PART 7. NOVEMBER, 1912.

THE BRITISH WARBLERS

A HISTORY WITH PROBLEMS OF THEIR LIVES

BY

H. ELIOT HOWARD, F.Z.S., M.B.O.U.

ILLUSTRATED BY HENRIK GRÖNVOLD

London
R. H. PORTER
7, PRINCES STREET, CAVENDISH SQUARE, W.

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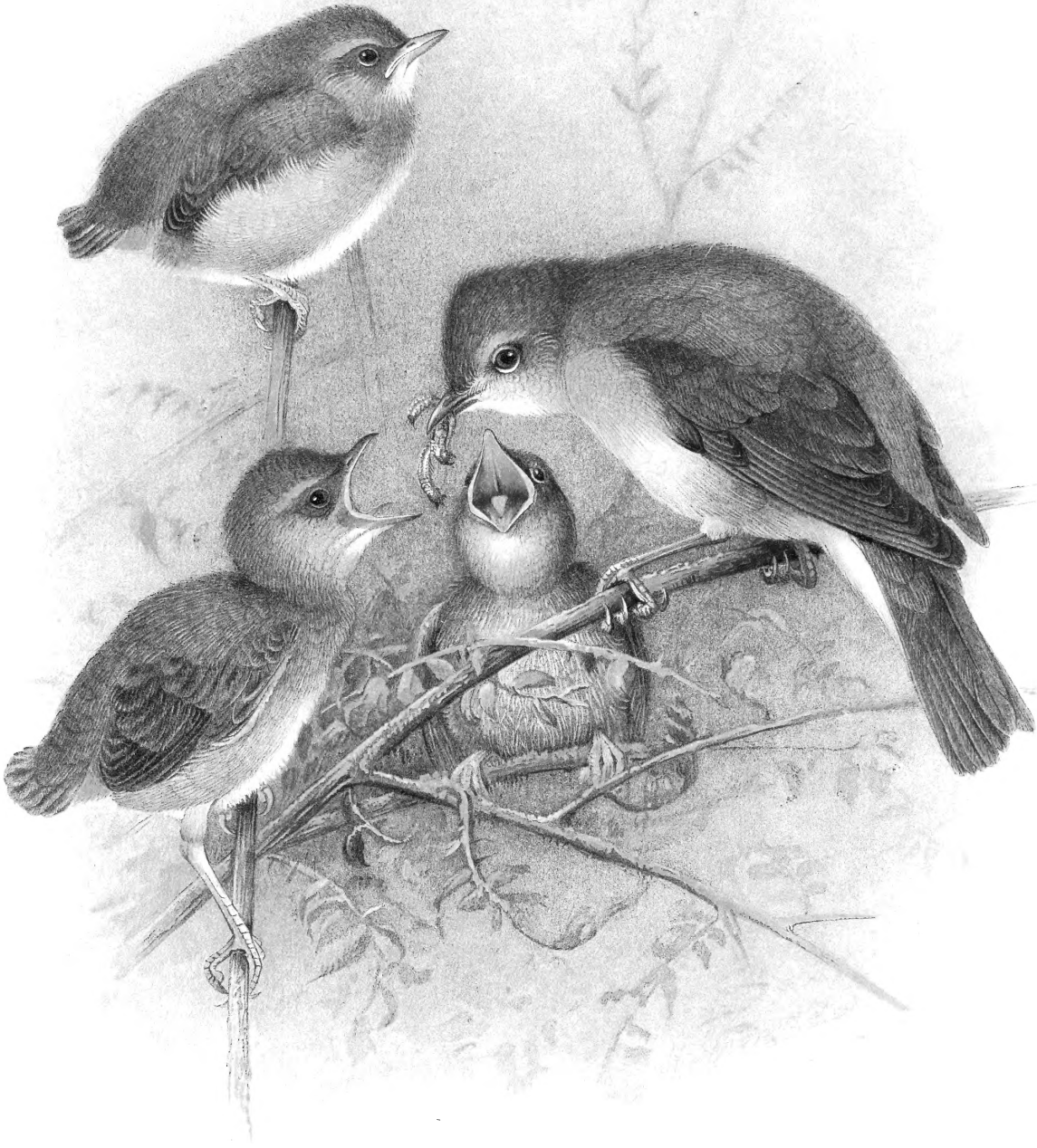

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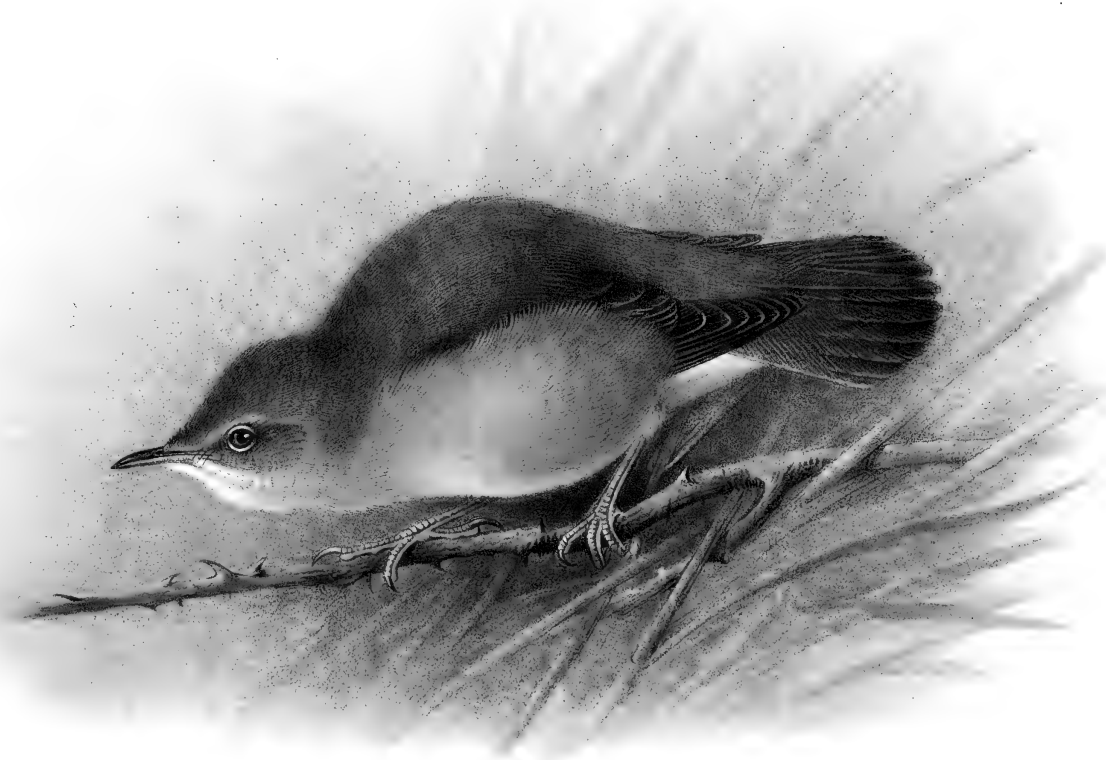
Showing approximately the arrival of the Marsh and Reed Warbler.



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MARSH WARBLER.

Calamoherpe palustris, *Gould, Birds of Great Britain,* vol. ii, 2 pp., pl. 74 (coloured figures of adults), 1872.

Acrocephalus palustris, *Yarrell, British Birds,* 4th Ed., vol. i, p. 373 (edited by Newton), 1873, and vol. iii, p. viii (edited by Saunders), 1884; *Dresser, Birds of Europe,* vol. ii, pp. 573-577, pl. 87, fig. 2 (coloured figure of adult), 1876; *Seebohm, British Birds,* vol. i, pp. 375-379, pl. 10, fig. 15 (egg), 1883; *Lilford, Coloured Figures,* vol. iii, p. 38, pl. 19 (coloured figure of adult), 1886; *Saunders, Manual of British Birds,* 2nd Ed., pp. 81-82 (woodcut), 1898.

Croatian, *Trstenjara Malakavka;* Danish, *Sumpsanger;* Dutch, *Bosch-riet-zanger;* French, *Rousserolle verderolle;* German, *Sumpf-Rohrsänger;* Italian, *Cannajola verdognola;* Hungarian, *Füzi nádarigó;* Russian, *Bolotnaja, Malinofka;* Spanish, *Canamera, Pinzoleta.*

DESCRIPTION OF THE PLUMAGE.

Adult Male in Spring.—The upper parts are of a uniform brownish tinge inclining more or less towards olive brown, the colour being rather darker on the crown, but more intense and slightly lighter on the rump and upper tail-coverts. The tail and flight feathers are brown narrowly edged with the same colour as the upper parts, the outer web of the primaries being tipped with greyish white, the outermost primary narrowly edged with light buff, and the innermost secondaries with the rest of the wing-coverts broadly margined with the same colour as the upper parts. There is a distinct buffish

white superciliary stripe, the lores are smoky grey, and the sides of the head olive brown. The under parts, including the under tail-coverts, are whitish washed with light buff—inclining to light olive buff in some specimens—on the upper breast and flanks and pale buff on the under tail-coverts. The under parts of the tail and wings are greyish brown, the shafts of the feathers being white; under wing-coverts and axillaries whitish buff. The upper mandible is dark lavender brown, lower fleshy buff darker towards the tip, and the flanges orange; mouth orange yellow; iris brown, the smaller feathers on the eyelid being buffish white. The feet are buffish flesh colour and the soles light olive yellow.

The sexes are alike in plumage.

After the autumn moult the colouring is richer.

Nestling.—The upper parts are brownish buff and the wings slaty brown, the larger feathers being margined with the same colour as the back. The under parts generally are yellowish buff, lighter on the abdomen but deeper on the flanks and under tail-coverts. The bill is pale pinkish brown and the gape yellow, this latter colour extending in a paler shade along the edges of both mandibles to the tip. Feet are pale pinkish brown; toes pale yellowish; hind part of feet yellow, brightest at the joint; under part of toes and claws yellow, upper part pale pinkish brown. The top of the mouth is dull orange, whilst the lower part is dull pinkish orange, the tongue being also orange with two narrow oval black spots at the base.

GEOGRAPHICAL DISTRIBUTION.

Though the bird is recorded as breeding in Kent, Surrey, Sussex, Buckingham, Hampshire and Cambridgeshire, and possibly Norfolk, the majority of the individuals seem to pass farther west for breeding purposes—that is to say to the counties of Oxford, Wilts, Somerset, Gloucester, and Worcester. And not only is it more plentiful in many

districts than is sometimes imagined to be the case, but, according to my experience, is gradually extending its range in a northerly direction. It is now eleven years since the bird first came under my notice on the northern boundary of the county of Worcester. A solitary individual then appeared in June, but after remaining a few days vanished. For some years following there was no further sign of the species, but it has now reappeared and, I hope, finally established itself in the district. There are places in both Worcestershire and Gloucestershire where it can by no means be described as uncommon, since it is an annual visitor in numbers which seem to be increasing. The Severn Valley appears to be especially favoured, but in saying this we must bear in mind how limited our knowledge of its distribution may really be, and how rare the bird was supposed to be until efforts were made to discover it. Many districts in which it has already been found nesting are eminently suited to its habits, and it is difficult to believe that in such places it is a casual visitor only. But just because it is an easy matter to assume that it has been overlooked, we must in the future scrutinise all the facts relating to its distribution the more closely, for otherwise we should be neglecting the bird with the most striking and highly developed vocal powers of all our birds. The gradual extension of its breeding range has a meaning in relation to the struggle for existence which we can scarcely afford to ignore. On migration it has been recorded from St. Kilda and Fair Isle. Concerning its distribution in the **Iberian Peninsula** little appears to be known beyond the fact that it is said to have bred towards the south, though the evidence is far from satisfactory. In **France** it is generally distributed, except in the western provinces. In all suitable localities in **Belgium**, the **Netherlands** and **Germany** it is common, but in **Denmark** scarce: it has occurred near Gothenburg. To the northern provinces of **Italy**, especially Piedmont, it is a common summer visitor, and though less common than the Reed Warbler in **Switzerland**, it is nevertheless generally distributed in all suitable localities, such as the

valleys of the Reuse, Simmat, and Thur, and in the neighbourhood of Zurich, Brunnen, and Schwytz. In **Austria** the bird is supposed not to be as numerous as in the adjoining countries. In **Hungary** it is generally distributed, and in parts of **Bulgaria** and **Turkey** abundant, but absent from **Greece** and not known to breed in the Mediterranean Isles. Throughout central and southern **Russia**, in **Poland**, and in the Baltic provinces, where we reach its northern breeding limit in Esthonia, it is generally distributed. We find it also in the provinces of Orenburg, Astrakhan, the vicinity of the R. Ural, the Caucasus and Trans-Caucasia, and specimens have been obtained in Persia in May, probably on the way to south-east Russia. It winters in **Africa** as far south as Natal and Pondoland.

LIFE-HISTORY.

Although this bird is so closely allied to the Reed Warbler that even an expert finds it difficult to identify the dried skins, yet the behaviour of the two species betrays no such remarkable likeness. It is true that we can recognise many points of similarity, but there are certain features which are strangely different and sufficiently distinct to prevent any confusion in distinguishing the living birds. The treatment of the life-history of the Marsh Warbler therefore demands that a series of comparisons shall be made with the corresponding behaviour in the life of the Reed Warbler, and in order to do this more completely it will be necessary to review some of the points of similarity and difference in the emotional behaviour of other members of this genus, and make some allusion to the biological questions arising therefrom.

If we study the life of any one species and keep a careful record of its actions day by day during the period of reproduction, we find that the greater part of its time is passed in the performance of certain actions, the purpose of which

is manifest, since they are either essential to its welfare or necessary for the attainment of reproduction. Every bird must search for and find sufficient food; again, every bird must be in possession of a suitable territory, and most birds must build a nest if incubation is to be carried out successfully, and any individual that came into the world imperfectly endowed with just those qualities requisite for a proper carrying out of the routine of activities, would either succumb or fail in the attempt at reproduction. The life of a bird is not, however, wholly spent in searching for food or in making preparations for its progeny; each species, in addition, behaves at certain definite times in certain definite ways, and it is this behaviour which we will now examine, limiting the investigation to those species whose peculiar but characteristic attitudes it is the purpose of these plates to demonstrate. It would be difficult to find a family more suitable for such an investigation, for, on the one hand, the nervous system of its different members is so framed as to produce a visible emotional behaviour seldom surpassed in bird life, and, on the other, the secondary sexual characters are not highly developed. The combination of these two characteristics in the same individual is important; for since the emotional behaviour reaches its highest degree of intensity, and the secondary sexual characters their greatest development during the period of reproduction, a direct relation between the two has always been deemed more than probable.

The period of reproduction is the period when behaviour is most emotional, and part of that period we often find referred to as one of courtship. We read of "the courtship being a prolonged affair," or that "courtship may thus be regarded, from the physiological point of view, as a means of producing the requisite amount of pairing hunger," or, again, "that it is the instinctive coyness of the female that necessitates all the arts of courtship," but of the term courtship no explanation is offered. The word is indefinite, implying a period of

hesitation which is assumed to be an essential prelude to conjugation. Elsewhere I have suggested that such a use of the term is open to criticism. And since it is possible that from the moment a sexually mature female enters the territory of a single male the question of reproduction is decided, providing always that she is not challenged and defeated by a rival of the same sex, I have referred, in the later parts of this work, to the whole of the period commencing with the arrival of the female and ending with the laying of the normal number of eggs as that of sexual activity. During this period the emotional manifestation, which is unequalled at any other period in volume though sometimes not in intensity, may perhaps be said to reach its climax during the actual discharge of the sexual function, and the manifold and peculiar antics and attitudes which we witness must be regarded as part of a whole—that is to say, as part of the sexual instinct. The problem, then, which requires a solution is the exact position that these activities occupy in the whole sexual process; but so long as we are ignorant of so many simple facts in the lives of so many species, it is scarcely likely that a satisfactory solution will be reached.

