all, only by means of exhausting journeys over the sea ice, and consequently have been abandoned by this species. When the females at length return, it is to take charge of the newly hatched chicks, leaving the emaciated males free to march off to the water and recover from their long fast (Stonehouse 1953). In the Adélie Penguin *Pucheranphus adeliae* the male takes charge of the newly laid eggs while his mate goes off to fish in the sea, returning about two weeks later. Since he had been ashore several weeks before laying began, the

male's period of fasting may extend to 40 days (Sladen 1953). From such an arrangement, the Emperor Penguin's peculiar method of incubation might be derived simply by extending the male's initial session to cover the two months required for hatching the eggs.

We are able to cite more numerous examples of less radical modifications of the incubation pattern, not involving a change in the participation of the sexes, which seem to have been made in response to fairly constant features of the environment. The infrequent change-overs and consequent long sessions, often amounting to many days together, of Adélie Penguins and many albatrosses, shearwaters, and petrels, are in at least many instances caused by the wide separation of the breeding ground on dry land from the foraging area on the high sea. When the penguins' nests are miles inland, the walking journey is time-consuming. The peril that the smaller petrels run from the big gulls whenever they approach land by day, or even on moonlit nights, has also been an important factor in reducing the number of changes of duty on the nest and in making the meals of the nestlings infrequent but copious.

In numerous other instances the environment, living and lifeless, has made attendance at the nest more constant, even if it has not lengthened the separate sessions. That male and female may share incubation, yet by no means keep the eggs constantly covered, is clear to anyone who has studied toucans, puffbirds, barbets, ovenbirds, and even some of the antbirds. When the eggs are hidden in a hole or closed nest there is no pressing need for one partner to remain in attendance until its mate comes to relieve it; in mild weather the periodic cooling of the eggs is no more harmful when both parents are responsible for them than when a single parent incubates taking alternating sessions and recesses. But when the nest is in a crowded colony whose members covet the sticks or stones which compose it, it becomes imperative to keep it constantly guarded lest it be carried off by thieving neighbours in the absence of the proprietors. Since these conspicuous colonies are often frequented by predators alert to snatch up unattended eggs or chicks, and Herring Gulls *Larus argentatus* may even eat the eggs and young of neighbours of their own kind (Tinbergen 1953), there is an additional motive for maintaining constant guard. Thus in colonial gulls, terns, herons, and other species, each parent remains on duty until its mate returns to relieve it, with a fidelity conspicuously absent among many birds whose nests are not exposed to these perils.

The surprisingly long sessions of diminutive manakins, antbirds, and other species of the tropical forest may be of value in reducing the number of comings and goings, each of which may reveal to the watchful eyes of snakes and other nest-robbers the position of a nest in itself inconspicuous. Far from the tropics, bitter weather may make continuous incubation imperative lest the eggs freeze. Although some northern birds nest in winter or



early spring while snow still covers the ground, the male does not on this account take a share in incubation, but rather supplies the female with so much food that she can sit almost uninterruptedly, as happens with the Pine Siskin *Spinus pinus* (Weaver & West 1943) and the Red Crossbill *Loxia curvirostra* (Lawrence 1949). Since other species of the Carduelinae which breed in midsummer or even in the tropics incubate in much the same fashion, with the female sitting for hours together while her mate regurgitates food to her, it may be doubted whether this system is really an adaptation for nesting in cold weather. The generally northern distribution of this division of the Fringillidae makes it probable that its mode of incubation is a response to nesting at low temperatures and has persisted even in species which later came to breed in milder months or lower latitudes. None of the obviously tropical branches of the Fringillidae, nor indeed any other tropical passerine known to me, exhibits comparable behaviour.

Another northern bird which nests amidst snow and ice is the Canada Jay *Perisoreus canadensis*. Lawrence (1947) watched two birds, presumably male and female, sit simultaneously and almost continuously in the nest, now one and then the other on top of its partner, in snowy weather in Canada; but Warren (1899) found only the female incubating while snow lay deep in Michigan. Incubation by the male is exceptional in the Corvidae. The behaviour of Mrs. Lawrence's jays may have been a response to severe weather; but in view of Warren's conflicting report, it looks like an abnormality rather than the custom of the species; and the fact that an egg was broken suggests that such double incubation is not a favourable arrangement. We must await further observations on this bird of the far north before drawing conclusions.

