PART 9. OCTOBER, 1914.

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
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See Notice to subscribers on back of title page

NOTICE TO SUBSCRIBERS.

The Author deeply regrets the delay in issuing this final part. The two coloured plates which should appear with this number were not delivered to time, and owing to the outbreak of the war it is impossible to obtain them.

They are now being executed here in the best manner and will be sent to subscribers in a separate cover as soon as they are ready.

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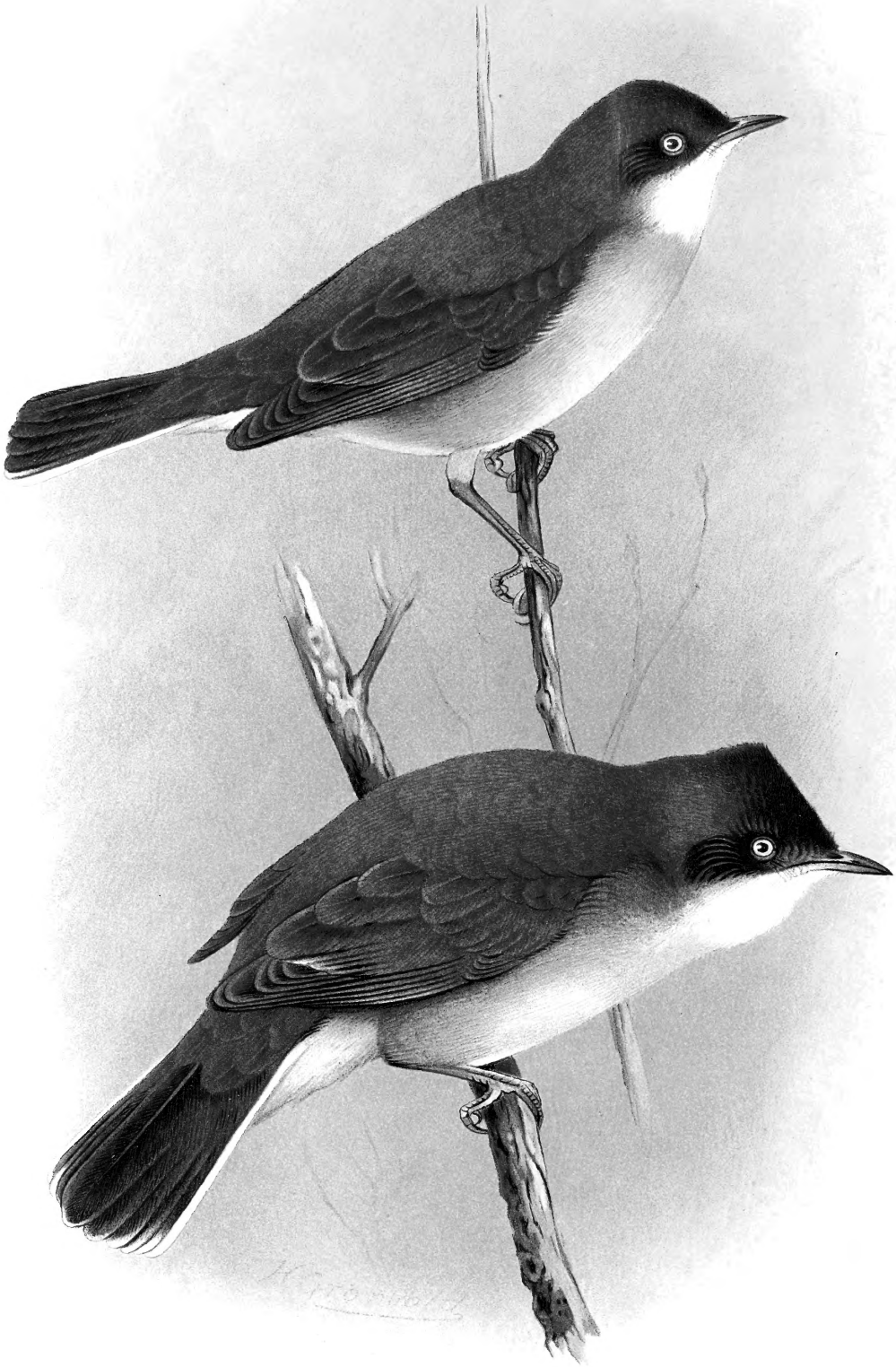
TWO MAPS

Showing approximate Geographical Distribution of Willow-Warbler, Chiff-chaff and Wood-Warbler during Summer and Winter.