If it were possible to induce one pair of each of our more common species of warblers to rehearse its life-history before an onlooker previously unacquainted with their habits, one feature which would perhaps command a large share of his attention would be the fact that each species has its own degree of response, which is constant even at the different emotional periods. He would notice that this pair was persistently sluggish in behaviour, while that pair was scarcely able to restrain its excitement on the slightest provocation. In all likelihood he would thereupon call to mind all he knew of human emotion, and possibly satisfy himself that an analogy was to be found in the behaviour of the different races of man. And so long as the analogy were limited to this particular feature, it would approximate in some measure to the actual facts. We enter in the latter part of April some wood in-

habited by various species, and seeing a male highly excited whilst following in the wake of a female, we carefully note the extent of its territory with the intention of re-visiting the spot at a later date. A month passes by and in that same territory we find a nest containing well developed young. By removing one of them and allowing it to flutter about on the ground, we find that we thereby produce in the parent birds an excitement approaching in intensity that which we noted a few weeks previously. Now such uniformity of response can be observed with little difficulty. If a male behaves consistently in an extravagant manner in the presence of a female, we may look with some confidence for extravagance in its behaviour at the excited assemblies of the males, or in the behaviour of both sexes, when the nest or young are intruded upon. The Blackcap and the two Whitethroats are extravagant in their actions during sexual activity, whilst under the influence of parental emotion, or when excited at the presence of a neighbouring individual of the same species, and they may be said to represent the one extreme, *i.e.*, the highest type of such behaviour; whilst the Reed and Sedge Warblers represent the other, the visible response being much less marked in their case. Between these two extremes ranges the motor expression of other members of the group. Approaching most nearly the degree of extravagance attained by the Blackcap or Whitethroat is the behaviour of the Grasshopper and Savi's Warbler, and perhaps on a level by itself is that of the Garden Warbler. Next in order we might place the reactions of the Chiff-chaff, Wood and Willow Warblers, leaving those of the Marsh Warbler midway between these three latter species and the comparatively unresponsive behaviour of the Reed Warbler. But in studying so elusive a subject as the emotions we have many difficulties to contend with, and the advisability of even attempting to allot a definite position in a hypothetical scale to this or to that species may be quite rightly called in question. The foregoing scale must consequently be regarded as an initial attempt

to reduce the emotional behaviour of the group to some order rather than a definite contribution to our knowledge of the subject. Why do I attribute a certain level of emotional development to such and such a species? Knowing, as we do, that in the case of human emotion a stimulus of an appropriate kind is necessary to produce a definite response, we can scarcely doubt that the same is true of the primary emotions of the lower animals. And since all knowledge of the emotion of a bird, in its subjective aspect, is beyond human understanding, how can we be sure that the comparisons are made under corresponding conditions, and are we therefore justified in even attempting to decide as to the relative position this and this species ought to occupy in any scale of emotion? I grant the difficulty, and even admit that the same individual does not always respond actively when under the influence of sexual or parental emotion. Perhaps my conclusions may be said to be based more upon impressions gained from a long acquaintance with the different species, than upon anything in the nature of tangible fact. And yet extravagant antics, which comprise an outstretching, flapping, and fluttering of wings, a spreading and raising of the tail, peculiar contortions of the body, and an equally peculiar employment of the vocal powers, are surely sufficient reason for assigning to the actor a different level in an emotional scale from one whose movements attract but little attention or excite but little wonder. Starting thus with the two extremes I have allotted the intermediate places as they seemed to me to be merited. The extremes may consequently be said to be based upon actual evidence, the intermediate stages being in some measure impressionist, though I hope not altogether so.

The similarity of the motor reactions at different emotional periods next requires consideration; it is a possible line of investigation from which something may come. The perceptual powers of animals are probably greater than we imagine. We think that we discern similarity in the behaviour arising in wholly different situations, yet some

feature may quite well escape our attention, a feature so small perhaps as to be beyond our powers of observation, but nevertheless sufficiently great to suggest a different meaning to the more delicate perceptual powers of a bird. We must, therefore, make due allowance for our own imperfections in this respect. Professor Lloyd Morgan suggests to me that the motor reactions may be only generically similar, that even they, as such, may very likely be specifically differentiated, and that the total complex of the emotional situation, involving factors so many and so varied, may be yet more markedly and distinctly differentiated. He sees no reason why a generic motor expression, supplemented by allied organic sensations, and qualified in experience by the total meaning of adaptive behaviour, should not be differentiated in different situations—the mating situation and the fighting situation—so as to bear its part with a difference in both. This of course is quite possible, but unsafe as it may therefore be to speak of specific similarity, I am nevertheless inclined to think that I have observed it on more than one occasion and in more than one situation. The emotional behaviour is most intense during sexual activity and while the young require the care and attention of their parents. The intermediate time is occupied almost wholly by incubation, and though this is a time of comparative quietude, yet even then there are frequent exhibitions of a similar behaviour, which, however, never reach a similar degree of intensity. Such exhibitions may occur at the assemblies of the males, when a territory is intruded upon by a neighbouring individual of the same or another species, or when a Cuckoo or some predatory bird approaches the locality in which the nest is situated. But for our present purpose we may disregard the minor exhibitions and compare those two in which the motor reactions are observed to be most in evidence. In the life-history of the Lesser Whitethroat this similarity has already been touched upon. I there stated that both the Whitethroat and Lesser Whitethroat, when anxious about their young, behaved in a

manner which differed but little from that of a few weeks earlier in the season. I can now amplify this a little. The Garden Warbler is not a particularly demonstrative bird; according to our emotional scale it occupies a position midway between the two extremes, and we have placed it in a class by itself. Two methods of expressing sexual emotion on the part of the male are known to me, the more commonplace of the two being that one in which the wings are partially extended, and this is the attitude that is assumed by the female when her nest is intruded upon, providing that the stimulus is sufficiently strong to produce the necessary response. The Willow Warbler is still less demonstrative, but both sexes assume a peculiar attitude previous to coition, and this attitude is again assumed by the female when excited about her offspring. The Grasshopper Warbler is more demonstrative than either of these two previous species. The male spreads and waves its wings during sexual activity, and a similar waving of the wings sometimes takes place in the case of both sexes when excited about their young. In comparing these two periods we must not lose sight of the fact that during sexual activity the motor reactions reach their greatest intensity in the male; but during incubation, or whilst the young still require the care of their parents, in the female; and as the female during sexual excitation shows traces of those reactions common to the male, so the male when excited about its young may affect attitudes similar to those of the female. That the sexual and parental emotion should reach the highest degree of intensity in the male and female respectively is what we should anticipate since it appears to be the rule throughout a considerable part of animal life. Similarity of the organic symptoms in different emotions is not unknown. Professor Lloyd Morgan refers to it as follows[1]: "It would seem then, if there be any truth in the considerations just hinted at rather than developed, that what is

[1] "Habit and Instinct," p. 201.

specially characteristic of emotion, as such, does not take its origin in the motor elements; and it becomes probable that it is the visceral elements which afford the differentiæ of emotion. If so, it is not the instinct-feeling in its motor aspect—what we may term the activity-feeling—that is concerned in the primary genesis of an emotion, but rather the concurrent and associated set of visceral actions. Let us see, therefore, whether observations on the active and emotional life of young birds throw any light upon this problem. Take the case of a young frightened moorhen. On land he runs away, and perhaps crouches in the rushes; in the water he dives, and comes up quietly under the bank and there stays still. The activities involved in running and diving are very different; must not the activity feelings be very different too? And yet we must surely suppose them to have a common emotional element. Again, when a moorhen catches sight of a worm and runs hard to secure it, the activity-feelings must, as such, one would suppose, be very similar to those experienced when the moorhen runs vigorously away from a goose. And yet in the one case he is frightened, and in the other case he is not. Here similar activity-feelings are associated with wholly different emotional states." Dr. Stout comments thus on the above passage: [1] "But Lloyd Morgan and others seem to suppose that visceral sensations at least are fairly constant in the same emotion on different occasions and in different circumstances. Now the problem is an obscure one; for visceral sensations are difficult to investigate. But so far as any distinct appeal to experience can be made, it seems that they also may be more or less similar in different emotions, and variable in the same emotion. The Maori women of New Zealand when they meet for festive purposes enjoy themselves by squealing and crying, so that a stranger would suppose them to be in a state of intense grief. One traveller tells how he was roused at night by the most doleful cries, and went

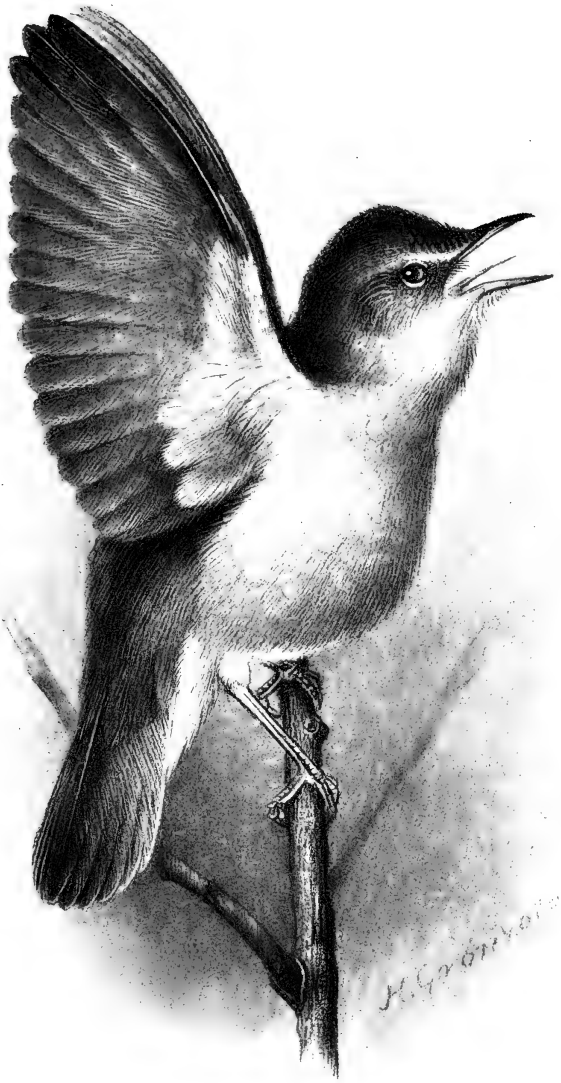
[1] "Manual of Psychology," p. 307.

out to see what human creature was in misery. He found that it was a woman rejoicing over a meeting with her long-lost son. Here the respiratory changes and increased secretion in the lachrymal glands were the natural expression of joy." Similarity of the organic symptoms at different emotional periods may therefore be more common in animal life than we imagine, but it remains to be seen wherein exactly its true significance lies.

We will now compare the motor reactions of the more closely allied forms amongst the warblers, and for such a comparison we could scarcely choose a genus that could afford more suitable examples. The various species in some cases resemble one another so closely that it is only with difficulty that an expert with dried skins before him can detect the very slight differences in shading and form, and if it were not for some specific type of behaviour, recognition in their natural surroundings would be well-nigh impossible. As instances of extreme resemblance we may take the Willow Warbler and Chiff-Chaff, the Reed and Marsh Warbler, and the Sedge and Aquatic Warbler, and of those which can be readily distinguished, but nevertheless are very much akin, the Blackcap and Garden Warbler, the two Whitethroats, and the Grasshopper and Savi's Warbler. Since there is such resemblance in their outward appearance we naturally ask ourselves whether it also obtains in their instincts, habits, and emotions. Now we have no palæontology to guide us as to the course mental evolution has taken, as we have in organic structures; the past is a sealed book, and I hold therefore that there is much to be learnt from such comparisons. In fact the only method left open to us is to examine and compare the results as they are presented in nature to-day, and decide whether they are such as we should expect to find according to the principles which we lay down. Let us first compare the instincts most familiar to us, namely those connected with reproduction. Both the Willow Warbler and Chiff-Chaff live in a similar environment and possess territories, the boundaries

of which they defend against intruders; they construct nests so similar that if it were not for the fact that those of the former are placed upon the ground and those of the latter slightly above it they would be indistinguishable, but even this slight difference does not appear to be absolute since the Willow Warbler sometimes builds above the ground. They make use of similar materials, frequently tearing off the bark of the honeysuckle which they weave into the foundation of their nests; in the manner in which they feed their offspring and clean the nest there is little or no difference, and their behaviour after the young are able to fend for themselves is identical. So it is with the Reed and Marsh Warblers. They possess territories which they defend so long as the young require their care; their nests are similar in construction and remarkable in type, the only difference being in the material used—which is due to the fact that they do not live in a similar environment—and in the manner in which they rear their young there is no perceptible difference. Much the same may be said of the Blackcap and Garden Warbler. Both possess territories, defend them, and remain in them until the young are fully fledged; both build in similar situations and construct nests which differ, if at all, but little, either as regards type or material; and both adopt similar methods in the care of their offspring. In the case of the two Whitethroats the nests are placed in slightly different situations, but beyond this the instincts connected with reproduction do not differ. So here we have four separate examples in each of which the reproductive instincts so nearly approach one another that there is nothing to prevent our regarding the species from this aspect as continuous forms. But besides these special instincts there are those connected with migration and bodily sustenance, and they are uniformly alike not only in those cases of close relationship, but practically throughout the whole genus. The laws of migration which apply to one apply to all, the same type of food is consumed, and the methods adopted in securing it are alike. We have

only to watch the oak trees when the *larvæ* of the *Tortrix viridana* are hatched to see the truth of this, for quantities of Blackcaps, Garden Warblers, Willow and Wood Warblers, and Chiff-Chaffs there find a living, or the alders adjoining some reed bed which, when the *aphides* are swarming, attract numbers of Reed and Sedge Warblers, Chiff-Chaffs, Willow and Garden Warblers. There remains the emotional behaviour upon which opinion is so divided. The continuity which we can almost trace in structure and instinct fails us here, and in place of it we are faced with facts of that contradictory kind which nature so often reveals. Those two small birds, perched on the same branch within a few feet of one another, flapping their partially expanded wings, we know at once to be a pair of Willow Warblers, for the Chiff-Chaff behaves differently. That bird, which rising from the hedge dances in the air as if suspended by an elastic thread, we recognise without difficulty, since its nearest of kin the Lesser Whitethroat has other means of expressing its emotions. And similarly we distinguish the Blackcap from the Garden Warbler, for each during times of excitement spreads out its wings and tail and raises its feathers in certain ways peculiar to it. Yet we cannot by such means distinguish between the Grasshopper and Savi's Warblers; their actions are identical; they spread and move their wings similarly, and if it were not for the difference in colour and in the pattern on the feathers, or the much more musical trill of the one, no one could say with certainty whether the bird he was observing belonged to this or to that species. Here is a somewhat different case. Let us imagine ourselves in the centre of some reed bed towards the end of May. Reed Warblers are all around. Beside us is a male, evidently sexually excited, uttering its metallic sounding song, and whilst doing so jerking its wings slightly outwards from the shoulder. Leaving it we enter an osier bed from which a more beautiful, more highly developed song is proceeding. To all appearances the owner of the voice is a Reed Warbler; it too is excited, singing to the



MALE MARSH WARBLER

ATTITUDE ASSUMED DURING THE
PERIOD OF SEXUAL ACTIVITY
THE WINGS ARE MORE FULLY EXPANDED
THAN IN THE CASE OF THE
REED WARBLER

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SWAN ELECTRIC ENGRAVING Co

utmost of its power, and at the same time rapidly raising, and as rapidly contracting, its fully expanded wings. By the fact of the fuller expansion of the wings we know that the bird is a Marsh Warbler, though it is only with difficulty that we can detect the subtle difference in the colour of the plumage. The behaviour of the two birds may seem to be very dissimilar, but a close examination of their actions reveals the fact that the difference is only one of degree. So that the motor reactions of the most closely related forms within this one family may be alike, or unlike, or differ only in degree. Shall we then say that each reaction has some special part to fulfil, and that that part is dependent upon just the particular way in which the reaction is to be found setting? Or must we take a broader view and say that the reactions as a whole have a part to fulfil, but that their utility is not necessarily consequent upon their being cast in any particular mould? Or yet a third view which would regard them as mechanical results of the way in which this or that nervous system has been framed? There are some who uphold the first of these propositions; who say that there is some relation between the plumage, *i.e.* the secondary sexual characters, and the attitudes assumed; they regard the antics of the male not as a physiological result of excitation but as the outcome of intelligence, and assert consequently that they are performed as a means to an end and that end is the fascination of the female. But if it be true that there is some relation between the plumage and the attitudes assumed, it must surely be the case that identity of structure and colour ought to correspond with identity of movement. Yet of none of the examples into which we have been inquiring can this be said to be true, for in the one that most nearly approaches it—the Grasshopper and Savi's Warbler—there is identity of structure and expression but not of colour. When, therefore, we consider that the attitudes may be alike when the plumage is different or wholly unlike when the plumage is similar, and at the same time bear in mind the manifold and diverse forms

the antics take in closely-related species, and the fact that they may be scarcely perceptible in one variety, whereas in another closely akin their very frequency and intensity compels our attention, we find little enough support for the first proposition in the lives of these particular species. This view, however, has in a great measure been discarded, opinion generally favouring the second proposition as being a more reasonable interpretation, since conscious display is discarded and replaced by a more mechanical process, which readily comes under the sway of natural selection. Thus Professor Groos in his "Play of Animals" develops a theory which is accepted by many as a provisional hypothesis. I quote it as summarised in his preface to the above work. "The disciple of Weismann who cannot accept Spencer's explanation of such phenomena must either cleave to Darwin's sexual selection, as Weismann himself does, or seek a new principle. Such a principle I believe I have found. It depends on two closely related facts. As sexual impulse must have tremendous power, it is for the interest of the preservation of the species that its discharge should be rendered difficult. This result is partly accomplished in the animal world by the necessity for great and often long continued excitement as a prelude to the act of pairing. This thought at once throws light on the peculiar hereditary arts of courtship, especially on the indulgence in flying, dancing, or singing by a whole flock at once. But the hindrance to the sexual function that is most efficacious, though hitherto unappreciated, is the instinctive coyness of the female. This it is that necessitates all the arts of courtship, and the probability is that seldom or never does the female exert any choice. She is not awarder of the prize, but rather a hunted creature. So, just as the beast of prey has special instincts for finding his prey, the ardent male must have special instincts for subduing feminine reluctance; and just as in the beast of prey the instinct of ravenous pursuit is refined into the various arts of the chase, so from such crude efforts at wooing that courtship has finally developed

in which sexual passion is psychologically sublimated into love. According to this theory, there is choice only in the sense that the hare finally succumbs to the best hound, which is as much as to say that the phenomena of courtship are referred at once to natural selection. It follows, too, that however useful attractive form and colouring may be in relation to other ends, they certainly contribute to that of subduing feminine coyness, and hence further the sexual life." And Professor Lloyd Morgan comes to the conclusion that[1]: "stripped of all its unnecessary æsthetic surplusage, at any rate so far as this implies an æsthetic ideal, or æsthetic motive, the hypothesis of sexual selection suggests that the accepted mate is the one which adequately evokes the pairing impulse." These opinions differ widely from the original theory of sexual selection, but even this modified form is not altogether free from criticism, as I shall endeavour to show in connection with the phenomena which we are now discussing. Since conscious display is discarded, the theory becomes, primarily, one of the development of emotion. It is assumed that the strength of the species is represented by the strength of its emotion, that the strength of the emotion is reflected in the intensity of the expression—that is to say in the movements, which are peculiarly attractive to the female, of the limbs and body of the male—and finally that inasmuch as the strength of different individuals is a variable quantity, so, at the other extreme, the capacity for movement will vary correspondingly, becoming consequently an index of the fitness of the individual to take its share in reproduction. Now this seems to me to be taking a great deal for granted. When we speak of a species being emotional all we mean to imply is that the visible expressional movement is well marked. Of internal organic changes we know nothing, though we believe that they too must be present and play an important part in the total emotional complex. In human emotion the expressional