*Incubation in relation to song and territory.* Of all the great divisions of birds, the Passeres is the group in which song reaches its highest development, and incubation by the male, who chiefly sings, is most conspicuously absent, although it does indeed occur in scattered families and species. We know that song is of importance in relation to the advertisement and defence of territory, and in this suborder we have the most numerous and careful studies of territorial behaviour. It is tempting to look upon the waning of incubation in the male as an adaptation which permits him to devote more attention to song and territorial defence. There is a rather widespread view that singing and non-incubation are causally related, and at one time I inclined to this opinion. But more mature reflection makes it appear untenable. The Tyranni are generally held to be more primitive than the Passeres and few of its members rank as songsters. Nevertheless, many of the American flycatchers and a few of the cotingas sing freely and even sweetly in the morning twilight, but through the rest of the day their songs are rarely heard except at moments of great excitement. A few renew their singing

in the evening twilight. In these families, spells of incubation in broad daylight would certainly not interfere with the males' vocal exercises.

Even in the Passeres, many good and persistent songsters incubate, and many which are practically songless fail to do so. Among the latter are crows, jays, and many tanagers, and honeycreepers. Some of the males that sing well and loudly continue to do so while taking their turns on the eggs. This has been frequently recorded for vireos of a number of species; and I have known a Pepper-Shrike *Cyclarhis gujanensis* to pour forth his song at the top of his strong voice while sitting in his open nest, continuing this for two hours. In the Rose-breasted Grosbeak *Pheucticus ludovicianus* (Ivor 1944) and the Black-headed Grosbeak (*P. melanocephalus*) males take a large share in incubating and frequently sing on the nest, in the latter species so loudly that Weston (1947) used the song, audible at several hundred feet, for locating nests. The boldly coloured and tuneful male grosbeaks are about the last birds one would expect to find incubating in a family in which even the most soberly attired male sparrows rarely sit on the eggs. Even female birds of many kinds often sing rather loudly while incubating. Laskey (1944) reported that female Cardinals *Richmondia cardinalis* sing loudly in the nest; and among those which I have heard are the Yellow-tailed Oriole *Icterus mesomelas*, Melodious Blackbird *Dives dives*, Blue-black Grosbeak *Cyanocompsa cyanoides*, Orange-billed Sparrow *Arremon aurantirostris*, Highland Wood Wren *Henicorhina leucophrys*, and others.

In many habitats silence at the nest does not appear to be essential to safety. Not only do sitting birds sometimes sing loudly, or shout out in answer to their mates, or murmur special low nest-songs; the nestlings themselves are frequently noisy when taking food and even while awaiting their meals. Many Tyranni and non-passerines practise the sweet but simple songs or calls of the adults before leaving the nest. Even when approaching the nest with the utmost hesitancy and circumspection, the parents are often exceedingly noisy, presenting a mixture of excessive caution and apparently foolhardy recklessness, which is understandable only if their behaviour has reference to predators which hunt with their eyes or noses rather than with their ears. The noisiness of these otherwise so discreet birds may not be prejudicial if their chief enemies are snakes, which have undeveloped hearing. Among the birds about me as I write, two members of the Sylviidae, the Long-billed Gnatwren *Ramphocaenus rufiventris* and the White-browed Gnatcatcher *Poliophtila plumbea* are fine songsters and the males regularly incubate; while most of the male tanagers and flycatchers neither have a song worthy of the name nor share in incubation.

As to defence of territory, this can be satisfactorily attended to (with or without song) even when both sexes incubate, as in the Wren-tits *Chamaea fasciata* studied in California by Erickson (1938), the Graceful Warbler *Prinia gracilis* watched in Egypt by Simmons (1954), the Black-headed



Grosbeak (Weston 1947), barbets, woodpeckers, kingfishers, and many other birds.