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TEXT.

PLATES.

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ORPHEAN WARBLER.

Sylvia orphea, *Hewitson, Eggs of British Birds*, 3rd Ed., vol. i, pp. 133-134, pl. 35, fig. 3 (egg), 1854; *Yarrell, British Birds*, 4th Ed., edited by Newton, vol. i, pp. 423-426 (woodcut), 1873; *Dresser, Birds of Europe*, vol. ii, pp. 411-416, pl. 64 (coloured figures of adults), 1874; *Lilford, Coloured Figures*, vol. iii, pp. 57-58, pl. 29 (coloured figures of adults), 1893; *Saunders, Manual of British Birds*, 2nd Ed., pp. 45-46 (woodcut), 1897.

Sylvia orpheus, *Seebohm, British Birds*, vol. i, pp. 390-393, pl. 10, fig. 4 (egg), 1883.

French, *Bec-fin Orphée;* German, *Orpheus-Grasmücke;* Hungarian, *Dalos poszáta;* Italian, *Bigia rossa;* Spanish, *Canarĭa.*

DESCRIPTION OF THE PLUMAGE.

Adult Male in Spring.—The crown is dull blackish grey blending on the hind neck with the brownish grey colour of the upper parts. The wings are dark brown, the primaries and outer secondaries being narrowly and the innermost broadly edged with the same colour as the back.

The primary coverts and bastard wing are brownish slate edged with the same colour as the back. The tail-feathers, with the exception of the outermost, are dull blackish brown edged with the same colour as the back, the outermost ones being white with black shafts and a blackish brown wedge-shaped spot on the inner web. The under parts are white, faintly washed with buff on the breast and distinctly washed with greyish buff on the flanks, and the abdomen proper is white. The under tail-coverts are greyish, broadly edged with whitish buff. The under side of the tail is greyish brown, the shafts of the feathers being brown except the outermost ones, which are white. The iris is bright sulphur yellow, the bill slate brown, and the feet brownish grey.

The female resembles the male, but the crown is not quite so dark and the outer edges of the flight-feathers are more buffish brown.

In autumn the crown is more greyish, and the under parts, especially the throat and upper breast, are washed with rosy buff, the flanks tending more towards rosy brown.

Immature.—The general colour is similar to that of the female, but the upper parts are of a more brownish colour and the outer edges of the flight-feathers and wing-coverts rusty buff.

GEOGRAPHICAL DISTRIBUTION.

There are four records of the occurrence of this species in **Great Britain**, two of which seem to be somewhat doubtful. The bird inhabits south-western **Europe** and north-western **Africa**. It is common in **Spain** and **Portugal**, and is found in southern and central **France**, **Luxemburg**, and in the western parts of **Switzerland**. In **Italy** and **Sicily** it is local, but it is absent from **Corsica** and **Sardinia**.

Eastwards a somewhat different race, with stouter and longer bill, occurs in **Dalmatia**, **Montenegro**, **Greece**, **Asia Minor**, **Palestine**, **Bokhara**, **Afghanistan** and **Turkestan**.

The eastern form winters in north-eastern **Africa**, **Arabia**, and **India**, but the western race winters probably in west **Africa** and the oases of the **Sahara**.

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DARTFORD WARBLER.

Melizophilus provincialis, *Meyer, British Birds*, folio Ed., vol. i, pl. 67 (coloured figure of adult male and egg) [1835-43] ; *Macgillivray, British Birds*, vol. ii, pp. 383-387 (woodcut), 1839 ; *Hewitson, British Oology*, 1st Ed., vol. ii, 1 p., pl. 147 (egg), 1838 ; *id., Eggs of British Birds*, 2nd Ed., vol. i, pp. 105-106, pl. 29 (egg), 1846 ; *id., id.*, 3rd Ed., vol. i, pp. 143-145, pl. 37 (eggs), 1854 ; *Gould, Birds of Great Britain*, vol. ii, 2 pp., pl. 59 (coloured figures of adults), 1862 ; *Lilford, Coloured Figures*, vol. iii, p. 48, pl. 24 (coloured figures of adults), 1887.