[1] "Animal Behaviour," p. 264.

movements visible to an external observer may be absent in slight, and sometimes in intense emotions. May not this be true of the emotion of a bird, and may not the relation between the strength of the emotion and the intensity of the expressional movement, which is here assumed, be open to question? Circumstances at least seem to show that such may be the case. For do we not observe in bird life numberless degrees of emotional reaction, ranging from almost imperceptible movements up to extravagant actions, corresponding to a sexual instinct the strength of which cannot well be differentiated in *x y z* and all the rest.

The proposition, as I understand it, is somewhat as follows: Not all the males are of equal strength; the stronger individuals are capable of greater sexual emotion. This emotion must somehow express itself, and does so in many cases by what are known as motor reactions. These reactions excite the female. The stronger the male the stronger the reaction and the greater chance that male will have of overcoming the reluctance of the female, pairing, and transmitting its greater strength to descendants, and the greater scope will there be for the development of secondary sexual characters, which will naturally result from greater strength and possibly contribute to a more effective pairing situation. And at first sight this would appear to be a reasonable interpretation of all the peculiar attitudes, antics, and vocal extravagances which are the subject of our investigation; but when we attempt to bring it into accord with the phenomena which we actually observe, the task is not altogether an easy one. Certain essential features of the theory are not very clear to me; for instance, there is no very definite expression of opinion as to whether the theory is one to explain the evolution of antics from movements that at some earlier period were not so pronounced, by the selection of variations all tending in the direction of greater activity; or whether it only claims to show how, having once arisen, they may now have a meaning in relation to something in the environ-

ment of the female. But it can scarcely be intended in this latter sense, as that would imply that the reactions came into being independently of the utility which the theory suggests. The central fact of the theory appears to be this, that the reactions are the agency by which the mating of the stronger individuals is secured. Let us then carry our minds back to some earlier period, and try to picture the appearance of a variation which possessing greater vitality reflected it in its emotions, stimulated the female, and thus gained an advantage in securing a mate. The weaker members insufficiently endowed with overt expressional movement would gradually disappear and the whole species become transformed. But since, on the average, it would only be those which possessed the power of reflecting their emotions in the highest degree which would attain to reproduction, competition would still continue, and the reactions would slowly increase in intensity *pari passu* with the selection of the stronger individuals until a level were reached when perhaps further increase might become harmful. This level would then be maintained by the elimination of those that failed to reach the necessary standard. The reactions have accordingly been developed just in so far as they represent increased emotion and thereby increased strength. Now with regard to some of the warblers the facts are as follow: There are ten species which for purposes of comparison can be divided into five pairs, the two Whitethroats, Blackcap and Garden Warbler, Grasshopper and Savi's Warbler, Willow Warbler and Chiff-Chaff, and the Reed and Marsh Warbler. All these pairs are severally very closely allied, but in the case of two of them the relationship is so close that one can only be distinguished from the other with some difficulty, and all may be said to be fairly equally distributed over Western Europe. Regarding these ten species as a whole we find it difficult to trace any uniformity in the intensity with which they manifest their emotions, and equally difficult to satisfy ourselves of any general resemblance in the particular form such manifestations take;

although the differences in their structure are but slight, and we have no reason, therefore, to anticipate any striking dissimilarity in behaviour, yet we can observe without difficulty quite a number of specific types of reaction. And examining the five pairs separately we notice that the reactions are alike in one case only, but in the remaining four widely divergent. No one who observes and compares the behaviour of the Blackcap and Garden Warbler, the Willow Warbler and Chiff-Chaff, the Marsh and Reed Warbler, or the Whitethroat and Lesser Whitethroat can deny that in each case the former bird is a superior exponent of the art of demonstration. Bearing in mind then the essential points of the theory—namely, that the reactions have been developed solely because they reflect vitality and are consequently useful in indicating the fitness of the individual to take its share in reproduction, and that they have been evolved in conjunction with an external factor—how shall we explain this remarkable disparity in their development? We can only do so if we say that a comparison between one species and another need not necessarily hold good, since it matters not how many different degrees of emotion bird life may supply so long as there exists for each separate species a certain specific standard of response to which it is necessary for every individual to attain if it is to have an average chance of reproducing. Of two closely allied forms, this one is excitable, flaps its expanded wings, spreads its tail and works itself almost into a frenzy; that one is passive, similar circumstances produce in its case only a modicum of excitement, only slight use is made of the wings, the tail is only moderately spread and the song is but little different from that heard on any ordinary occasion. In each case the behaviour must have a similar meaning through which it has reached its present development. And since in both cases it must be assumed, *ex hypothesi*, to represent equivalent emotion and equivalent strength and to serve its purpose equally well in its own particular sphere, the explana-

tion of the difference lies outside the province of utility indicated by Professor Groos; there must be some other factor which, exercising independent control, arrests development here or allows it to proceed there to the verge of extravagance. I therefore suggest that the reactions may be by-products of this factor which regulates the intensity of the activity feelings, and that after all there may be something to be said for the third proposition—the view that would regard them as having arisen independently of any question of utility. The infinite number of specific types of reaction lends some support to this view. How frequently we can distinguish a species merely by some particular way in which it behaves in the breeding season! The Greenfinch, Yellow Bunting, Tree Pipit, Meadow Pipit, Snipe, Ruff, Redshank, Black-tailed Godwit and a host of others we can recognise, each one by its own particular mode of conduct. The reactions reflect the emotions—says the "utility" hypothesis—excite the female and are thus of some use, but why should they have taken the form of a spreading of the tail in this case, a waving of wings in that, or a fluttering in mid-air in a third? It is evident that there is something here which requires an explanation if we regard them thus, and it is evident that the assistance of some further factor, which can guide the reactions into certain definite channels, must be assumed in order to complete the explanation. In one passage Professor Groos seems to recognise the difficulty of attributing utility to the reactions and almost approaches the conclusion that they may be but incidents of the nervous system having no special part to fulfil. [1] "We must admit," he says, "that in most cases the actual basis for the arts of courtship is to be found in general excitement reflexes, or even in those of quite a different origin. This basis consists partly in such reflex motions as result from any strong excitation such as restless fluttering, running about, skipping and

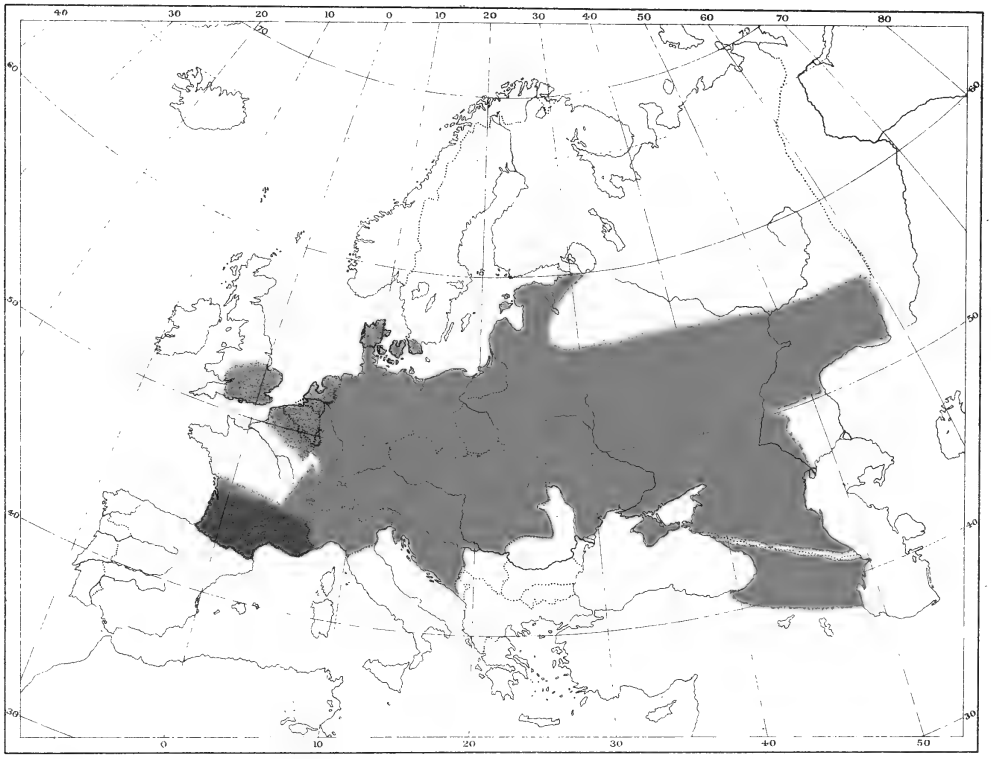
[1] "The Play of Animals," p. 247.

trembling, and further in the reflexes that are commonly awakened in the face of an enemy, such as inflation, erection of hair or feathers, lifting the voice, &c. These are obviously the material from which Nature has derived the peculiar arts of courtship in all their variety, and these arts as we have seen are then extended to occasions which have no sexual meaning." But surely the restless fluttering, running about, skipping, trembling and so forth *are* the peculiar arts of courtship; at least, I am aware of scarcely any sexual behaviour that could not justly be included under one of these headings.

The detailed life-history of the Marsh Warbler, which now follows, entails a repetition of certain features of behaviour to which allusion has already been made, and if the foregoing discussion fails in its first purpose to make clear the necessity for such comparisons as we shall presently institute, it will, I hope, serve to show the complexity and difficulty of the subject, and how much remains to be explained. Owing to its peculiarly close relationship to the Reed Warbler, few birds have been of greater interest to me than the Marsh Warbler, and I find it difficult to analyse its habits and instincts, or institute comparisons between its behaviour and that of the Reed Warbler without being constantly awakened to the fact that some lesson is to be learnt from its life. In the following account the different phases of its life-history will therefore be compared, wherever possible, with those which correspond to them in the life of the Reed Warbler.

The latest of all our summer migrants to arrive at its breeding haunts, it is said to reach Oxfordshire during the last few days of May or, more usually, the first few days of June, and this agrees with my own experience of the bird in Worcestershire, where I have observed it in the Severn Valley. In that district May 30th is the usual date of arrival, but in other parts of the country it has been known to arrive some few days earlier. In Gloucestershire the average date for fresh

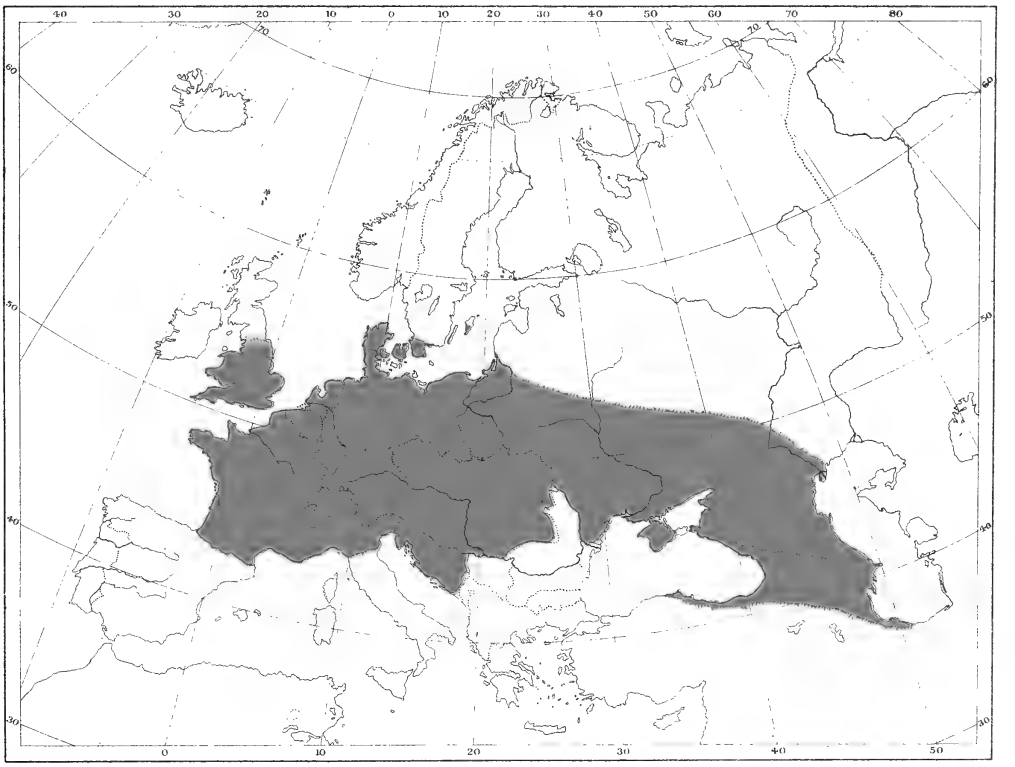
BRITISH WARBLERS.



First half of April
Last half of April
First half of May
Last week in May and first half of June

MAP SHOWING APPROXIMATELY THE DATE OF ARRIVAL OF THE MARSH WARBLER IN CERTAIN PARTS OF EUROPE.

BRITISH WARBLERS.