*Incubation and the sex-ratio.* Monogamy, with the equal participation of the sexes in all reproductive activities after laying, is ideally suited to a species in which the sexes are present in about equal numbers. When there is an excess of males or females, either some must refrain wholly from reproduction, or the sexes must take unequal parts in nesting. In the Black-eared Bush-tit *Psaltiriparus melanotis* supernumerary males aided mated pairs in caring for the young and sometimes even in building, but I found no evidence of actual polyandry (Skutch 1935). The attendance of extra males or females at the nests of mated pairs has been recorded as an exceptional occurrence in a few species; but usually a strongly unbalanced sex-ratio is associated with polygamy, which normally gives a larger proportion of the population some share in perpetuating the kind. When males are more numerous than females, as in the tinamou *Crypturus variegatus* (Beebe 1925), the jacana *Hydrophasianus chirurgus* (Hoffmann 1949), and apparently also the painted snipe *Rostratula* (Mayr 1939), each female may lay eggs in a number of nests, leaving to a male the whole responsibility of hatching them and caring for the young. By putting the males to work in this fashion, a female may produce more eggs and young than if she laid only as many eggs as she and a single male could together hatch and attend. But in the phalaropes, where also the male takes over the domestic duties, there appears not always to be a preponderance of this sex (Mayr 1939). Likewise in the tinamou *Nothoprocta ornata*, of which the male alone incubates, Pearson & Pearson (1955) saw no indication of either polygyny or polyandry; while in the tinamou *Nothocercus bonapartei* Schäfer (1954 b) found the two sexes in about equal numbers, although one male incubated the eggs which three females laid in a single nest. Such an arrangement is hardly advantageous for the species and doubtfully so for the male who shoulders all the responsibility of reproduction; and it is difficult to explain except as an inheritance from an ancestral stock in which females predominated. Likewise the male Rhea *Rhea americana* takes charge of the eggs laid in a common heap by several females, which suggests an excess of the latter sex.

Usually, however, the presence of several females to each male leads the latter to desist from all participation in nesting and confine his attention to courtship alone. Unfortunately, we know very little about the sex-ratio in pheasants, birds of paradise, manakins, humming birds, and other groups with well developed arena displays or courtship assemblies along with the male's complete withdrawal from nesting activities. In some of the colonial, polygynous passerines, including species of Icteridae and Ploceidae, the relative paucity of males is well attested (Moreau & Moreau 1938; Skutch 1954). It is probable that the colonial oropendolas, grackles, caciques, and other Icteridae sprang from monogamous ancestors in which the males

had already lost the habit of incubation, and that the incidence of a strongly unbalanced sex-ratio, with accompanying polygyny, led the males to desist also from feeding the young, as they do in monogamous members of this family.

When there is a strongly unbalanced sex-ratio, the failure of the less numerous sex to incubate has an advantage which is not obvious in most species in which a single parent sits, for it permits breeding by many individuals which would otherwise remain childless. The aberrant behaviour of the males of some normally monogamous species suggests how polygyny might arise. A male Starling *Sturnus vulgaris* shared incubation at two nests but later fed the young at only one (Schüz 1943). Male Song Sparrows *Melospiza melodia* and Robins *Erithacus rubecula* do not incubate; but a bigamous male of the former attended the young of both his wives (Nice 1937); and a bigamous male of the latter might have done so if he had not disappeared before the brood of his second mate hatched (Lack 1953). In this connection, Brewer's Blackbird *Euphagus cyanocephalus* is of special interest because of the family in which it belongs. In California, Williams (1952) found that the sex-ratio of this icterid varied from year to year; and the greater the excess of females, the more instances of polygyny he observed. Unlike the typical polygynous or non-pairing Icteridae, the male blackbirds fed the young in the nests of several mates at the same time. In cases like this, a sustained increase in the number of females might lead the male so to divide his time between them that he would in the end quite fail to attend eggs and young, as in those passerines which exhibit the most highly evolved polygyny.