Melizophilus undatus, *Yarrell, British Birds*, 4th Ed., edited by Newton, vol. i, pp. 398-405 (2 woodcuts of bird and nest), 1873 ; *Dresser, Birds of Europe*, vol. ii, pp. 441-446, pl. 69 (coloured figures of adult and young), 1875.

Sylvia undata, *Seebohm, British Birds*, vol. i, pp. 414-417, pl. 10, fig. 7 (egg), 1883.

Sylvia provincialis, *Booth, Rough Notes*, vol. ii, pp. 67-68, 1885.

Sylvia undata, *Saunders, Manual of British Birds*, 2nd Ed., pp. 55-56 (woodcut), 1897.

French, *Pitchou Provençal ;* German, *Provence-Grasmücke ;* Italian, *Magnanina* Portuguese, *Cheide ;* Spanish, *Colorin Caganchina.*

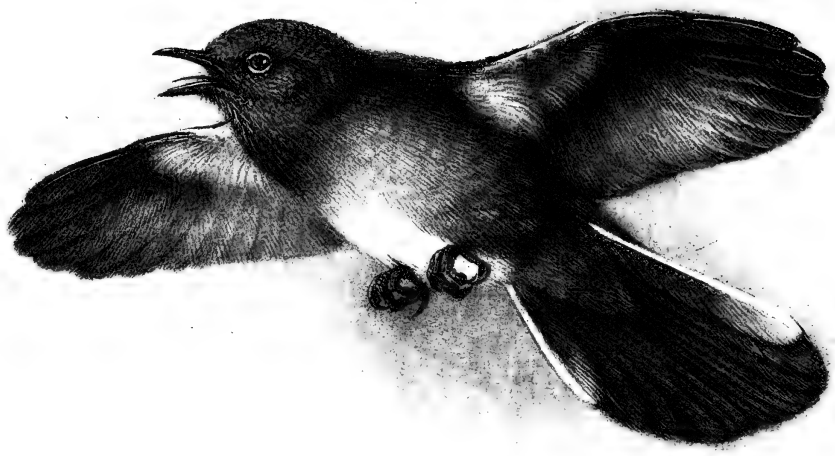
DESCRIPTION OF THE PLUMAGE.

Adult Male in Spring.—The upper parts are dark chocolate brown but rather more slate colour on the crown. The wing-coverts are the same colour as the back, the flight-feathers dark brown, the innermost secondaries rather broadly edged with rusty brown, and the remainder narrowly edged with the same colour. The bastard wing is slate colour with narrow whitish edges to the feathers and the axillaries are whitish. The tail is slate colour, each feather being edged with brownish grey becoming lighter towards the tip, and the outer web of the outermost tail-feather is whitish towards the tip. The shafts are dark slate. The space in front of the eye

is dark slate and this colour continues under the eye and becomes ashy grey on the ear-coverts and sides of the neck. The throat, under parts, and flanks are rusty chocolate, the feathers on the throat having whitish shaft lines. The abdomen is whitish, the under tail-coverts smoky brown narrowly tipped and edged with whitish, the under side of the tail slate colour, and the inner web of the outermost tail-feather the same colour. The bill is dark horn brown, flanges and the base of the lower mandible reddish, and there is a dark reddish brown ring round the eye. The feet are brownish flesh colour.

Adult Female.—The upper parts are a uniform brown colour, slightly darker and more greyish on the forehead. The wing-coverts are the same colour as the back, the flight feathers brown, the innermost secondaries being edged with light brown, whilst the remainder are narrowly edged with whitish brown on the outer webs. The tail-feathers are greyish brown narrowly edged with brown, the outer web of the outermost tail-feather being light greyish toward the tip and the inner web brown with a wedge-shaped spot near the end. The shafts are brown. The throat, under parts, and flanks are light rust colour, the throat being spotted with whitish and the flanks slightly washed with brown. The abdomen is whitish, the under tail-coverts brown, and the under side of the tail greyish, each feather being narrowly edged with light grey. The space in front of the eye is grey, divided from the crown by a narrow whitish stripe. The ear-coverts are brown, the sides of the neck brown slightly washed with ash colour, and the moustache stripe almost light ash colour. The bill is light horn colour.