Latter part of April and first half of May

MAP SHOWING APPROXIMATELY THE DATE OF ARRIVAL OF THE REED WARBLER IN CERTAIN PARTS OF EUROPE.

eggs is from June 18th to 24th. Nests with eggs have been found in Somersetshire on June 26th, in Buckinghamshire on June 14th, in Surrey on June 14th, in Kent on June 22nd, and in Cambridgeshire on June 14th. As far then as can be gathered from these records, the last week in May and the first week in June is the normal period of arrival in England, whereas the last week in April and the first week in May is the normal period of arrival of the Reed Warbler—so that, broadly speaking, the former bird may be said to be one month later in arriving at its breeding quarters than the latter. Nevertheless it is improbable that the period of arrival is confined solely to these two weeks. The migration is, doubtless, a far more protracted affair, and if we possessed sufficient records we should very likely find individuals still arriving in the middle of June. I am arguing from my experience of other species, of the Reed Warbler especially, and also from the conditions which prevail in the North of Holland where males continue to arrive up to the middle of June. The species is not sufficiently plentiful in England to enable one to reach a very definite conclusion. In the case of the Reed Warbler observation shows that the period of arrival extends to upwards of a month—that is to say until the latter part of May, and it would therefore seem as if the first of the Marsh Warblers and the last of the Reed Warblers reach their destination approximately at the same time. We will now turn our attention to the Continent. In the Island of Texel my experience is that they may be looked for in the early part of June, but even as late as the 20th of that month fresh arrivals are still in evidence appropriating territories in the various spinneys and osier beds. Denmark is reached towards the end of May, but Heligoland is passed on migration according to Gätke at the commencement of that month. The South of France witnesses their return as early as the end of March or the beginning of April. Naumann states that in Germany they commence to sing during the first week in May, and Dr. Otto Herman informs me that they may be expected in Hungary

about the same time, Professor Goeldi that they reach Switzerland from the middle of April to the middle of May, Count Salvadori that they arrive in Northern Italy during the latter half of April and the beginning of May, and M. Buturlin that Poland is reached towards the end of April, Southern Russia from the middle of April to the middle of May, the Baltič Provinces during the first half of May, Central Russia about the middle of May, and the Province of Kasan towards the end of that month. Here, then, we have a peculiarly contradictory set of facts. Let us see what the variation amounts to. In England, the normal period of arrival is the end of May, or the commencement of June, in Texel the early part of June, but in Germany and Hungary the beginning of May, one month earlier, that is to say, than the normal period in Western Europe; whilst in Switzerland it is the middle of April and in the South of France the commencement of that month, almost two months earlier than the average date of arrival in this country. Assuming that all these dates are approximately correct, we have a variation which is probably unsurpassed by any other migrant —at least it is not approached by those with which I am more especially familiar. Variation in the case of all migratory species must and does occur up to a point. The more southern parts of Europe are, as a rule, the first to witness the return of these heralds of spring, and even the territories in the southern counties of England are, on the average, appropriated somewhat earlier than those in the north. But in all such cases the difference in time may be more conveniently reckoned in days than in weeks, still less in months. As an example, we have the Reed Warbler which arrives in Hungary about April 20th, ten days or so before it may be expected in England, and the Reed Warbler, be it remembered, is closely related to the Marsh Warbler, a fact which makes the variation in the case of the latter species even more significant. There is nothing to account for this extreme variation; there is nothing, so far as we can judge, in the reproductive instincts of the

Marsh Warbler to prohibit the development of an earlier, and probably more advantageous, habit of nest building. Such a development may, indeed, be gradually taking place; for if at some earlier period the nesting instinct of this bird was similar to that of the Reed Warbler, we have an explanation of this curious variation. We can account for the comparatively late arrival of the Reed Warblers. They, in the majority of cases, construct their nests upon reeds which only attain the necessary height late in the season. Some, it is true, make use of the old reeds only, but not early in the season, since any tendency in the direction of too early nesting would be held in check by the fact that such nests could not fail to be more conspicuous, and therefore more liable to destruction. The habit of late arrival has, in their case, simply conformed to the needs of their environment. The Marsh Warblers on the other hand no longer depend for the construction of their nests upon the growth of any particular plant; they are no longer subject to the same selective agency, and consequently we find the instinct of migrating at a more or less definite period subject to considerable variation. To them earlier nesting may now be an advantage, since the likelihood of two broods being reared in one season is greater, and so the tendency towards an earlier arrival may be receiving encouragement instead of being checked; hence the extreme variation. If the individuals which breed in England and the western parts of Europe gain any advantage by their late arrival, how can we explain the fact that those which inhabit other parts of Europe, where the conditions of existence are very similar, arrive so very much earlier? In contrast with this remarkable variation we have the relative constancy in the date of arrival of the Reed Warbler throughout western Europe. Thus England is reached at the end of April or the first week in May, France, Hungary, Germany and Switzerland about the middle of April, Denmark at the commencement of May, while Heligoland is passed on migration in May. So that the arrival of this species in the various

countries alluded to may be said to occur approximately within a period of three weeks—a striking difference when compared with the corresponding period of two months during which the Marsh Warbler is arriving.

The localities frequented by the Marsh Warbler are different from those in which we are accustomed to find the Reed Warbler. The latter bird inhabits the dense masses of *Arundo phragmites*, and sometimes, it is true, when such conditions are not available, the withy beds that are found along the banks of our larger rivers; but for the Marsh Warbler the dense reed beds never seem to possess a similar attraction. There are records of the nest having been found amongst reeds—to the authenticity of which, however, some doubt is attached—and in Texel I was taken amongst the reeds in order to hear the males singing, but no trace of them was to be found; and it is doubtful whether my friends were really acquainted with the species. In the choice of a situation for breeding purposes a close proximity to water is by no means a necessity, for sometimes they inhabit steep banks, where a year or so previously the trees have been felled and the ground has become thickly overgrown with such bushes as hazel, elder, and ash, and carpeted with a luxuriant undergrowth, or even thick hedgerows surrounding orchards. On the other hand, they may be found along the very banks of a river, providing that the vegetation and bushes are sufficiently dense to afford protection. However, the osier bed seems to be preferred to any various descriptions, usually damp, sometimes surrounded by other situation, and by this term I mean small plantations of or even partially filled with water, but always having a relatively drier portion which can be resorted to by the birds for the purpose of reproduction. In Texel there are many of these small plantations in which the willows and other trees have been allowed to grow to a considerable size, but they are resorted to nevertheless so long as the undergrowth is sufficiently dense. I recollect two males inhabiting one such

withy bed, at one end of which the common reed was growing in profusion. The reeds were not infrequently entered by the male who owned that part of the plantation, and by the female also, but, as far as it was possible to judge, solely for the purpose of finding food. The situation chosen for reproduction is clearly not confined to any particular locality, nor is any special tree or vegetation a necessity. We may look for and expect to find the birds in wooded banks, in damp or wet osier beds, in hedgerows or along the banks of a river. The choice of a breeding territory seems therefore to be in a condition of instability similar to that which prevails in the date of arrival in different countries.

As is the custom amongst other migrants, males arrive before females. This does not imply a strict division in the times of arrival of the sexes; the first arrivals are males, but in the latter part of the migratory period the sexes seem to accompany one another. How long after the first males the first females commence to arrive, I am unable to say. Since the species is the latest of the migrants, and it is therefore important that reproduction should be commenced as early as possible after the territories have been appropriated, the period during which the sexes are separated is probably not very great. Mr. Warde Fowler is of the opinion that males arrive in Oxfordshire a few days only before the females, and this agrees with my own experience in Worcestershire, which nevertheless is somewhat limited on this particular point.

Each male upon arrival takes up a certain position in the osier bed, plantation, or overgrown bank in which it has settled; and this position constitutes a breeding territory which is adhered to, and more or less defended from intrusion so long as the young require the care of their parents. One instance only has come under my notice of a male occupying a territory, singing there regularly, but ultimately deserting the locality, and I am inclined to think that the cause of desertion in this particular case was the fact that the position chosen was not altogether suitable to the needs of the bird.

It was amongst some willows growing in the water with little or no undergrowth close at hand that could afford adequate protection for the nest. That a male should have appropriated such a territory seemed to me at the time unusual, and therefore I was scarcely surprised when, after singing regularly for about ten days, and frequently intruding upon a neighbouring territory, it wandered one morning up an adjoining hedgerow and disappeared in search of a new home, which I believe it eventually found in a plantation approximately a mile away. Each territory has its boundaries which are jealously guarded by the owner. But these boundaries must not be regarded as clearly defined. The conception, that is to say, of a boundary must not be that of a line which is at no time crossed by the owner, or which cannot be crossed by an intruder without a commotion resulting. Such a conception would imply powers altogether beyond the mental capacity of a bird. These boundaries must be thought of in a wider sense than this, although it is remarkable how well defined they sometimes are. I have already pointed out that the territories are the result of a natural law, and that it is unnecessary to regard the individual bird as being in any way cognisant of a territory as such. The securing and defence of a territory is not an individual acquirement, but is rendered possible by congenital nervous dispositions which have been gradually evolved by selection and determine their possessor to act in this particular way. Neither is it essential for the principle of territory that there should be absolute boundaries, or that an intruder should never be allowed to enter a neighbouring preserve without being attacked. All that is required is that on the average those individuals which are the more active in attacking and driving away such other individuals as approach them too closely should be left in possession of a territory, and thereby gain some advantage; and the advantage in the case of the migrants arises from the fact that an ample supply of food for the helpless offspring is secured. The dimensions of the territories of the Marsh

Warblers vary considerably. I have sometimes been impressed with the remarkably small area which is embraced, fifteen square yards in one instance being almost sufficient to enclose the wanderings of the male. So small an area is noteworthy when compared with that of other species living in a similar environment. However, I am not in possession of the daily records of a sufficient number of pairs to justify any very definite conclusion upon this point. Nevertheless if at some earlier period the bird had been an inhabitant of reed beds, building its nest therein, the dimensions of its territory must necessarily have been small, as in the case of the Reed Warbler; and although these dimensions would certainly have been gradually modified to suit the new environment, yet a reversion in certain cases to the former conditions would be neither impossible nor unlikely, especially if the change had been of comparatively recent occurrence.

Before the arrival of a female, the male will be found to be constantly moving around his territory, and if his wanderings are carefully watched, it will be seen that they are not quite so aimless as they may at first appear, but subject to some routine. A certain tree or bush is selected and regarded as a favourite resort. From this tree excursions are made into different parts of the territory, but even these excursions bear evident traces of that tendency towards routine so common in animal life, for the short journeys are often made in the same direction, the same bushes are selected and forced to give up part of their stock of insect life, and then only is a return made to the tree more especially favoured. In having a head-quarters, therefore, the bird resembles the Reed Warbler, and for the matter of that many other species too. Various trees are made use of for this purpose, alders, willows, or even clumps of tall decayed vegetation; and previous to the arrival of a female more time is spent in this one spot than in the remainder of the territory, and of that time a considerable portion is passed in the exercise of those vocal masterpieces in which the bird excels.

To an observer unacquainted with their habits, the males might appear to be pugnacious and to be constantly quarrelling with their neighbours. The word "pugnacity" however implies a wilful and useless bickering, a quarrelling more for pleasure than for a purpose, and casts an unjust reflection on the character of the bird. I do not mean to say that of its frequent pursuits of other species none could justly come under the heading of "play," but that in the majority of instances there is a true cause, having its root in the question of territory. Various species are flown at, attacked, and pursued; Hedge Sparrows, Sedge-, Reed- and Garden-Warblers, Whitethroats and Chiff-Chaffs all run the risk of a small encounter when they enter the domain of a male; and if we are to judge by attitude he is not always irritated in a similar degree by such intrusions, for sometimes he neither raises his feathers nor spreads his tail. Perhaps it would be more correct to say that the presence of a bird of another species seldom brings about that extreme irritation which results in attitudes bearing only one interpretation, but that the intrusion of a neighbouring male of his own kin frequently does so. This objection to the presence of another male in his territory can be witnessed not only when a female is present, but even before her arrival. At the same time it is more in evidence in its active form and more intense when she is present. Nor is it unnatural that this should be so, for sexual emotion has then reached its maximum development, creating a high degree of irritability which would be reflected in and would increase the intensity of every motor reaction, no matter what the stimulus. The attitudes which result follow similar lines to those of the majority of other species, but they are decidedly more intense than those of the Reed Warbler. To describe instances of extreme excitement: a male enters the territory of his neighbour; the owner, a little distance away, threatens, scolds, opens his wings and then flies towards him, upon which he beats a retreat. Or a male, espying an intruder, flies towards him, and settling a few feet away raises the feathers on his

MALE MARSH WARBLER
ATTITUDE ASSUMED DURING SEXUAL ACTIVITY
OR WHEN ANGRY AT THE PRESENCE
OF AN INTRUDER

PUBLISHED BY R H PORTER

SWAN ELLIOTT HOLLOWAY & Co

back and head, spreads and jerks his tail, singing excitedly whilst doing so, whereupon the intruder usually retires and the commotion ceases. I have seen a male on the approach of a Sedge Warbler spread out his wings and tail in a similar manner. In many cases in which a male intrudes upon a neighbouring territory, the owner, flying to the same tree, settles beside him, but does nothing further in the way of active expostulation; yet this seems to have the desired effect, for the intruder as a rule retires and the object of the owner is thereby achieved. It must not be forgotten that the retreat of the intruder is all that is required. And that this should often be accomplished without recourse to battle is an advantage to the species as a whole. Two males with territories adjoining may be equal in strength; they may have been compelled to fight earlier in the season when challenged by other claimants to respective positions, or they may not have had to face a rival. Supposing, however, that they are of equal strength and both equally fitted to reproduce, what effect could incessant and severe struggles have other than a harmful one? Energy would thereby be wasted, and no inconsiderable strain imposed upon the physical strength of the birds just at the moment when a greater strain was being placed upon their nerve force, and this could scarcely fail to reflect itself upon the strength of the offspring. He, therefore, who makes a study of some particular species, and watches the behaviour of males with adjoining territories, expecting to see constant and earnest struggles, expecting, whenever the males approach one another closely, to hear and see unmistakable signs of conflict, expecting even to witness with but little difficulty a vanquished male succumb to its injuries, will certainly be disappointed, and he will do well to bear in mind this fact, that, for the welfare of the species, conflicts could easily become too frequent and could even be carried too far, if Nature had not ordained otherwise.

What with one species and another there is thus frequent commotion. The excitement, as mentioned, takes the form of

a raising of feathers, a spreading and jerking of the tail, an extension of the wings, and excited singing. This latter phase is by no means infrequent, the song at such a time being just as beautiful as under ordinary conditions, though clearly the expression of an entirely different emotion. One such commotion I will now describe, although the cause was shrouded in mystery owing to the density of the foliage and vegetation, coupled with a scarcity of light, and it must remain but an incident until fortune again favours and enables me to witness another of a similar kind. It happened in Texel, in one of the numerous osier beds that are dotted about the island. Listening at daybreak to the song of a male in a small osier bed my ear occasionally caught, coming from afar, the unmistakable notes of other males. These sounds I located in a larger plantation, but as it was then past 4 a.m. I determined to visit the place at daylight the following morning. This I did, and on arriving at about 2.30 a.m., heard violently excited singing proceeding from the throat of more than one male. At first there appeared to be three birds, but ultimately I came to the conclusion that there were only two. Making my way amongst the bushes I approached to within a few yards of first one and then the other, and found each one restlessly moving about within a small area. They fearlessly perched on the branches a few feet above my head, and by looking upward I could see the outline of their forms against the sky and make out their attitudes, which represented intense emotion of some kind. Their vocal productions were remarkable and defy description; it seemed as if their whole strength was concentrated upon the effort to produce the sounds. One listened to the true song of the species, then to perfect imitations of first one species, then another, and one saw, whilst the song was being produced, the wings partially expanded and jerked upwards, or even waved with a slow motion up and down. Both males were often within a short distance of one another, and fighting there may have been at times, but the density of the foliage and scarcity of light

prevented my following their movements. As the light increased the excitement dwindled, and both birds gradually lapsed into silence. I then made a search for a female, but without success. That the one male possessed a territory, and made his headquarters in a tall alder tree I proved to my own satisfaction, but on the following morning one male only was singing, there being no trace of the second, and the excitement of the first one was by no means so intense as on the previous day. Owing to this episode occurring at the end of a brief stay in the island, I was unable to complete the record of the sexual life of the two males, and in the absence of such a record it will be well, perhaps, to refrain from further speculation. One point, however, may be mentioned in connection therewith. The plantation was only a short distance away from another of a similar kind in which there were also two occupied territories. The owner of one of these was paired, the nest built, and two eggs laid, but the other male is the one which calls for attention. He had been in the territory a week at least, but not continuously, sometimes he was there, sometimes undoubtedly absent; but his presence always seemed to be a source of irritation to the other male, and generally terminated in a conflict. After one such encounter I noticed that he deserted his territory altogether for a time. Now the ground that he occupied did not appear to be altogether suitable for breeding purposes. It embraced a corner only of the plantation, and that corner was covered for the most part with tall trees, beneath which there was little in the way of dense vegetation, small bushes, or withies, in which a nest could be suitably placed. It is possible, therefore, that this bird was the second male referred to as being in the aforesaid plantation, and that being in an unsettled condition on account of not possessing a suitable territory, he was roaming backwards and forwards between the two plantations. An instance of a similar kind has recently come under my notice in the case of another species, the male apparently possessing two territories, in each of which he spent part of his time.