The evolution of polyandry from a stock in which the female alone attends the nest might be difficult; but if we assume equal participation by the sexes or exclusive charge by the male as the primitive condition, it is easy to imagine how a situation such as we find in the tinamous and jacanas arose. In the first case, we might suppose that the female on her absences from incubation is courted by an unoccupied male and, deserting her nest, goes off with him to start another brood, while her first mate continues to care for her first set of eggs and the young he hatches from them. With an increasing number of males to distract her from domestic obligations, this desertion of nests and mates would happen more frequently, until the female laid sets of eggs only to abandon them to the care of her latest associate. If, however, we assume full charge of the nest by the male as the primitive arrangement, we need only to suppose that as males became relatively more numerous the females laid more often in order to provide work for all of them. These probable routes of the evolution of both polygyny and polyandry require some individual adjustments or original behaviour by the birds themselves; or at least the process would be accelerated by such spontaneous responses to the novel situations which a growing disparity in



the numbers of the sexes would create. But if we adopt the concept of "organic selection" (Huxley 1942; Skutch 1955), which postulates the gradual replacement of individually acquired behaviour by supporting mutations, we need not have recourse to Lamarckism.

*Conclusions.* The rarity of incubation by the female alone in the more primitive groups of birds makes it highly improbable that this was the original condition in the avian stock. A survey of incubation habits in the whole avian class leads to the conclusion that incubation by the male, or by both sexes, was the ancestral method. If we assume that male incubation was the original mode, we must further suppose that in the evolution of such families as jacanas and phalaropes, in which the male is largely or wholly responsible for the eggs, the female acquired and then lost the habit of incubation; for these families belong to an order in which incubation by both sexes is the prevailing method. On the whole, the probable view is that in ancestral birds both sexes shared incubation, and that from this original and still predominant condition some stocks diverged in the direction of greater participation by the male, others in the direction of greater participation by the female.

Where there is great disparity in the numbers of the sexes, the advantage of shifting all or at least most of the labours of the nest to the more abundant sex is fairly obvious, because it permits fuller participation of the whole adult population in reproduction. In the Emperor Penguin, abstention from incubation by the female is an adaptation to breeding by an unusually large bird with a very long period of helpless dependency in an extraordinarily rigorous environment. But with this outstanding exception, and that of Gould's Hummingbird which nests at high altitudes in the Andes, the incubation pattern in its major feature, the participation of the sexes, is surprisingly unresponsive to ecological conditions, although many less radical changes may be traced to such influences. In many situations where incubation by both sexes would seem to be highly advantageous, as among birds which nest on high tropical mountains or amid snow and ice in the north, a single sex takes charge of the eggs if this is the family tradition.

On the other hand, in most monogamous birds in which only the female incubates, it is hardly possible to point to any advantage which the species has derived from the male's aloofness from the eggs. When I reflect upon a great variety of birds that I have studied and found only the female incubating, I can think of exceedingly few in which the male's sitting would be detrimental. In areas where snakes with poor hearing or nocturnal mammals are the chief predators on eggs and young, he might even sing while incubating without jeopardizing the eggs. Possibly in some of the biggest and most brilliant tanagers, as the Scarlet-rumped Black Tanager *Ramphocelus passerinii*, the Scarlet Tanager *Piranga olivacea*, or the bright red Summer Tanager *P. aestiva*, the male would imperil the nest by his eye-

catching attire; yet after hatching, these males often visit it with food, and in movement they are even more conspicuous than when quietly sitting. And in many other tanagers the female, who alone incubates, is hardly less colourful than the brightest males. No male bird whose nest I have studied in the tropics has seemed to be so burdened with the maintenance of territory that he could not well have spared four or five hours a day for incubation; and indeed the incubating females were in some cases as much concerned with territorial defence as their idle mates. In sum, I believe that neither the safety of the nest nor the integrity of the territory would be diminished if the males of the majority of passerine species with which I am familiar took to incubation.