Nestling.—The general colour is somewhat like the adult female. The upper parts are earth brown, slightly darker on the crown, but lighter and washed with ashy brown on the nape, rump and upper tail-coverts. The wings are greyish brown, all the feathers being edged with rusty brown. The tail-feathers are greyish brown. The sides of the head are



MALE DARTFORD WARBLER

ATTITUDE ASSUMED DURING THE PERIOD

OF SEXUAL ACTIVITY

ashy brown, the throat uniform rusty buff and the remainder of the under parts the same colour, only slightly more greyish on the upper breast, more rusty buff on the flanks, and more whitish on the abdomen. The under side of the tail and wings is brownish lavender and the smaller under wing-coverts lavender buff.

GEOGRAPHICAL DISTRIBUTION.

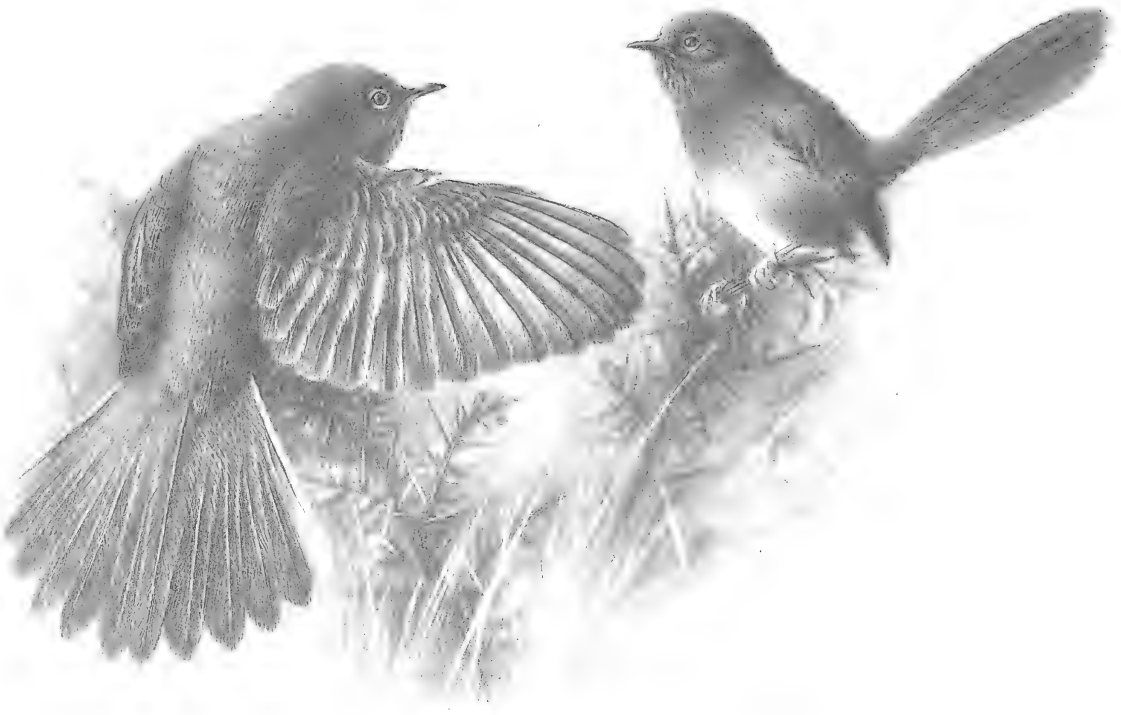
In **England** this species is resident. It is found in Hampshire extending to the Isle of Wight, Dorsetshire and possibly Wiltshire, Surrey, Berkshire, Sussex, and in smaller numbers in Cornwall, Essex, east Suffolk, Shropshire, and probably Oxfordshire. It is also found in the **Channel Islands**, but from **Ireland** there is only one record, a specimen having been obtained at the Tuskar Lighthouse. The bird is principally an inhabitant of south-western **Europe**. In **Spain** and **Portugal** it is locally common, but it is absent from north-eastern and central **France**, though found in the north-west, south, and at the base of the Pyrenees. Its eastern range in **Europe** does not seem to extend beyond **Italy**, where it occurs in the central and southern provinces, as well as in Corsica and Sardinia. There are records of its occurrence in Malta, and on migration Gätke reported it in **Heligoland.** In **Morocco, Algeria,** and **Tunis** it is common in places.