We shall probably be safe in assuming that the first females arrive very shortly after the first males. And an important point to be noticed with regard to the period of sexual activity is that the emotion displayed is far more intense than that which corresponds to it in the life of the Reed Warbler. This emotion results in motor reactions, which appear to be considerably different from those of the latter species, but, nevertheless, the difference is one of degree only. It must further be noticed that the presence of the male may evoke in the female a similarly intense sexual emotion, which will result in motor reactions bearing some resemblance to those of the male. Upon the arrival of a female the male still makes use of his headquarters, though perhaps in a lesser degree. Whenever able to tear himself away from following in her wake, he returns to his special tree—the favoured haunt of his bachelor life—and there sings or preens his feathers. As a rule it is the male that follows the female rather than the reverse. One catches glimpses of her as she passes, close to the ground, through the bushes, reeds, willows, or dense vegetation, and of him in close attendance. Then for a time they disappear from view, and there are long periods of silence, relieved only by an occasional spasmodic outburst of song. The male will then, perhaps, return to his headquarters, and, after singing there for a time, go again in search of her. Upon discovering her there may be some excitement, momentarily they seem to fly at one another, the male uttering a short warble during the performance. This flying at one another may be better described as a dance in mid-air, and is pretty to watch. Sometimes he will sing as he flies in her direction, and often, instead of the usually more or less rapid flight, makes use of a slower flapping flight. During the outbursts of song, which occasionally he seems unable to resist, he shows whilst following her signs of evident excitement, jerking his wings or even raising them considerably. In the latter case the movement is altogether slower and not in the nature

of a jerk. On these occasions the song may gradually become more and more feeble until it develops into a quiet warble, audible only a few yards away and much like that of the Blackcap. Both sexes make use of a quiet note which is evidently a call, as it is used constantly by one or the other as they wander in search of food during periods of quiescence. The male has yet another method of expressing his emotion, which is peculiar and verges on the ludicrous. It generally occurs after he has been absent from the female for a time. Flying rapidly towards her and settling beside her, he concentrates all his efforts in violently producing a few bars of his song, and whilst doing so sways his body from side to side with his feathers tightly compressed, his bill pointing upward and widely opened, and his neck considerably stretched. A great part—perhaps the greater part—of the time which the male and female spend in close companionship is a tranquil one. It must not be supposed that the whole of the period of sexual activity, or even that the first few days of that period, is one of constant excitement. So far is this from being the case that if it were possible to estimate correctly the aggregate time during which emotional behaviour dominated the situation, it would be found to form but a very small part of the routine of their daily life. The outbursts of emotion are short, spasmodic, and irregular in occurrence, rather than constant or even prolonged; and it is difficult to say in which sex they are first aroused. Much, if not all, depends, I believe, upon the female in such matters. She is, so to speak, the medium by which Nature prevents a too liberal yielding to the sexual impulse; not, however, through the instrumentality of coyness, as suggested by Professor Groos, but rather by the aid of some physiological disposition which controls the sexual emotion. One sees the male approach the female in a manner which makes his intentions clear, and one sees her face him with lowered head and feathers erected, an attitude which makes her intention equally clear. One sees her, on the other hand,

fluttering her wings rapidly, raising her tail, and continuing thus for some seconds, an attitude indicative in many species of a desire for coition. Her sexual emotion is expressed in another but more peculiar form. This is an alternate stretching of the wings, and although the degree of expansion is only slight yet the movement is sufficiently conspicuous, and is slowly executed. I have seen her when under the influence of excitement behave still differently, but the direct stimulus was not clear, and therefore it is impossible even to suggest what the emotion may have been. That she was labouring under the influence of some considerable emotion was evident, for she spread her tail and waved her wings slightly, an attitude similar to that affected by the male. Now all these various ways by which the sexual emotion of both sexes is betrayed are not confined to one day, or a few days, after the arrival of a female; they are not, that is to say, antecedent only to conjugation, but occur throughout the whole of the period of sexual activity. At the risk of repeating myself I will again define what is meant by this period. It comprises the whole of that time between the arrival of a female in a given territory and the laying of the full complement of eggs. Where a second brood is produced, either from natural causes or as the result of the first brood being destroyed, there is a recurrence of this activity, and, consequently, of emotional behaviour. But this need not be considered here, since it is a repetition only of that which occurs during the first period. The activities referred to are in evidence throughout the whole of the period, but their intensity becomes gradually less and less marked. The song is neither uttered so frequently nor so violently, the periods of silence become longer, the flying at the female by the male occurs less frequently, and ultimately the excitement in a great measure disappears. The gradual diminution in the song during this period is interesting. I recollect one instance in which it almost ceased upon the arrival of a female, and this case is not without a parallel

FEMALE MARSH WARBLER

EXPANDING ITS WINGS ALTERNATELY

DURING SEXUAL ACTIVITY

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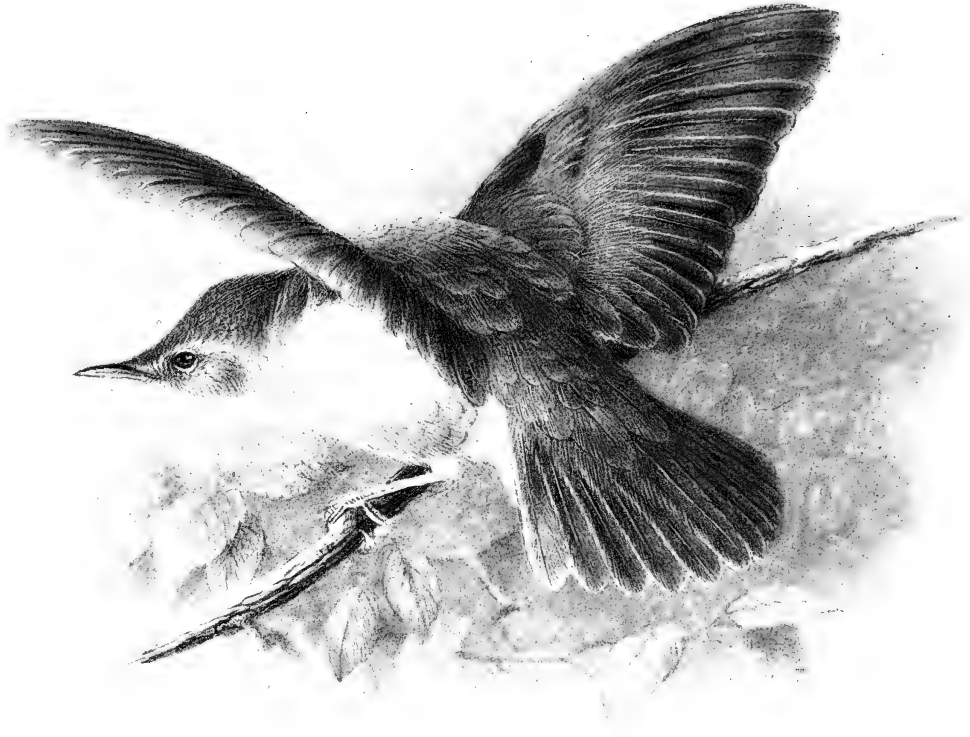
in the lives of other species. What place are we to assign to song in the sexual process? In the life of the Willow Warbler I suggested that it might be of some use in connection with the territory, and the means whereby the females are made aware of the presence of males fit to reproduce. But supposing we say that song has a meaning in relation to something in the sexual environment of the female; supposing, that is to say, that her instinctive sexual response will only follow a certain presentation—a necessary part of which is formed by the song—how shall we explain this marked diminution of the song before coition has taken place, and before therefore the utility we postulate can possibly have come into play? Even the gradual slackening of the song is, in accordance with this view, not altogether easy to understand; for may it not be argued that a waning sexual instinct would require an even more vigorous presentation to arouse the necessary response, and that as the period of sexual activity progressed so the intensity of the song ought to increase rather than diminish? And yet the converse may be said to be possible, namely, that a response once aroused would be more readily awakened on subsequent occasions.

There is a point with regard to the sexual behaviour which deserves mention. I became acquainted with this species in Holland before I had an opportunity of doing so in this country, and I was there impressed with the attitudes the males habitually assumed, with, in fact, the intensity displayed in overt expressional movement. Of these attitudes the most striking was that one in which the wings were rapidly raised above the back and as rapidly closed, and has already been referred to. I therefore expected to find that the attitudes assumed by the males in this country would be similar to those already observed, but this expectation has not altogether been fulfilled. How far failure has been due to insufficient observation is difficult to say, but the way is clearly open to error, since we can never be quite sure that the conditions under which we observe different individuals entirely

correspond. Each year we are learning more about geographical races; we find slight differences in structure and colour where previously none were supposed to exist, and these peculiarities seem to be common to all the individuals of a species inhabiting a certain area. We also find peculiarities in the song of the same species in different districts. And if there are differences in structure, colour, and song, why not in the nervous system? It is generally, and probably rightly, supposed that the instincts of a species are more or less constant throughout the whole of its range. A motor reaction, however, is part of an emotion, and an emotion, though it accompanies an instinct, is a separate manifestation. An instinct is uniform just because it is of vital importance to the species as a whole and therefore subject to a rigid selection. But it is possible that these reactions may not be of selection value, and consequently subject to a greater variation than we imagine.

Before finally leaving this interesting phase of the bird's behaviour, we will analyse a little more closely the relation of attitude and vocal extravagance to emotion. This is a somewhat difficult undertaking, involving as it does the dangerous proceeding of attempting to put oneself in the place of the bird. Nevertheless it is important that we should attempt, as far as possible, to separate these activities, to trace out the emotion to which they correspond, and instead of taking a broad view of the behaviour as a whole, make some effort to reduce it to order. We are accustomed to use the term "display" to embrace the whole of the visible signs of the complex emotional system of a bird, and if there are facts which seem to be outside its province we find for them a ready explanation under the heading of "play"—practice, that is to say, for the more serious side of life. But we can scarcely make use of so loose a definition as "display" if we desire to resolve this emotional behaviour into its constituent parts. Let us take the song first, and for this purpose it is only necessary to consider it in its more emotional aspect. Violent



FEMALE MARSH WARBLER

ATTITUDE ASSUMED DURING THE PERIOD

OF SEXUAL ACTIVITY

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singing may occur when the male settles beside his mate and sways his body from side to side, or when with ruffled feathers he flies towards an intruding male. Now it is manifest that the stimulus which evokes these feelings is very different in these two cases. In the former it is the presence of a female, in the latter the presence of a male. May we not therefore infer that the feelings themselves are different in origin? In the former case it is not altogether clear what the emotion is which is set free. That the presence of the mate is desired is evident, and this could not well be associated with feelings otherwise than of pleasure; consequently we cannot be far wrong in assuming that the emotion is sexual in origin. In the latter case we see our way more plainly; for correlated with the vocal effort is a certain ruffling of feathers and spreading of the tail which we know to be often the prelude to a skirmish, and, arguing from our own standpoint, the emotion must be akin to anger and probably corresponds to the instinct of pugnacity. In the former case the feelings are evoked by a desire for the presence of a mate, in the latter by a desire for the absence of a male. A contrast is thus presented; yet the reactions are similar. The relation of attitude to emotion runs on parallel lines, but here the emotion is not quite so easy to diagnose. The peculiar jerking of the wings which is correlated with excited singing first deserves attention. It occurs when two males are in proximity to one another. The stimulus to the emotional behaviour is clearly the presence of the other male, but what the specific emotion is which is thus aroused we can never know by direct observation, and consequently must rely upon induction. The presence of an intruding male is generally a cause of suspicion to the owner of a territory; such presence is not desired, causes irritation, and must therefore call forth an emotion of a corresponding type. But the jerking of the wings may also occur when the male is seized with a sudden passion after conjugation has taken place. No intruding male is then at hand to cause irritation, but the female is only a few yards

away and she must be the stimulus unless the emotion is spontaneous, arising, we know not how, from the sexual condition of the male. In either case the feelings which prompt the bird to action can scarcely be those of displeasure, and we have indisputable evidence that the movement of the wings *can* be associated with a pleasurable emotion, since the female flutters them at a moment when her desires are perfectly clear. So that here again there appears to be a similarity of response under the influence of a dissimilar emotion. The presence of another male or of an individual of another species may cause a general relaxing of the feathers and a spreading of wings on the part of the male, and this attitude sometimes appears to be the prelude to an attack, but the emotion, whatever it may be, disappears upon the retreat of the intruder. Why should the presence of an individual of another species influence the behaviour of the male? We shall find this question difficult to answer. The passing of a stranger through his territory may possibly evoke different emotions at different times and yet produce similar motor reactions. This is just the difficulty. There is the playful tendency, so common in the higher animals, which might be readily awakened by a harmless intruder of another species. On the other hand, the question of territory may here also dominate the situation and the intrusion may be genuinely resented. Who can say with any degree of certainty in which direction we are to look for the real factor? And with this first step undetermined, what useful purpose can be served by attempting to locate the true emotion? Attention may nevertheless be called to this one point; the attitudes affected by the male upon the intrusion of an individual of another species are similar in all respects to those caused by resentment at the approach of another male of the same species.

In one instance that came under my notice a male Sedge Warbler took possession of the same territory as a Marsh Warbler; and, further, made use of the same willow tree as his headquarters. This tree was situated only a few yards

away from the nest of the latter bird. As usually happens, the Sedge Warbler was most pugnacious and resented the presence of other species, especially in the one particular tree. The burden of his anger generally fell upon the Marsh Warblers, and no discrimination was made between the sexes, both male and female being frequently attacked and pursued. The Marsh Warbler as a species is not of a very peaceable disposition, and the result of this was that for some days at least that particular corner of the osier bed was in constant commotion. The Sedge Warbler was undoubtedly more often the aggressor, pursuing his opponents this way and that in the territory, and judging by their frequent retreats the Marsh Warblers must have been afraid of him. Yet at times one or the other, or perhaps both, made some show of resistance. Most of the skirmishing occurred in the special willow, and in fact seemed to originate in the Sedge Warbler's jealousy of that particular tree. Occasionally the quarrel ended in the refusal of the Marsh Warbler to retire from his headquarters, for spreading his tail he would scold vigorously at his opponents only a few feet away. Even after he had obtained a female the Sedge Warbler still maintained his pugnacious attitude, though perhaps in a lesser degree.

The period of sexual activity no doubt varies in the case of different individual pairs according to the early or late arrival of the female, and possibly according to her physical condition. I have not had opportunities of studying a sufficient number of pairs to make a correct estimate of the average duration of this period possible, but according to my experience hitherto it would seem to be approximately eight days. Still more difficult is it to state with any degree of accuracy how long after her arrival the female actually commences to construct her nest, but in some cases a commencement is made on the following day. In attempting, however, to estimate either of these periods one might easily be deceived. The female is at all times more skulking in her habits than the male. She creeps amongst the dense vegeta-

tion or thick foliage, and therefore might readily escape detection. In fact it is necessary to rely to some extent on the behaviour of the male in order to assure oneself of her presence, so that to observe her plucking the first piece of decayed vegetation with which to form the foundation of her nest is no easy matter. The male takes but a small part in the actual construction of the nest, his behaviour being in this respect similar to that of the male Reed Warbler, who labours but little to obtain the necessary material and weave it into the nest. But although he seems unwilling to share this work with his mate, yet he takes great pains to follow her closely, whenever she is engaged in searching for material or in deciding the actual position the nest is to occupy. In thus accompanying her closely when at work he resembles not only the male Reed Warbler but the males of other species also; and this habit of keeping a close attendance upon the female, of following her from tree to tree and bush to bush, desirous apparently of being a spectator of all her work and acquainted with all her movements, must be sexual in origin. After the nest has been built and laying has commenced the peculiarity is not so striking; true it is that he can often be seen beside her, but the craving for her companionship does not seem to be then so pronounced. His actual conduct during these few days gives us some insight into the true meaning of this close companionship, for we can frequently witness those playful contests which we know to be characteristic of sexual activity. The responsibility for these contests does not always rest with the male, but there is no doubt that we can more often mark their beginnings in him, although at times they seem to be almost mutual. One sees on such occasion a spreading and raising of wings on the part of one of the sexes, followed by a flying together and a touching of bills, accompanied by an uttering of the call note or a few phrases of the song. Of the two the male is more frequently the one that quivers his wings, and on his approach the female is sometimes accustomed to spread her tail and

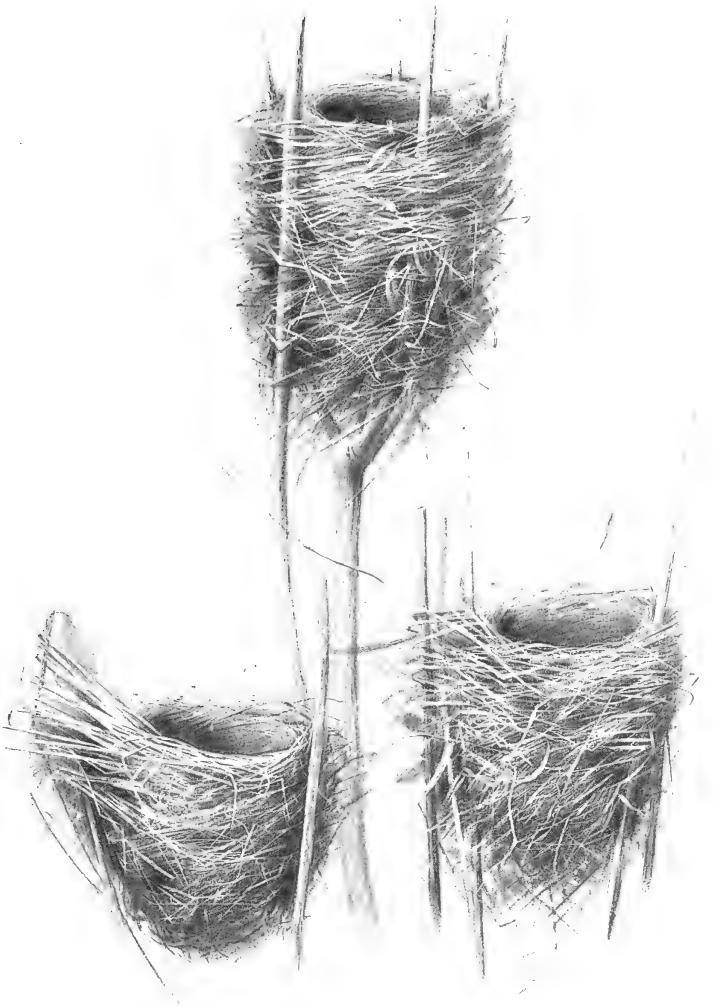
fluff out the feathers both on her breast and flanks. All these antics are the special accompaniments of the sexual instinct, and we can well imagine that it would be during this short period—that is to say, previous to the actual discharge of the sexual function—that the instinct would reach its maximum development. Nor is it unreasonable to suppose that after each discharge there should be a lessening in the intensity of the instinct accompanied by a decrease of the motor reactions; observation at least seems to show that this really is the case.