On the other hand, when I recall how many manakins, cotingas, American flycatchers, icterids, and other birds of tropical America raise without the least male assistance broods of the same size as most of their neighbours in which pairs are regularly formed and the males help at the nest, I am led to believe that few passerine species, at least in the lowlands, would be adversely affected if the males, which now feed the nestlings but do not incubate or brood, were to relinquish feeding as well. In the more favourable tropical environments, a single parent seems in many instances quite capable of adequately reproducing the species, and the assistance of the male is not strictly necessary, except for fecundation. Hence incubation or non-incubation by the second parent seems in many instances to be non-adaptive. When as a result of mutations a male bird loses the incubation habit, the mutant persists simply because this new departure is not injurious, not because it adds to the efficiency of reproduction. In migratory species breeding at high latitudes, the urgency of rearing in a short season many offspring to replace high annual losses might place a premium upon the specialization of functions which results when the female alone incubates and the male is free to devote all his attention to the establishment and maintenance of territory; but in these birds with their larger broods the male's aid in feeding the young is imperative. But tropical birds, like tropical people, manage to survive without being so efficient as the inhabitants of more rigorous northern lands. It is probable that, in the Passeriformes at least, non-incubation by the male began in the tropical groups, as a mutation neither useful nor harmful, and later happened to give some slight advantage—if it is an advantage—to species which undertook a long and perilous annual journey to breed at high latitudes.

As we have seen, incubation by a single parent is advantageous to species with a strongly unbalanced sex-ratio if it is combined with habits which permit a fuller participation in reproduction by the more numerous sex, as in polyandrous tinamous and jacanas and polygynous Icteridae and Ploceidae. But an unbalanced sex-ratio is itself a misfortune which can only weaken the monogamous species in which it arises by diminishing its reproductive



capacity. Such a disparity in the numbers of the sexes should give an advantage to any subsequent mutation that threw the weight of family cares on the more abundant sex. Thus non-incubation by one of the sexes seems in many instances to be either useless, or if advantageous, it is so merely because it serves to compensate for other genetic accidents which upset the sex-ratio.

It is instructive to compare incubation habits with the use of distraction displays. On the whole, the latter are given only by birds whose nests are so situated that they are likely to be of some use in luring away predators (Armstrong 1954; Skutch 1954). But the male's participation in incubation varies in a largely capricious fashion, so that usually we can point to no good reason for his behaviour in this respect. The reason why distraction displays are usually adaptive and incubation patterns, at least in the matter of the participation of the sexes, appear rarely to be so, seems obvious. It is not beyond the mental powers of birds to learn by experience that they can entice an enemy from the nest by a slow and conspicuous retreat in front of the animal; but we can hardly expect them to understand the relation between temperature and the development of an embryo unseen within the shell. Hence birds' intelligence has had some influence upon the evolution of distraction displays by the method of organic selection; whereas, since in many environments the participation of both sexes in incubation is not essential, incubation patterns have been free to vary more or less at random, without the initiative of mind nor close control by natural selection.

Still, as ornithologists we have no reason to regret the accidental loss of the incubation habit by so many male birds, because it has added greatly to the diversity of bird behaviour and consequently to the fascination of our studies. Whether, as Selous thought, there is greater charm in watching the female build and incubate while her mate sings close by, or in watching the two take equal shares in all the activities of the nest, is a question of taste which admits no argument. We should be grateful that both arrangements are available for our contemplation. Moreover, the release of the male from incubation, and finally from all association with the nest, opened the way for the evolution, largely under the influence of sexual selection, of marvellous courtship habits and wonderful adornments, which in some instances have become so lavish that the bird who wears them is physically incapacitated for attending eggs or young.

#### SUMMARY.

A classification of the known methods of incubation of the birds of the world, on the basis of the division of labour between the sexes and the apportionment of time on the eggs, shows that practically every feasible pattern has been adopted by one species or another.

A review of the evidence suggests that incubation by both sexes was the primitive method among birds.

Among passerines, there appears to be little correlation between incubation by the male and his possession of a brood-patch. Some males which regularly incubate lack it, whereas others which fail to incubate develop it.

There is also poor correlation between the form of the nest (whether open or covered), the coloration of the two sexes, and their participation in incubation.

Participation of the sexes is not generally correlated with the environment. The non-incubation by the female Emperor Penguin and the sharing of incubation by the male Gould's Hummingbird, seem to be instances of response to rigorous climates.

Except possibly in migratory birds whose breeding season is short, incubation by the male seems compatible with efficient territorial defence. Some males and even females sing loudly from the nest, apparently without betraying it to predators.