LIFE HISTORY.

I am not in a position to interpret the intricacies of this bird's behaviour with any approach to scientific accuracy. I can only give the impressions left upon my mind after spending a comparatively short time in their midst at an early stage in their sexual process. Of the later stages in that process—that is to say, of the behaviour leading up to the actual discharge of the sexual function, of the building of the nest, and of the rearing of the young—I know nothing;

and I regret this, for even a slight acquaintance is sufficient to show that the species stands high in the scale of emotional development.

In England the bird inhabits wide stretches of common land where heather and gorse grow in profusion, the favourite resort of Stonechat and Meadow Pipit. It is the only warbler that stays with us throughout the year, but whether it remains in family parties or in pairs during the winter, or whether it pairs for life, I am unable to say. Towards the end of February they can be seen in couples, male and female together, and their behaviour seems to show that they are then paired. One can observe the different pairs in the same position day after day, and there is little doubt that they own territories after the manner of other species. For the size of the bird the territories are large, some 250 square yards or so in extent, but it is by no means easy to follow the same pair for a long period, since they move rapidly from place to place and diving into the thickest parts of the heather and gorse are soon lost to sight. Where a number of different pairs occupy adjoining territories there is evidence of much emotional reaction on the part of the males, the meaning of which is not easy to determine in the absence of daily records of the whole period of sexual activity, but the question of territory seems to dominate the situation. Each day one witnesses a more or less similar routine. For periods of varying lengths neither song nor call-note can be heard nor manifestation of excitement seen. But suddenly a change comes over the scene, the birds move restlessly about their respective territories, males come into contact with one another, and we then have the conditions which lead up to an emotional situation. I found these emotional scenes of frequent occurrence at the latter end of February and during the first few days of March, and yet the majority of the males affected seemed to be paired. One or two females were sometimes close at hand, but there was often no visible sign of their presence, and I have no reason to believe that the



MALE DARTFORD WARBLER & FEMALE

stimulus to the emotional manifestation in the male was supplied directly by them. Let us examine these emotional scenes more closely. Sexual no doubt they are in origin, in so far as the sexual instinct is the source of all this behaviour, but the instinct more immediately aroused is clearly that of pugnacity. There is a deal of quarrelling and sometimes much fighting. The males follow one another closely from bush to bush, and meeting upon the top of some holly or fir tree or prominent gorse bush, utter their scolding note, warble, or sing, with their feathers in the meantime tightly compressed. And when the scene becomes more animated, both males, at different moments or perhaps together, expand one wing and hold it momentarily fully expanded, or expand both wings alternately with great deliberation. The expansion of one wing can be frequently witnessed and may occur whilst the birds are on the ground hopping round and about one another. At any moment, too, their emotions may increase in intensity until the situation becomes one of active hostility. Thereupon they fly at one another often amongst the thick heather, and one can hear the snapping of bills and observe scenes which are customarily associated with hostility. What relation can these activities bear to the female if the males that take part in them are paired and have each their respective mates ? I have even observed a male desert the company of his female, when another male was close at hand, and become an actor in such a scene, so that we cannot regard the presence of an unpaired male as an essential condition of the situation, if, that is to say, my observations are correct. In the absence of sufficient data, one is forced to bring to bear upon the problem knowledge derived from other species. And knowing the part that the struggle for territory plays in the lives of so many different species, we are justified, I think, in believing that it is responsible for the manifestations which we witness.

I mentioned the expansion of one wing or the alternate expansion of both wings in the case of the male during periods

of active hostility. This is the most interesting phase of emotional reaction which I have witnessed, but then I am ignorant of what takes place when their behaviour is dominated by the sexual or parental instinct. It may be that the reactions are similar at different emotional periods, or it may be that the expansion of one wing is a particular expression of the emotion which corresponds to the instinct of pugnacity, and if this is so it is the most remarkable of all the manifestations that I have yet observed in bird life.