Whether the female first selects a position for her nest and then goes in search of material is difficult to determine, but judging by her behaviour this does not appear to be her method of procedure. For this is what occurs: she tears off dead material of some kind, and flies from place to place holding it in her bill. Making her way into some thicket, she reappears, having left therein the material she was carrying. For a time she is then lost to view, but presently comes again into sight in the same vicinity carrying a further supply of dead grass. This time, however, she wanders about in uncertainty, and finally deposits it in an entirely different situation, albeit only a few yards away. This spirit of uncertainty ultimately deserts her; a position is found suitable to her requirements, and forthwith she sets about her task in earnest, going repeatedly in search of material, and upon returning therewith fixing it rapidly; thus the nest gradually begins to assume some shape. Regarding the psychology of the bird's behaviour it is perhaps wise to say but little. Is the whole situation a conscious one, and, if so, how far conscious? Does the bird, that is to say, reflect upon the possibilities of this position or of that, ultimately come to a decision, and forthwith commence to build? Or is the mental process an altogether more simple affair, congenital rather than individual, having its origin in some internal impulse called forth by the sight of the requisite situation? Personally I am inclined to the latter view. It is true that in

the fact of the bird flying from place to place, and even making initial attempts at construction, we seem to be presented with evidence of conscious deliberation. Hence some may affirm that she carries in her imagination a mental image of the nest she is about to construct, and thus decides in advance as to the relative merits of the various situations. But a young bird is capable of constructing a nest antecedent to experience, and manifestly has no mental image before it, and cannot well make use therefore of any such complicated process of reasoning. Is it then necessary to demand such a power for the adults?

The nest is placed in various situations—in perpendicular osiers, amongst common nettles (*Urtica dioica*), cow parsnip (*Heracleum sphondylium*), meadow-sweet (*Spiræa ulmaria*), wormwood (*Artemisia absinthium*), dogwood (*Cornus sanguinea*), tall grass, and not infrequently in young ash plants. In giving the results of his long experience with these birds in Oxfordshire, Mr. Warde Fowler writes as follows: [1] "But here I may remark that it is not every kind of osier willow that suits our bird; I have never found the nest in any but the *Salix triandra*, which sends up pliant perpendicular shoots quite close to each other. The other osier to be found in all withy beds (*S. viminalis*) is in every way less suitable. If the osiers in the favourite breeding place have been cut, and the season is late, the birds will be in serious difficulties, and will search for suitable sites in hedges and ditches, and have recourse to nettles, wild parsnip, or even beans, as we have seen. Here, of course, they run far greater risks than in the dense vegetation of the osier-bed, where I have hardly ever known a nest destroyed or even discovered by the ploughboys who are constantly about the spot. The difficulties met with by my birds during the last few years lead me strongly to believe, apart from other evidence, that the Marsh Warbler is not, and cannot be, a more abundant bird than we

[1] *Zoologist*, vol. x, p 406.



NESTS OF THE MARSH WARBLER

SHOWING VARIATION IN STRUCTURE

PHOTOGRAVED BY E. H. PORTER SWAN ELECTRIC ENGRAVING CO.

commonly think. What it really loves best, and rarely finds in England except in some parts of Somersetshire and Cambridgeshire, where it first attracted notice, is a large space of flat alluvial ground, with convenient bits of cover, such as thick bunches of tall plants scattered here and there." My experience does not altogether bear out the foregoing statement, for it shows that the species not only can but does adapt itself to a variety of situations. Perpendicular shoots of osiers or indeed of any plant are not a necessity. In Texel the bird is plentiful enough in the well grown plantations, and in this country it often nests in similar situations. Instead of being confined in a great measure to reed beds, like the Reed Warbler, it is capable of inhabiting varied situations, such as are afforded in abundance by many counties in England. No reason for its comparative scarcity can therefore be assigned to any lack of power of adaptation.

For reasons which I shall presently give, the actual dimensions of the nest and the methods employed in securing it to the supports require detailed description. The nest is circular in shape, tapering downwards almost to a point. The full diameter varies from 3″ to $4\frac{1}{4}$″ in one case up to from 4″ to 5″ in another; the interior diameter is less variable, being approximately 2″. The outside depth again varies considerably, for whereas one example will measure $3\frac{1}{4}$″ another will be fully $4\frac{3}{4}$″. The same is true of the depth of the interior, which varies from $1\frac{1}{2}$″ to $1\frac{7}{8}$″ in one case up to 2″ or $2\frac{1}{2}$″ in another. The walls of the nest may be from $\frac{1}{2}$″ to 1″ full in thickness. The nest is composed of dead grasses of various thickness, and various descriptions, and there may or may not be a lining of hair, fine roots, or even an admixture of both. Unlike that of the Reed Warbler, its appearance is untidy, an untidiness due no doubt to the material used, for the Reed Warbler makes use of the seed heads of the common reed, which cannot fail to give the nest a neater appearance. In the case of both species the quality of the workmanship is on the whole very similar, as is also the method adopted

in securing the nest to the supports. At the same time this method in the case of the Marsh Warbler is subject to a variation which is referred to by Mr. Warde Fowler as basket-handles, the nest having thereby the appearance of being slung from the supports, since the dead grass which actually forms the sling is slightly above the top of the nest; but it is by no means always adopted. The nest is frequently placed in a fork from which rise four or five perpendicular stems, and although it would clearly be secure without any actual attachment to the stems, yet the bird takes infinite pains to weave the grass round the supports after the manner adopted by the Reed Warbler. Now some of these special features in the construction of the nest are of considerable importance when we bear in mind the nature of the environment and the peculiarly close relationship of the bird to the Reed Warbler. In my description of the latter species I gave my reasons for believing that the depth of the nest was a factor of no small importance for the welfare of the species, since thereby the young—not the eggs as is sometimes suggested—were prevented from being precipitated into the water. I further stated my ground for the belief that we need have no hesitation in attributing the development of this peculiarity to natural selection, nor in regarding the regularity in this type of structure as the outcome of the same principle. As to whether the depth is to ensure the safety of the young or of the eggs opinions may differ, but no one can well dispute the fact that one or the other must be the cause of the development, and for our present purpose that is sufficient.

What then does an examination of the nests of the Marsh Warbler reveal? It reveals all the peculiarities of those of the Reed Warbler—complete adaptations to a special environment—but with this difference that the constancy of type has been replaced by variation, the adaptive characteristics of the structure being in a condition of instability. But when we here speak of the adaptive characteristics, we manifestly make use of a wrong term, since they are not adapted to the

present environment of the Marsh Warbler. It may be remembered that the Reed Warbler's nest is usually built on from three to seven stems of the common reed; there is no support for it beyond that which is supplied by the architecture of the bird, and we consequently find it bound securely to the reeds, the material being woven round the stems and intertwined into the nest. If it were not thus secured it is evident that disaster would befall the offspring; and so natural selection has eliminated the careless worker, with the result that a definite type of structure has been evolved. The swaying of the reeds is the indirect cause of the depth, but there is no excessive swaying to be found in the situations chosen by the Marsh Warbler. Young withies are pliant, but do not bend before the wind like a hollow reed, and what could offer greater security from this danger than dense vegetation or young ash plants? We have then to ask whether it is possible to conceive of any useful purpose being served by these corresponding features in the nest of the Marsh Warbler; and we can satisfy ourselves that nothing is to be gained either by an excessive depth or by a careful attachment to upright supports, since the present environment calls for none of these factors to ensure the safety of the offspring; and surely something in the nature of proof of their inutility is to be found in the fact that they are constant when the nest is situated in reeds, but subject to remarkable variation when recourse is had to a situation of a different kind. If some particular character has been developed by selection owing to its having served some useful purpose in relation to the environment, and if upon new conditions arising the selective agency is withdrawn, the stability of that character will be replaced by fluctuating variability and gradually fade away during the process of modification to suit the new conditions. Bearing this in mind, what traces of the former nesting instinct should we expect to find, if the Marsh Warbler had at some earlier period resorted to reed beds for the purpose of procreation,

but had, for reasons unknown to us, recently adapted itself to its present environment? The answer to this must be that we should anticipate those conditions of instability which are so clearly revealed to us; instability, that is to say, in just those particular features which were of adaptive value under the former conditions of existence. Since no useful purpose is any longer served in the excessive depth of the nest and in the method of weaving it to the upright supports the selective agency has been withdrawn, and we consequently find nests varying considerably in depth, and varying, too, in a remarkable degree in the manner whereby they are secured. We find them, on the one hand, placed in a fork and tightly woven to the upright supports, and, on the other, flimsily slung by slender basket handles. And just as the former type is unnecessarily secure, so the latter—one might almost say—is foolishly insecure. In one instance I watched with growing anxiety a nest that daily became more tilted owing to the grass that formed the handles becoming stretched. Disaster however in this case overtook it from another source. The method of attachment of which we are now speaking is in reality similar to that adopted by the Reed Warbler and some individuals of this species, though when first seen it appears to be very different. The situation in a great measure determines the type. If the bird builds in a dense thicket of dogwood, where there is a difficulty in finding three or more shoots close together, it has to make the best of the position. The weaving instinct being strong within it, it threads the grass round the nearest supports, which instead of being upright are often bent, and the result is the flimsy handles referred to. When a nest rests on no solid foundation and is dependent solely on the supports from which it is slung, it is possible, especially in wet weather, that the weight of the bird brooding her well-grown young will aggravate the weakness and thus bring about a catastrophe. This appeared to be taking place in the case referred to. It seems then as if a stronger structure than

this will have to be generally evolved in the future, though perhaps not so needlessly strong as is sometimes the case even now. One other feature with regard to the nest deserves mention, and this is the depth of the foundation. Every nest is by no means alike in this respect; for whereas in one case the foundation may be of the normal depth, in another there may be a solid platform of dead grass measuring between two and three inches. So that here again the variation is considerable, and it is difficult to see what useful purpose can be served by the increased labour that is sometimes bestowed upon it.

From four to five eggs appear to be the normal clutch of the species. On the average one egg is laid every twenty-four hours, either during the night or the early hours of the morning. Incubation lasts about twelve days and during this period the excitement of the male becomes appreciably less. He nevertheless shows signs of irritation when his territory is intruded upon by another male of his own or another species, and displays it in the manner already described. His song decreases gradually in strength, being confined in a great measure to the early hours of the morning, and even then it can scarcely be compared to its former glory. Both sexes share in the duties of incubation, and they often relieve one another approximately every half-hour. While one of them is engaged in incubating, the other occupies its time in searching for food, preening its feathers, or pursuing an intruder. The changing of places is done stealthily. The relieving bird does not fly directly to the nest, but approaches it slowly by hopping from stem to stem through the dense undergrowth, so that one is oftentimes made aware of the change solely by the shaking of the various plants as the bird travels amongst them. The one that is being relieved slips off the nest quietly and disappears, leaving scarcely any trace of its departure. How far they are aware of one's presence and how far their conduct is affected thereby is difficult to say, but they are decidedly more timid than the Reed Warbler under similar

circumstances, and this shyness continues throughout the whole period of reproduction. If I cut away the undergrowth and make a clear opening so as to be able to observe them at the nest, I find that they have difficulty in overcoming their natural timidity. Only when one stands some distance away can they be persuaded to approach the nest, and this distance requires to be much greater than is necessary in the case of the Reed Warbler. During incubation it is impossible to be too careful in taking up one's position, and even when a post from which observations can be taken has been successfully reached, it is essential that little or no movement should be made if suspicion is not to be aroused. I am inclined to doubt whether the birds really become reconciled to the human presence after the young are hatched, for it will be noticed that they then carry out their duties hurriedly, over anxious apparently to finish the task they have in hand. One of the sexes is more timid than the other, though it is difficult to determine which, but since in the case of the Reed Warbler it is the male that is the more nervous, it is probably the male that lacks courage in this species; all this timidity tends to show that the temperament of the bird is different from that of the Reed Warbler, and it is interesting to note that the greater timidity seems to be correlated with a greater nervous development in other directions. It may here be mentioned that the male, when approaching the nest in order to relieve his mate, sometimes utters a few phrases of his song, and also that the presence of a Red-backed Shrike (*Lanius collurio*) near the nest seems to cause him much anxiety, which he shows by moving restlessly to and fro and vigorously uttering his scolding note so long as it remains in the vicinity.

There is considerable variation in the length of time that the young of different pairs remain in the nest. Development appears to be more rapid in one case than in another. One nest will be deserted at the end of ten days, whereas another will still be a nursery at the end of fourteen. Ten days is

approximately the time the young Reed Warblers remain in the nest, and it is difficult to understand why, in the case of this species, the period should be increased in certain instances by three days. Climate may be connected with this variation, for development would probably be more rapid when the temperature was high and food consequently abundant. But it is well to remark that in one instance which came under my notice the young occupied the nest for close upon fourteen days, and during that period the conditions were exceptionally favourable for rapid development, insect life being abundant and the temperature abnormally high. In order to get at the truth of this variation a large number of separate pairs require to be observed

Both sexes share in the task of tending the offspring, but one of them, as already observed, is more timid than the other, and it is therefore not altogether easy to determine just how the labour is divided; whether, that is to say, the male not only brings food and cleans the nest, but also takes his part in brooding the young. The task of brooding is performed largely, if not wholly, by the parent that is the less shy; this can clearly be seen. And since it is probable, from our knowledge of other species, that the female would naturally be more anxious to carry out this task, it is probably she who, as previously hinted at, is the less timid throughout. Yet even she is decidedly more nervous than the female Reed Warbler, for arriving at the nest with food she will remain for a long time close to, or actually upon the side of it, unable to make the final effort to deliver the food she is carrying. One or two of the young, occasionally three, are fed by one parent at a time. Their usual custom, however, is to feed two and remove the *fæces* from one. In the earlier stages of their growth, the young are not fed so frequently, brooding being then more important. But these conditions gradually become reversed, until the time of both parents is largely occupied in securing the necessary food. The interval between

the departure of a parent from the nest and its arrival with a fresh supply of insects varies considerably. Sometimes it appears to be in no great hurry and may not return for twenty minutes or more, whilst at other times it seems to be equally anxious that there should be no delay, and consequently returns in from five to six minutes. The parents as a rule approach the nest separately, but occasionally they arrive together, and when this occurs the same offspring may be fed by both of them. Defæcation usually ensues a few moments after the young one has been fed, and the parent waits for this to happen, and then carries the *fæces* away or swallows them. The routine of feeding is very similar to that which occurs in the case of the Reed Warbler; the bird, that is to say, which is the more hungry, is the more vigorous in stretching out its neck, and the more liable consequently to receive food. We can therefore explain the behaviour of the parents at the nest without imputing to them any intelligent control. There still remains, however, one point in connection with the care of the offspring, which, though appearing to be purposeful, may nevertheless be one of those beautiful adjustments of Nature, the development of which can be referred to selection. It is this: defæcation usually ensues after food has been supplied by the parent, who then carries the *fæces* away and thus prevents the contamination of the nest. Now it often happens that the parent divides each supply of food that it brings between two of the young, and no doubt economy is thus effected in the time and energy which it is compelled to devote to securing the necessary food. But it is clear that if both the young were to eject the *fæces* forthwith the parent could not conveniently remove them and Nature's object would not thereby be attained. If, however, the methods adopted by the parents be closely observed, it will be noticed that the various insects are not divided equally between the two offspring, but that one receives a larger proportion than the other. It may well therefore be that there is some relation between the method thus adopted and the ejection of the

fæces. A certain quantity of food may be necessary to set the machinery at work, to stimulate, that is to say, the nerves which control defæcation; and this quantity may only be supplied to the first of the two offspring, and the second, though partially satisfied, may neither receive sufficient to bring about a similar result, nor to allay the hunger to such an extent as would make it incapable of the necessary effort to obtain the major share at the next opportunity. The whole system has probably been built up to bring about a certain definite result, and that result is the cleanliness of the nest. I have already called attention to the importance of cleanliness in this respect, and have pointed out that young birds could scarcely thrive in an insanitary nest. The perfection of the system can be better understood if we imagine the present regular method abolished. The young would then be fed accidentally, defæcation would occur at no specified time, the *fæces* would be overlooked, and the nest consequently contaminated. Perfect as the system is, even now it does not always ensure complete cleanliness, for the *fæces* are occasionally allowed to remain in the nest. Experiments made with leaves placed in the nest bring about results very similar to those already referred to in the life of the Reed Warbler. A leaf is picked up by the parent and held for a few moments; it is then dropped, but again picked up and perhaps carried away or again dropped. Even when the *fæces* are there awaiting removal a leaf may be carried away in place of them. However, it is well to state that considerable hesitation is displayed in their attitude towards such an obstruction; no doubt the interruption of the instinctive procedure is sufficient to account for their bewilderment.