When the sex-ratio is strongly unbalanced, the failure of the less numerous sex to incubate makes it possible for a larger proportion of the adults to reproduce. But in a number of species in which polygamy or polyandry occurs, the sex-ratio is not known to be unbalanced.

Many modifications in the incubation pattern, especially those involving the participation of the sexes, appear to be non-adaptive, and to persist because they do not decrease reproductive efficiency.

#### REFERENCES.

- ADDICOTT, A. B. 1938. Behavior of the Bush-tit in the breeding season. *Condor* 40 : 49-63.
- ALLEN, R. W. & NICE, M. M. 1952. A study of the breeding biology of the Purple Martin (*Progne subis*). *Am. Midl. Nat.* 47 : 606-665.
- AMADON, D. & ECKELBERRY, D. R. 1955. Observations on Mexican Birds. *Condor* 57 : 65-80.
- ARMSTRONG, E. A. 1952. The behaviour and breeding biology of the Shetland Wren. *Ibis* 94 : 220-242.
- ARMSTRONG, E. A. 1954. The ecology of distraction display. *Brit. J. Anim. Behav.* 2 : 121-135.
- ARMSTRONG, E. A. 1955. The Wren. London.
- BAILEY, R. E. 1952. The incubation patch of passerine birds. *Condor* 54 : 121-136.
- BEEBE, W. 1925. The Variegated Tinamou *Crypturus variegatus*. *Zoologica* 6 : 195-227.
- BENT, A. C. 1940. Life histories of North American cuckoos, goat-suckers, hummingbirds, and their allies. U. S. Nat. Mus., Bull. 176.
- BENT, A. C. 1950. Life histories of North American wagtails, shrikes, vireos, and their allies. U. S. Nat. Mus., Bull. 197.
- BLAIR, H. M. S. 1936. On the birds of east Finmark. *Ibis* (13) 6 : 280-308, 429-459, 651-674.
- CONDER, P. J. 1948. The breeding biology and behaviour of the Continental Goldfinch *Carduelis carduelis carduelis*. *Ibis* 90 : 493-525.
- DAVIS, D. E. 1940. Social nesting habits of the Smooth-billed Ani. *Auk* 57 : 179-218.
- DAVIS, D. E. 1945. The occurrence of the incubation patch in some Brazilian birds. *Wilson Bull.* 57 : 188-190.
- DELACOUR, J. 1951-52. The Pheasants of the World. 2 Vols. London & New York.
- ERICKSON, M. M. 1938. Territory, annual cycle and numbers in a population of Wren-tits (*Chamaea fasciata*). *Univ. Calif. Publ. Zool.* 42 (5) : 247-334.
- FORBUSH, E. H. 1929. Birds of Massachusetts and other New England States 3. Boston.
- FRIEDMANN, H. 1929. The Cowbirds. Springfield & Baltimore.
- FRIEDMANN, H. 1932. The parasitic habit in the ducks, a theoretical consideration. *Proc. U.S. Nat. Mus.* 80 (18) : 1-7.
- GOODWIN, D. 1948. Incubation habits of the Golden Pheasant. *Ibis* 90 : 280-284.
- GOODWIN, D. 1953. Observations on voice and behaviour of the Red-legged Partridge *Alectoris rufa*. *Ibis* 95 : 581-614.
- GRINNELL, L. I. 1944. Notes on breeding Lapland Longspurs at Churchill, Manitoba. *Auk* 61 : 554-560.
- GULLION, G. W. 1954. The reproductive cycle of American Coots in California. *Auk* 71 : 366-412.
- HOFFMANN, A. 1949. Ueber die Brutpflege des polyandrischen Wasserfasans *Hydrophasianus chirurgus* (Scop.). *Zool. Jb.* 78 : 367-403.