A feature of the bird's behaviour which arrested my attention was the general resemblance that some of its movements and some of its notes bear to those of the Whitethroat; the call-note especially is remarkably alike in the two species, but there is a difference which can readily be detected though with difficulty put into words. At times the song resembles that of the Stonechat almost as much as that of the Whitethroat, but the quiet warbling during periods of emotion might easily be mistaken for the warbling of the Whitethroat at a corresponding period. The resemblance in the behaviour of the two species is most marked in the aerial flight or dance. The Dartford Warbler springs up into the air whilst singing and remains poised as if suspended upon wires, and a similar performance is a strong characteristic of Whitethroat behaviour. But the position of the Dartford Warbler whilst in the air is somewhat different from that assumed by the Whitethroat; it is more horizontal and the wings are more fully expanded.

Much of their time is occupied in searching for food, principally amongst the heather, where for long periods they are hidden from view. They are by no means shy and it is possible to approach them closely at all times, whether they are slowly wending their way amongst the heather, or washing themselves in convenient pools of water, or singing, or even when their movements are restless and their behaviour highly emotional.

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ICTERINE WARBLER.

Hypolais icterina, *Yarrell, British Birds*, 4th Ed., edited by Newton, vol. i, pp. 360-363 (woodcut), 1873; *Dresser, Birds of Europe*, vol. ii, pp. 521-525, pl. 81 (coloured figures of adult and young), 1874; *Lilford, Coloured Figures*, vol. iii, p. 32, pl. 16 (coloured figure of adult), 1886; *Saunders, Manual of British Birds*, 2nd Ed., pp. 75-76 (woodcut), 1897.

Hypolais hypolais, *Seebohm, British Birds*, vol. i, pp. 381-384, pl. 10, fig. 13 (egg), 1883.

Dutch, *Spotvogel;* French, *Bec-fin à poitrine jaune;* German, *Gelber Spottvogel;* Hungarian, *Sárga füzike;* Italian, *Canapino maggiore;* Norwegian, *Bastard-Nattergal;* Russian, *Penotschkasadovaja;* Swedish, *Gulbröstad sångare.*

DESCRIPTION OF THE PLUMAGE.

Adult Male in Spring.—The upper parts generally are pale olive green, but the upper tail-coverts are rather more olive brown. The wings are brown, the primaries being edged with pale greyish green and narrowly tipped with white, whilst the secondaries are edged with the same colour, which becomes paler on the innermost secondaries. The primary coverts and bastard wing are of a uniform brown colour, the secondary coverts brown broadly edged with pale greyish green, and the median coverts are the same colour as the upper parts. The tail is brown, the outer edge of each feather being pale greyish green. The superciliary stripe is light yellow, the lores yellow, the cheeks brownish yellow, and the under parts pure light yellow washed with brown on the sides of the upper breast. The axillaries and under wing coverts are white washed with sulphur yellow. The under side of the wing is light brown, the inner edges of the feathers being whitish with a trace of yellow; the under tail-coverts

light yellow and the under part of the tail light greyish brown. The iris is brown, the upper mandible light horn brown, and the lower buffish flesh colour. The feet are bluish grey. The sexes are alike in plumage. In autumn all the colours are purer, but the upper parts are rather more brown.

GEOGRAPHICAL DISTRIBUTION.

This bird is an accidental visitor to the **British Islands**, the records coming principally from the eastern counties of England and from Fair Isle. That it appears here so seldom is the more curious since it breeds commonly on the Continent.

It is found in north-eastern **France** as well as in the central and southern parts. To **Belgium, Holland,** and throughout the greater part of **Germany** it is a common summer visitor, and generally distributed in suitable localities in **Switzerland.** Its range extends as far as the Arctic circle in **Norway,** and it breeds sparingly in **Sweden** up to Wermland. In **Hungary** it is seldom seen in summer, though it breeds in suitable localities in **Italy.** Eastwards it appears to be fairly common in **Dalmatia, Montenegro** and **Bulgaria,** but not common in **Greece.** Whilst rare in **Finland**—it occurs as far north as Kuopio—it is evidently a common breeding species in **Poland**, the **Baltic Provinces**, and **Central Russia.** Its range in the East extends to the Orenburg region, and it has occurred in the Kirghij Steppes. In the southern parts of **Russia** it is less common, and the records from the **Crimea** and the **Caucasus** are few. It winters in tropical **Africa.**

LIFE HISTORY.