The young are completely naked at birth, no down being visible, and the eyelids are sealed. For the first two days or so no very great change in their growth is perceptible, but on the third day the primaries become visible. Between the third and fourth days a considerable change takes place, the feathers sprouting on all the tracts, and the primaries being

about ¼″ in length. A day later the feathers are bursting and show the brown colour, the primaries being then about ⅓″ in length; and a faint high-pitched note is uttered on the approach of the parents with food. The sixth day shows but little alteration in their appearance, but by the seventh day they become more restless, peck here and there, constantly open their bills, flap their wings, and make efforts to struggle one above the other. On the eighth day they are well feathered. On the ninth day they are very active, frequently preening their feathers, stretching their wings, and uttering their call note. Some will now be found to be stronger than others, and by more active struggling secure the topmost position. Not all of them leave the nest at the same time; the stronger are the first to scramble away amongst the undergrowth and on the ground, aided but little by their wings. At this age they are difficult to find, scattered as they are in the dense vegetation, but in a few days their wings are sufficiently strong to enable them to perch amongst the bushes, and they then sit close to one another on the same branch. Their call note is uttered frequently or even continuously during this period, but it is almost inaudible fifteen yards away. No doubt when defæcation has taken place, and hunger again asserts itself, the uttering of the call note increases and enables the parents to divide their attentions equally amongst their offspring.

The vocal powers of the male are remarkably developed. In the life of the Blackcap I ventured to suggest that it was difficult to conceive of more beautiful notes being uttered than those produced by that species. However, a closer acquaintance with the vocal powers of the Marsh Warbler compels me to modify this statement somewhat. For us the æsthetic value of a song is quite an individual matter, subject to wide divergence of opinion. But for science it matters but little so long as some common ground for agreement can be found regarding that more important consideration, the question of relative development. We ought, that is to say,

to subordinate questions of æsthetic value to an inquiry as to the degree of specialisation attained by any particular song. In fact we must do so. For if we take our own conception of what is beautiful as the criterion of development, and say that the vocal powers of a certain species have reached a higher level of perfection just because the sounds produced appear to us the more pleasing, we manifestly postulate a direct relation between beauty and development, and assume that the bird forms an æsthetic standard analogous to that found in man. Such a method of approaching the subject might quite rightly be called in question. Must we then give up all attempts to interpret the vocal powers of birds in terms of development? Not necessarily. For if we try to conceive of a song apart from æsthetic emotion and the effect in us of association, all that remains upon which we can base our opinion as to its objective nature is the range of notes, the modulation, and the power of imitation displayed. But the imitative faculty is possessed by different species in different degrees; one bird, capable of but small power of song, introduces numerous notes of other species; another, having command of numerous strains covering a wide range, shows little imitation, whilst a third adds to numerous strains of its own an equal number of those of other species. No one would care to affirm that the Parrot or the Starling is a beautiful songster, yet each is capable of reproducing sounds of varying descriptions, and the former bird in confinement is said to imitate correctly songs having a proper musical notation. No one, on the other hand, would care to deny that the Nightingale is a beautiful songster, yet it indulges in but little imitation. So that the question is clearly beset with difficulties when we look at it from the evolutionary standpoint, and no useful purpose can be served by attempting to assign a definite position in a scale of development to this species or to that. We must take a broad view of the vocal powers as a whole, and perhaps we shall not be far wrong in provisionally accepting as the

maximum development the power of producing numerous strains embracing a wide range of notes correlated with a power of imitation, embracing in its turn not only the notes but the phrases of other species. If we are content to do this, we need have no hesitation in placing the Marsh Warbler in the foremost rank; and this is what concerns us more immediately.

No one acquainted with its powers and those of the Reed Warbler could deny that it surpasses the latter both in song and imitation. There is, indeed, but little in common between the true songs of the two species. Instead of the laboured efforts of the Reed Warbler we listen to a flow of song exhibiting a range of notes and modulation approached by few other species; some of the phrases own a peculiar charm—I believe that they could be reproduced only by some kind of stringed instrument—and they possess an additional interest from the fact that they are identical with certain phrases in the song of the Icterine Warbler (*Hypolais icterina*). I recollect on one occasion being puzzled as to the identification of a bird owing to the similarity in the two songs, and was only able to decide to which species the owner of the voice belonged when it fluttered out of the foliage. The imitative faculty of the Marsh Warbler probably surpasses that of any other species found in the British Islands. On various occasions I have listened to imitations of the following: Swallow (*Hirundo rustica*), House-Sparrow (*Passer domesticus*), Hedge-Sparrow (*Accentor modularis*) song and call note, Greenfinch (*Ligurinus chloris*), Chaffinch (*Fringilla cœlebs*), Goldfinch (*Carduelis elegans*), Linnet (*Acanthis cannabina*), Blue Titmouse (*Parus cæruleus*), Great Titmouse (*Parus major*), Blackcap (*Sylvia atricapilla*) alarm note, Nightingale (*Daulias luscinia*), Sedge Warbler (*Acrocephalus phragmitis*), Reed Warbler (*Acrocephalus streperus*), Savi's Warbler (*Locustella luscinioides*), Garden Warbler (*Sylvia hortensis*), Chiff-Chaff (*Phylloscopus rufus*) call note, Willow Warbler (*Phylloscopus trochilus*) song and call note, White-

throat (*Sylvia cinerea*) call note, Pied Wagtail (*Motacilla lugubris*), Blue-headed Wagtail (*Motacilla flava*), Yellow Bunting (*Emberiza citrinella*), Green Woodpecker (*Gecinus viridis*), Oyster-catcher (*Hæmatopus ostralegus*), Black-tailed Godwit (*Limosa belgica*), Common Tern (*Sterna fluviatilis*), Common Redshank (*Totanus calidris*), Lapwing (*Vanellus vulgaris*), Meadow-Pipit (*Anthus pratensis*), Skylark (*Alauda arvensis*), Redstart (*Ruticilla phœnicurus*), Starling (*Sturnus vulgaris*), and Magpie (*Pica rustica*). The imitations are to a large extent copies of sounds produced by the inhabitants of the surrounding district. For instance, the cries of the Black-tailed Godwit, Redshank and Oyster-Catcher are reproduced in Holland where those birds are everywhere abundant. Any cry, call note, or song is liable to be reproduced immediately, if only it is uttered sufficiently close to a male that is singing, or if it happens to be particularly loud or distinct, and as a rule no hesitation is shown by the imitator in incorporating the alien sound with its true song. So easily does the imitation flow from the throat of the bird, and so natural a sequence does it seem to be of the vocal effort, that an observer who had not just heard the sound which was copied might readily regard it as a revival of phrases previously associated. Nevertheless the majority of the imitations are due to revival. This can be proved in two ways. Firstly by the fact that a species is sometimes imitated which does not inhabit the surrounding neighbourhood, as for instance when a male in a midland county reproduces the song of Savi's Warbler, and secondly by noting the sequence of imitative strains. This latter feature requires some further consideration. The question is sometimes asked whether the sequence is always similar in the same individual. I have satisfied myself that it is not. The cries of different species are not reproduced in rotation but are interspersed throughout the song in no definite order. From time to time, whilst listening to different males, I have rapidly written down the species

imitated as far as it lay in my power to distinguish them, and the results plainly show a lack of any definite sequence. Two examples will suffice to illustrate my meaning. In the first case the imitations were produced in the following order: Sparrow, Blackbird, Whitethroat, Sedge Warbler, Sparrow, Whitethroat, Green Woodpecker, Blue Titmouse, Redstart, Blackbird, Whitethroat, Greenfinch, Swallow, Whitethroat, Blackbird, Swallow, Chiff-Chaff, Hedge Sparrow, Blue Titmouse, Swallow, Greenfinch, Sparrow, Greenfinch, Green Woodpecker, Blackbird, Sparrow, Whitethroat, Chaffinch, Starling, Thrush, Hedge Sparrow, Blue Titmouse, Whitethroat, Swallow, Sparrow, Thrush, Whitethroat, Hedge Sparrow, Blue Titmouse, Whitethroat, Greenfinch, Willow Warbler, Thrush, Hedge Sparrow, Green Woodpecker. And in the second as follows: Blue Titmouse, Swallow, Sparrow, Swallow, Blue Titmouse, Greenfinch, Blackbird, Willow Warbler, Sedge Warbler, Chaffinch, Pied Wagtail, Nightingale, Starling, Blue Titmouse, Sparrow, Redstart, Starling, Sedge Warbler, Sparrow, Swallow, Chaffinch, Whitethroat, Swallow, Starling, Greenfinch, Willow Warbler. There is nothing in the nature of a uniform sequence here; the most that can be said is that in certain instances imitations of the same *two* species are to be found in the same sequence. It must not be supposed that the above imitations were produced in a continuous stream unbroken by the true song of the species. Even when the bird *is* in an imitative vein it would, perhaps, be more correct to speak of imitations being intercalated among phrases of the song, than of phrases of the song being intercalated amongst extraneous imitations. Both the males were singing in Worcestershire about 2.30 a.m., and whilst the imitations were being produced the majority of the birds copied uttered no sound within hearing; some would probably not have been astir at that hour of the morning. It is evident, therefore, that there is mental retention and revival of some kind; for it must be borne in mind that it is not only an alien note that

is incorporated with the song, but often a phrase or a number of phrases from a highly specialised song—sometimes even a complete song of simple type—and where phrases are introduced those phrases are in their proper sequence. Let anyone attempt to combine and recombine without pausing an equivalent number of tunes, and he will find that some effort is required to do so. There is much yet to be learnt about the power of imitation. For how long is a bird able to retain an alien song in its memory, and to what extent does it add to its store as the season advances? Nothing in the way of a decisive answer can be given to these questions. But the key to the first is to be found in the answer to the second. When the males first reach their destination do they reproduce as many alien cries as they are accustomed to a few weeks later in the season? That they do so is scarcely likely; for as the days pass by new notes must be so frequently copied as to become associated with the song, thereby extending the list of imitations. The tendency to reproduce alien phrases must be founded on a congenital basis. Given this tendency, the rest, it may be said, will follow in due course. There is much to be said for this contention. We observe the acquirement actually taking place in the case of birds kept in captivity, and we find that such acquirements are so retained as to be subsequently reproduced; we also observe a similar process at work in Nature, as when the cry of some species is immediately reproduced by the imitator. At one time or another every imitation must have been an act of individual acquirement. Now we start with a congenital basis, of the origin of which we are completely ignorant. The young bird born in June leaves this country a few weeks later without having had an opportunity of exercising its vocal powers, and probably unacquainted with its ancestral song. In the winter months it hears the songs of many foreign species, of some of our own summer migrants, and possibly even of its own species. With the rise of the sexual instinct its vocal powers begin to develop, and

it then migrates to its breeding home. Assuming that its vocal powers lie dormant during the winter months, it is evident that when it reaches its destination in the spring it can have acquired no imitations, and therefore commences the period of sexual activity with its true song *plus* the imitative tendency undeveloped. Supposing, however, that the development of this faculty occurs at an earlier stage in the life of the bird than we are assuming to be the case, then the imitations ought to represent not only the songs of species that migrate to northern countries, but also the cries and call notes of those indigenous to the African continent. Now so far as an appeal to experience can be made, each male upon arrival is capable of reproducing the notes of other species, and, to a large extent, the imitations are of the songs of the birds of the surrounding district, but I cannot state definitely that any one individual to which I have listened was a bird of the previous season. In all, I have heard thirty-two different species copied, and no one male to which I have listened has reproduced the cries of more than seventeen. Of these thirty-two, no less than eleven are constantly introduced into the song of the males both in this country and in Holland; and of these eleven again the notes of the Blue Titmouse, Swallow, Starling, Linnet and Sparrow are habitually reproduced. They are the more common species of the surrounding neighbourhood, we may say, and consequently would be more liable to be imitated, but we must not overlook the fact that an instrument capable of copying such widely divergent sounds as the notes of the Blue Titmouse, Magpie, Starling and Green Woodpecker, and the song of the Nightingale, is qualified to imitate almost any sound to be found in bird life. How can we explain this similarity in the strains reproduced? Is there, as suggested in the life of the Blackcap, an innate proclivity to copy some sounds in preference to others? Until definite evidence is produced showing that the acquired imitation of one generation can become the congenital variation of the

next we must, I think, assume that this is the case, and that each individual acquires the imitations during its lifetime. An interesting experiment might be made with young Marsh Warblers if they could be successfully reared in confinement.

It is difficult to understand what part, if any, imitation in the limited sense in which we are here discussing it can play in furthering the life of the individual. The only explanation we have is that these modifications of the song evoke in different degrees the pairing impulse of the female, but even when we interpret this in a very broad sense it is not altogether easy to reconcile it with the facts we have at our command. If these diverse modifications of song have differential effects, such effects must be due to the quality, quantity, or both, of the imitations. Those individuals, in brief, which start life with an instrument capable of more perfect reproductions will acquire a greater number of imitations and consequently be more likely to secure mates. But we can scarcely assume that imitations, however perfect they may be, will arouse the pairing instinct of the female in a greater degree than the true song; and so the development of the imitative faculty must run parallel with the development of the vocal powers in other directions, the one supplementing the other from the point of view of this theory. Now since the acquirement of imitations is a matter of experience, and since observation shows that some imitations are susceptible of revival, the older birds will have predominant opportunities of securing mates, the younger, no matter how well they may be endowed congenitally, being at a disadvantage in competition with their more experienced rivals. This factor of experience then will to some extent neutralise the beneficial effects arising from the possession of a slightly more perfect instrument, though perhaps not altogether so, for it may be argued that over a long period of time those individuals which were not so perfectly endowed would on the average be at a disadvantage; the point however is a debatable one. Another difficulty arises from the peculiar similarity in the strains

imitated of which we have been speaking, and which cannot well supply the conditions necessary to produce differential effects upon the female. For, however broadly we interpret this view, however confidently we assert that imitations, broadly speaking, create a more effective pairing situation, yet inasmuch as of two individuals it will always be the one that has acquired more numerous or more perfect imitations which will attain to reproduction, there must result a constant tendency towards variation which can scarcely make for the similarity that we observe. If we had sufficient knowledge of the vocal powers of those species in which the faculty was highly developed, we might possibly find that it always followed certain definite lines, that it was, so to speak, the outcome of a certain type of vocal development. A song, for instance, in which articulation is conspicuous and the utterances distinct may lend itself more readily to imitation than one in which the flow of phrases is more continuous. If this were really the case, the tendency to imitate song need not necessarily be of service to the individual, but only the result of a definite type of instrument, and on this view the similarity referred to would become more intelligible. But evidence on many points is still needed. We require information concerning the behaviour of the males in their winter home. Do they there sing and copy indigenous species? We need information concerning the course of and the time occupied in the migratory journey, and definite knowledge as to whether each individual male, upon arrival at its breeding home, introduces imitations into its song, and to what extent variation occurs in the quality and quantity of such imitations. There is room for much observation here.

Of the call notes it is necessary to say but little. The most common one is not an unmusical sound, and is similar in some respects to the corresponding note of both the Reed and Sedge Warblers, but rather more distinctive than either of these. It is uttered at various times and by both sexes, and can be

heard during courtship, when an intruder enters the territory, or when the parents are anxious about their young. A similar sound therefore seems to be indicative of different emotional states, but although similar to our ears it may in reality be specifically distinct to the keener perceptual powers of the bird.

In the summer their food consists entirely of insects, *larvæ* of various descriptions forming their staple diet. The young are principally fed on green *larvæ*, *chironomidæ*, and even *chrysalides*.