- HUXLEY, J. S. 1938. Darwin's theory of sexual selection and the data subsumed by it in the light of recent research. *Am. Nat.* 72 : 416-433.
- HUXLEY, J. S. 1942. Evolution, the modern Synthesis. London.
- IVOR, H. R. 1944. Bird study and semi-captive birds: the Rose-breasted Grosbeak. *Wilson Bull.* 56 : 91-104.
- KENDEIGH, S. C. 1952. Parental care and its evolution in birds. *Illinois Biol. Mon.* 22.
- LACK, D. 1953. The Life of the Robin. Rev. ed. London.
- LASKEY, A. R. 1944. A study of the Cardinal in Tennessee. *Wilson Bull.* 56 : 27-44.
- LAWRENCE, L. de K. 1947. Five days with a pair of nesting Canada Jays. *Canadian Field-Nat.* 61 : 1-11.
- LAWRENCE, L. de K. 1949. The Red Crossbill at Pimisi Bay, Ontario. *Canadian Field-Nat.* 63 : 147-160.
- LAWRENCE, L. de K. 1953. Nesting life and behaviour of the Red-eyed Vireo. *Canadian Field-Nat.* 67 : 47-77.
- LEWIS, H. F. 1921. A nesting of the Philadelphia Vireo. *Auk* 38 : 26-44, 185-202.
- LOCKLEY, R. M. 1942. Shearwaters. London.
- LORENZ, K. Z. 1952. King Solomon's Ring. London.
- LOW, J. B. 1945. Ecology and management of the Redhead, *Nyroca americana*, in Iowa. *Ecol. Mon.* 15 : 35-69.
- MANNING, T. H. 1942. Blue and Lesser Snow Geese on Southampton and Baffin Islands. *Auk* 59 : 158-175.
- MAYR, E. 1939. The sex ratio in wild birds. *Am. Nat.* 73 : 156-179.
- MEWALDT, L. R. 1952. The incubation patch of the Clark Nutcracker. *Condor* 54 : 361.
- MOORE, R. T. 1947. Habits of male hummingbirds near their nests. *Wilson Bull.* 59 : 21-25.
- MOREAU, R. E. 1936. The breeding biology of certain East African hornbills. (Bucerotidae). *J. E. Africa Uganda Nat. Hist. Soc.* 13 : 1-28.
- MOREAU, R. E. 1937. The comparative breeding biology of the African hornbills (Bucerotidae). *Proc. Zool. Soc. London*, 1937 (A) : 331-346.
- MOREAU, R. E. 1949. The African Mountain Wagtail *Motacilla clara* at the nest. *Ornithologie als biologische Wissenschaft* : 183-191.
- MOREAU, R. E. & MOREAU, W. M. 1938. The comparative breeding ecology of two species of *Euplectes* (Bishop Birds) in Usambara. *J. Animal Ecol.* 7 : 314-327.
- MOREAU, R. E. & MOREAU, W. M. 1940. Hornbill studies. *Ibis* (14) 4 : 639-656.
- MOREAU, R. E. & MOREAU, W. M. 1941. Breeding biology of the Silvery-cheeked Hornbill. *Auk* 58 : 13-27.
- NICE, M. M. 1929. The fortunes of a pair of Bell Vireos. *Condor* 31 : 13-18.
- NICE, M. M. 1937. Studies in the life history of the Song Sparrow I. *Trans. Linn. Soc. N. Y.* 4 : i-vi, 1-247.
- PARKES, K. C. 1953. The incubation patch of males of the suborder Tyranni. *Condor* 55 : 218-219.
- PEARSON, A. K. & PEARSON, O. P. 1955. Natural history and breeding behaviour of the tinamou, *Nothoprocta ornata*. *Auk* 72 : 113-127.
- PUTNAM, L. S. 1949. The life history of the Cedar Waxwing. *Wilson Bull.* 61 : 141-182.
- RAND, A. L. 1938. Results of the Archbold Expeditions. No. 22. On the breeding habits of some birds of paradise in the wild. *Am. Mus. Novit.* 993 : 1-8.
- RICHDALE, L. E. 1943. The Kuaka or Diving Petrel, *Pelecanoides urinatrix* (Gmelin). *Emu* 43 : 24-48, 97-107.
- RUST, H. J. 1920. The home life of the Western Warbling Vireo. *Condor* 22 : 85-94.
- SCHÄFER, E. 1953. Estudio bio-ecológico comparativo sobre algunas Cracidae del norte y centro de Venezuela. *Bol. Soc. Venezolana Cien. Nat.* 15 : 30-63.
- SCHÄFER, E. 1954a. Der Vogel mit dem Stein auf dem Kopf. *Kosmos* 50 : 9-13, 118-124.
- SCHÄFER, E. 1954b. Zur Biologie des Steisshuhnes *Nothocercus bonapartei*. *J. Orn.* 95 : 219-232.
- SCHÄFER, E. 1954c. Sobre la biología de *Colibri coruscans*. *Bol. Soc. Venezolana Cien. Nat.* 15 : 153-162.
- SCHÜZ, E. 1943. Brutbiologische Beobachtungen an Staren 1943 in der Vogelwarte Rossitten. *J. Orn.* 91 : 388-405.
- SIBLEY, C. G. 1946. Breeding habits of megapodes on Simbo, Central Solomon Islands. *Condor* 48 : 92-93.