The resemblance in the external characters of the Marsh and Reed Warblers and the contrast which is presented to us in much of their behaviour only serves to stimulate our interest in the two birds. We wish to know more of their relationship, why they resemble one another in this particular feature or differ in that. We wish, in fact, to be able to interpret more of the mystery of their development. Have they diverged from some early ancestor along separate paths? Or has the separation been of more recent occurrence? In the pursuit of evidence bearing upon this question of development we must not lose sight of specific behaviour. The behaviour is the outcome of an inherited nervous system; it is the output, so to speak, of a certain type of machine. And surely if we desire to trace the course which the evolution of any particular machine has taken, we do not fix our attention solely upon the material of which that machine is composed and its outward appearance, but take into our consideration also the quality of the work turned out, the details of its mechanism, the productive capacity, and the changes in the relations between the machine and the surrounding conditions which have made development imperative. So ought it to be with regard to the development of species. Not only must we take into account structure and colour but also analyse and carefully compare the output of each inherited nervous system as expressed in song, in the reproductive parental and migratory instincts and the emotional behaviour

which accompanies them, and in the degree of adaptation to environment attained. The comparisons which we have made are not then without meaning. They bear testimony to a condition of instability in the behaviour of the Marsh Warbler which leads us to believe in the possibility of some change having recently been effected. We came to the conclusion, it may be remembered, that the nest of the Reed Warbler was a beautiful illustration of adaptation to a special environment. Its depth allowed the reeds to sway without jeopardising the safety of the young, its shape allowed of its depth, and the means by which it was carefully woven to the reeds made it amply secure from all excessive movements. But upon examining the nest of the Marsh Warbler we found that constancy of type, which so often betokens adaptation, replaced by fluctuating variability; we found examples of both deep and shallow types, nests on the one hand carefully woven to upright branches where the necessity for so doing was not obvious, and on the other insecurely slung to the surrounding branches; and just as the former entailed a needless waste of energy, so the latter courted needless disaster for the offspring. We found, in short, certain conditions prevailing which admitted of but one interpretation, namely, that the nesting instinct was not properly adjusted to the environment now inhabited by the bird. And with regard to the period of arrival we saw that this too was subject to remarkable variation in different countries. For the late arrival of the Reed Warbler there is a cause. It builds in a special situation, and until the new reeds are of a certain height, the facilities for building are not so great, nor is the same measure of protection afforded; consequently the date of arrival is adjusted to the growth of the reeds. On the other hand the Marsh Warbler gains no advantage by so late an arrival at its breeding haunts, but rather exposes itself to all the disadvantages inseparable from late nesting. For it the conditions are equally favourable to reproduction a month earlier in the season, which is shown by the fact that individuals *do* arrive

in certain districts at the commencement of May. Thus it seems as if the period of arrival were not yet adjusted to the environment in which the bird now finds itself, but that a gradual adjustment is taking place.

Impressed with the possibility of some change having recently been effected, we turn our attention to the points of similarity or difference in the characters of the two species, hoping thereby to find some indication of the nature of the change. Structure and colour tell us but little beyond the intimacy of the bond; they point to the probability of the two forms having originally been the same, but they afford no clue as to which is the more recent development. The emotional behaviour gives greater hope of success, for although the song and motor reactions of the Marsh Warbler are widely differentiated from those of the Reed Warbler, we nevertheless find in the former the rudiments of the special features characteristic of the latter. We may say of the Marsh Warbler that there is a general heightening of the manifestation at all emotional periods. The song is more vigorous, possesses a wider range of tone, includes a greater number of imitations and is produced with but little hesitation. The visible organic symptoms of the emotions which accompany the instinct of pugnacity and the reproductive and parental instincts are more suffused with feeling tone, more frequent in occurrence, and appear to be more readily provoked. May we not therefore speak of its nervous system as a higher and probably more recent development? Now we concluded from our examination of the dates of its arrival in different countries, the variation in its nest-building instinct, and the small dimensions of its breeding territory, that its environment may have been at one time similar to that now inhabited by the Reed Warbler. Assuming then that we are thus far correct in our speculations we shall find it difficult to conceive of such a development of the nervous system and such a change of environment as a coincidence and nothing more. We are justified in believing that there must be some relation between

the two, since the possession of certain congenital nervous dispositions determines the actions which are adapted to promote the welfare of the species; but of the nature of that relation we are ignorant. Did the change of environment precede, was it coincident with, or subsequent to the change in the nervous system? Our answer to this question will depend in a great measure upon the view we hold with regard to the development of living forms from others of a simpler type. From our inquiries into the life-histories of the two species we believe that they may have been at some earlier time even more closely related than they are to-day, and we believe that the Marsh Warbler is the more recent modification. According to the theory of continuous variation this result must have been brought about by a number of successive steps or gradations, each one of which possessed some definite value in the struggle for existence and was thus left free to develop. And those who hold that this is the only means by which one form can have passed into another will point to the variation in the nesting instinct in proof of their assertion; and doubtless they will be justified in doing so, for there we have indisputable evidence of the process at work. But the fact of the nesting instinct being in a condition of instability shows that sufficient time has not yet elapsed to complete the adaptation, and consequently the change from one environment to the other must be regarded from this point of view as of more or less recent occurrence. A difficulty arises here. The vocal powers and motor reactions of the two species are separated as regards development by a very considerable interval, and in the case of the Marsh Warbler they are not subject to variation to such an extent as the nesting instinct but seem to have reached a condition of comparative stability. On the hypothesis of gradual transition such an interval must represent an infinite number of gradations, which, in their turn, must have required a long period of time for their completion, and I find it difficult to imagine that time which was insufficient to complete such a simple but nevertheless very

necessary adaptation as the nest-building instinct was sufficient to bring about by slow degrees the change which we observe in the nervous system. How can we reconcile these two sets of facts unless we assume that the change of environment did not necessarily precede, nor was coincident with, the transition from one type of nervous system to the other? Such an assumption may very likely be correct, but we cannot then speak of the environment as either the directing cause or the limiting cause of the specific difference. There is, however, no reason, as has been frequently pointed out, why a variation should not be neutral, should persist, that is to say, and develop so long as it is not harmful. Herein lies a possible explanation of our difficulty.

Those who are inclined towards the mutation hypothesis will no doubt ask why one should trouble about these difficulties. *Natura facit saltum* they would say, and what better example could be found of this principle? It is an attractive solution of our dilemma. We no longer need concern ourselves about the gulf which appears to separate the emotional system of just these or those two closely related forms, and we can even discuss with equanimity the possibility of the change of environment preceding and even acting as a stimulus to the change in the nervous system. The doctrine of mutation assumes that specific differentiation does not take place in any definite direction, that mutations are produced independently of their adaptive value, and that they may survive provided that they do not prejudice the existence or annul the fertility of the individual. The comparisons we have made in the foregoing pages can scarcely be said to afford any direct support for this theory; they show, it is true, that the relationship between these two species is in some ways difficult to understand if recourse be had solely to continuous variation as an explanation, but to this extent, and this extent only, can they be said to support the mutation hypothesis.

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GREAT REED WARBLER.

Acrocephalus turdoides, *Gould, Birds of Great Britain*, vol. ii, 2 pp, pl. 72 (coloured figure of adult), 1870; *Seebohm, British Birds*, vol. i, pp. 361-366, pl. 10, fig. 14 (egg), 1883; *Lilford, Coloured Figures*, vol. iii, p. 34, pl. 17 (coloured figure of adult), 1886; *Saunders, Manual of British Birds*, 2nd Ed., pp. 83-84 (woodcut), 1898.

Acrocephalus arundinaceus, *Yarrell, British Birds*, 4th Ed., edited by Newton, vol. i, pp. 364-368 (woodcut), 1873; *Dresser, Birds of Europe*, vol. ii, pp. 579-583, pl. 88 (coloured figures of adult and young), 1878.

Danish, *Rördrossel;* French, *Rousserolle;* German, *Drossel-Rohrsänger;* Portuguese, *Chinchafoes;* Spanish, *Carrisalero;* Dutch, *De groote Karakiet;* Hungarian, *Nagy nádirigó;* Italian, *Cannareccione;* Russian, *Trost-janoidrosd;* Swedish, *Trastsangare.*

DESCRIPTION OF THE PLUMAGE.

Adult Male in Spring.—The upper parts are buffish rusty grey, slightly more greyish on the crown and nape, but more of a buff colour on the rump and upper tail-coverts. Flight and tail feathers are brown narrowly edged with the same colour as the back, innermost secondaries and the rest of the wing-coverts being broadly margined with this colour. There is a light buffish grey superciliary stripe, the lores are buffish grey, and sides of the head brownish grey. The throat and abdomen are white, crop whitish buff, and sides of the upper breast greyish buff, the latter colour shading into pure buff on the flanks and under tail-coverts. The underside of the wings and tail is greyish brown, the feathers of the latter being tipped with light greyish buff, while the under wing-coverts are pure buff. Iris is dark brown, the small feathers on the eyelid whitish, the upper mandible dark horn colour, and the lower brown at the tip but shading into buff flesh

colour at the base. The flanges and the mouth are orange, the feet dusky flesh colour washed with lavender, the claws brown, and the soles olive yellow.

The colouring of the female is similar to that of the male. In the autumn the colouring becomes more intense, the upper parts being strongly washed with olive yellow, and the under parts rusty buff.

Nestling.—In colour the nestling is much like the adult after the autumn moult. The upper parts, however, are less olive, and the under parts more brownish. The iris is light greyish brown, the bill lavender, and the flanges light yellow. Feet are light flesh colour.

GEOGRAPHICAL DISTRIBUTION.

It is not a little remarkable, considering how numerous this bird is in **France, Belgium** and **Holland**, that on a few occasions only has it been known to visit our shores. Why so narrow a strip of sea should form such an impassable barrier we do not know. Northumberland, Shropshire, Norfolk, Kent, Surrey, Sussex, Hampshire, and probably also the Scilly Isles, all possess records of its occurrence, but no instance of its breeding.

In **Spain** and **Portugal** it is common except in the central plateau, and also in **France** except in the extreme west. Throughout **Belgium, Holland, Germany, the Austro-Hungarian Empire**, and **Italy**, it is generally distributed and common, but scarce in **Denmark**, and scattered over the low ground only in **Switzerland**. In parts of the **Balkan Peninsula** it is common, but very scarce in Macedonia and **Greece**, and though breeding in Sicily does not do so in Corsica and Sardinia. In **Poland** it is numerous, and we find it in the western part of the Baltic Provinces, in the provinces of Jaroslav, Smolensk, Tula and Tambov, in the north-eastern part of the provinces of Perm and Orenburg, in the delta of the River Ural, and throughout Southern Russia generally to the Caucasus. In

Asia it breeds in **Asia Minor**—Tristram says also in Palestine, but this requires confirmation—and seems to pass through **Persia** on migration; while to the south it is resident in **Algeria**, **Morocco** and **Tunis**. As a species it is found not only in Transcaspia, Turkestan, the Kirghiz Steppes and Volga mouth in the west, but also in the Argun, the oases of Central Asia, North and Central **China**, **Korea** and **Japan**. These races, however, differ subspecifically. It winters in **Africa** as far south as the **Transvaal** and **Natal**, and migrates through the **Malay Peninsula** to the Sunda Islands, Andamans, and Philippines.

LIFE-HISTORY.

Of the habits of this species I can add little or nothing that is new, my acquaintance with the bird being limited to occasional visits to its haunts. It is to be found where the common reed grows in profusion, in the dense masses of which it is readily concealed. Arriving at its breeding haunts towards the end of April, it is supposed not to commence reproduction until approximately a month later. No doubt there is a variation in this respect comparable to that which obtains in the case of the Reed Warbler; some individuals arrive early, and possibly commence to breed without much delay; others may be later, accustomed perhaps to build their nests in the new growth of reeds. Even as late as the second week in June individuals can still be seen busily engaged in the construction of their nest. The powerful song and the comparatively large size of the bird make it a conspicuous figure as it flies from place to place, bending down the reeds with its weight, and tend to impart a measure of boldness to its behaviour, which does not seem to me to be altogether merited. My experience is that the bird is shy and retiring, only too anxious to conceal itself in the jungle of reeds as one approaches it closely. When undisturbed it climbs to the top of some reed, and pours out its peculiar croaking song.

The greater part of the construction of the nest is the work of the female. I have never seen a male sharing this duty with her, but like the males of so many species he follows her closely whilst she is engaged in searching for building material. The nest is composed for the most part of pieces of reed which the female herself breaks off, and these pieces are bound together with pond weed or sheep's wool if it can be obtained close at hand. In Texel, for instance, the bird flies out on to the adjoining meadows in search of wool, and whilst on these short excursions sometimes settles upon telegraph wires. The nest is woven to about six upright stems of the reed, and, so far as shape and structure are concerned, is very similar to that of the Reed Warbler, though considerably larger.

The song, which is loud and uttered frequently, resembles to some extent the croaking of frogs.

In April the bird can be seen searching for food amongst the seed heads of the reeds, and in Hungary it is not uncommonly found inside the eel nets, which are there hung on the reeds to dry, evidently attracted by the aquatic insects within.

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AQUATIC WARBLER.

Calamodyta aquatica, *Gould, Birds of Great Britain,* vol. ii, 2 pp, pl. 76 (coloured figures of adults), 1871.

Acrocephalus aquaticus, *Yarrell, British Birds,* 4th Ed., edited by Newton, vol. i, pp. 380-383 (woodcut), 1873; *Dresser, Birds of Europe,* vol. ii, pp. 591-596, pl. 89 (coloured figures of adult and young), 1876; *Seebohm, British Birds,* vol. i, pp. 357-360, pl. 10, fig. 18 (egg), 1883; *Lilford, Coloured Figures,* vol. iii, p. 42, pl. 21 (coloured figure of adult), 1888; *Saunders, Manual of British Birds,* 2nd Ed., pp. 87-88 (woodcut), 1898.

Danish, *Vandsanger;* French, *Bec-fin aquatique;* German, *Seggen Rohrsanger;* Hungarian, *Csikosfejü nádiposzata;* Italian, *Pagliarola;* Norwegian, *Starrsangaren;* Polish, *Gajowka wodniezka;* Russian, *Karnyschewka wertljawaja;* Spanish, *Arandillo.*

DESCRIPTION OF THE PLUMAGE.

Adult Male in Spring.—The upper parts are yellowish buff, each feather having a blackish broad centre spot which gives the bird, when the plumage is in perfect order, a striped appearance. The yellowish buff is richer and brighter on the rump and upper tail-coverts where the spots are narrower. On the back two lighter stripes are formed by the whitish edges of the outer back feathers. The forehead is almost orange buff, and a light buff stripe, very distinct, runs down the centre of the crown bordered on each side by a broad black line with narrow buff edges. A whitish buff superciliary stripe is very conspicuous, the lores are greyish buff, sides of the head buff, and the uppermost ear-coverts blackish, forming a streak behind the eye. The least wing-coverts are brownish buff, the greater wing-coverts blackish, broadly edged with yellowish buff, and the bastard wing blackish. The primaries and their coverts are lavender brown tipped

with a lighter brownish grey, whereas the secondaries are blackish, edged with light yellowish buff. The tail-feathers are dark brown, edged with dull brownish buff, and the under tail-coverts uniform buffish white. The throat and abdomen are whitish, and the rest of the under parts yellowish buff, with or without smaller longitudinal spots on the upper breast. The under side of the wings is lavender brown, the shafts of the feathers being white. The upper mandible is dark brown, and the lower the same colour at the tip, but buffish flesh at the base. Iris is brown, and the feet buffish flesh colour.

The adult female is similar in colouring to the adult male, and when very old has a wash of yellow on the light markings of the head.

In winter the yellowish buff is much richer.

In the case of the young bird the buff is greyer on the upper parts, and the black centres of the feathers are less distinct. The under parts are buffish white, but otherwise the colouring is similar to that of the adult.

GEOGRAPHICAL DISTRIBUTION.

This species is but an accidental visitor to **Great Britain** and nearly all the authentic instances of its occurrence have been in autumn. Most of the records come from Sussex, but it has been obtained in Leicestershire, Kent, Norfolk, Hampshire, the Isle of Wight, Cornwall, and one was taken at the Bull Rock Lighthouse, Co. Cork.

In **Spain** it breeds in Andalusia, and it is found in **Portugal** in spring, summer, and autumn. While it is not an uncommon breeding species in the south of **France** it becomes scarce towards the north, and in the departments of Somme and Nord occurs on migration only. Although a rare visitor to **Belgium** and **Holland**, it passes Heligoland frequently on migration. In **Denmark** and **Schleswig-Holstein** it breeds occasionally, but in parts of the **German Empire** it is not of uncommon occurrence, and becomes even numerous in Silesia.

It is said to be less abundant than the Sedge Warbler in both **Switzerland** and **Italy**. In **Greece** and **Montenegro** it is a bird of passage only, but in **Bulgaria** not uncommon in the Dobrudscha District, and Hungary is visited principally on migration, although some individuals remain throughout the summer.

In **Poland** it is fairly common in the east, but a rare breeding species in the west. The province of Plock appears to be its stronghold, but it also occurs in the provinces of Warsaw and Suwalki, the latter being the northernmost breeding limit of the species. In **Western Russia** it is found in the provinces of Volhynia, Minsk, Kiev, Bessarabia and on the Kinburn peninsula. In **Eastern Russia** it occurs in the province of Perm, near Ekaterinburg in the province of Ufa, and probably in the province of Orenburg near Cheliabinsk. In **Algeria** and **Tunis** it is probably resident.

The winter is passed in **Greece** and **Asia Minor**, but principally in **North Africa**.