- SIMMONS, K. E. L. 1954. The behaviour and general biology of the Graceful Warbler *Prinia gracilis*. *Ibis* 96 : 262-292.
- SKEAD, C. J. 1954. A study of the Cape Wagtail *Motacilla capensis*. *Ibis* 96 : 91-103.
- SKUTCH, A. F. 1935. Helpers at the nest. *Auk* 52 : 257-273.
- SKUTCH, A. F. 1953. The White-throated Magpie-Jay. *Wilson Bull.* 65 : 68-74.
- SKUTCH, A. F. 1954. Life histories of Central American Birds. *Pacific Coast Avifauna* 31 : 1-448.
- SKUTCH, A. F. 1954-55. The parental stratagems of birds. *Ibis* 96 : 544-564, 97 : 118-142.
- SLADEN, W. J. L. 1953. The Adelie Penguin. *Nature* 171 : 952.
- SMITH, S. 1950. The Yellow Wagtail. London.
- SPINGARN, E. D. W. 1934. Some observations on the Semipalmated Plover (*Charadrius semipalmatus*) at St. Mary's Islands, Province of Quebec, Canada. *Auk* 51 : 27-36.
- STODDARD, H. L. 1946. The Bobwhite Quail. New York.
- STONEHOUSE, B. 1953. The Emperor Penguin *Aptenodytes forsteri* Gray. I. Breeding behaviour and development. *Falkland Islands Dep. Surv. Sci. Rep.* 6 : 1-33.
- SUTTON, G. M. & PARMELEE, D. F. 1954. Nesting of the Snow Bunting on Baffin Island. *Wilson Bull.* 66 : 159-179.
- SUTTON, G. M. & PARMELEE, D. F. 1955. Summer activities of the Lapland Longspur on Baffin Island. *Wilson Bull.* 67 : 110-127.
- TINBERGEN, N. 1939. The behaviour of the Snow Bunting in spring. *Trans. Linn. Soc. N. Y.* 5 : 1-94.
- TINBERGEN, N. 1953. The Herring Gull's World. London.
- VAN FLEET, C. C. 1919. A short paper on the Hutton Vireo. *Condor* 21 : 162-165.
- WALLACE, A. R. 1871. Contributions to the Theory of Natural Selection. 2 ed. London & New York.
- WALLACE, A. R. 1872. The Malay Archipelago. 4 ed. London.
- WARREN, O. B. 1899. A chapter in the life of the Canada Jay. *Auk* 16 : 12-19.
- WEAVER, R. L. & WEST, F. H. 1943. Notes on the breeding of the Pine Siskin. *Auk* 60 : 492-504.
- WESTON, H. G., Jr. 1947. Breeding behavior of the Black-headed Grosbeak. *Condor* 49 : 54-73.
- WILLIAMS, L. 1952. Breeding behavior of the Brewer Blackbird. *Condor* 54 : 3-47.
- WITHERBY, H. F. *et al* 1938. The Handbook of British Birds. London.
- WYNNE-EDWARDS, V. C. 1952. Zoology of the Baird Expedition (1950). I. The birds observed in central and south-east Baffin Island. *Auk* 69 : 353-391.