I have had no opportunity of really studying this bird, and can therefore only suggest to those more fortunately placed that there seems to be here a fruitful field for investigation. Is its behaviour response similar to that of either the Willow Warbler, Chiff-chaff, or Wood Warbler, and, if not, in what

respects does it differ? The song at least bears no resemblance to that of these other species; it is a highly specialized production, abounding in peculiar phrases and combinations which appeal to the human ear, and the power of imitation seems to be highly developed. The most interesting feature of its vocal development is the remarkable similarity between its true song and that of the Marsh Warbler; in fact the resemblance is so great that one may readily fail to identify the owner of the voice. The songs of both species rank high in any scale of vocal development, and it is possible—though I cannot speak with any great authority on this point—that the power of imitation possessed by the Icterine Warbler is as great as that of the Marsh Warbler. It is clear from the casual observations which I have been enabled to make from time to time that the bird stands high in the scale of emotional development; the conflicts, the restless movements, the passionate uttering of the song into which is infused much feeling tone, all betray that excitable condition of the nervous system which, judging by experience, leads to interesting behaviour in many directions.

GENERAL SUMMARY AND CONCLUDING REMARKS.

A BRIEF summary will be sufficient to recall some of the more important points scattered throughout the preceding life histories. Of the twenty-six species included in this work, all, with the exception of the Dartford Warbler, are migratory, and of the remainder, eleven visit us annually for the purpose of reproduction.

From about the middle of March until the latter part of June individuals of one species or another continue to return to these islands, the van of the advancing army being led by the Chiff-chaff, whilst the Marsh Warbler—the least common—is the latest to appear in its accustomed breeding haunts. In the case of every species the first arrivals are males; one instance only of a female returning to this district before a male has come under my notice and is referred to in the life of the Blackcap. The period of arrival is protracted, varying in the case of different species, varying too in the same species in different seasons, and though the earlier arrivals are males, yet it cannot be said that there is any definite division between the times of arrival of the sexes, since the last of the males and the first of the females appear approximately at the same time. It must, however, be admitted that an element of uncertainty is here introduced which varies in degree according to the locality wherein such observations are made; for inasmuch as every male cannot be so fortunate as to secure a territory forthwith, some will be compelled to wander in search of a home, and no one can distinguish between such a wandering male and one that had recently completed its migratory journey.

Why should males be so strongly impelled to reach their breeding grounds? An answer to this question is, I believe, to be found in the necessity for occupying a breeding territory. Each male, that is to say, must secure a position wherein the rearing of its offspring can be safely accomplished, and this is the first and most important step towards reproduction. I must explain what is meant by a "breeding territory." Let us suppose that we watch a male of one of our common species—a Reed Bunting for instance—and accurately record its movements each day during the first few hours of daylight from about the second week in February, what do we find? Not that its behaviour is of a casual description, not that it is here to-day and gone to-morrow, but that all its movements are subject to a routine which becomes increasingly definite as the season advances. There it is in the same plot of ground, in the same bush or clump of bushes, taking short flights first in one direction and then in another, attacking other males that come within a certain radius and exhibiting in all its actions a strong disposition to make its own just that one particular corner of the universe. Those few acres wherein it performs this routine of activities and awaits a female I have termed a breeding territory, the dimensions of which vary, according to the species and according to the environment, from the few square miles of the larger birds of prey, to the few square inches on a ledge of rock which is all that the Guillemot requires. I have, perhaps, in the earlier parts of this work, expressed myself unguardedly when speaking of boundaries, and the critic is perfectly justified in taking me to task for seeming to imply a definiteness which does not really exist. In the history of the Marsh Warbler I therefore tried to make it clear that the word should be interpreted somewhat liberally. The conception of a boundary must not be that of a line definitely delimiting an area the exact extent of which the bird is cognisant of, but of the normal extent of range which has become habitual and has, I suppose, been

determined in part by acquired experience, though founded on a congenital basis. Now this theory of breeding territory raises questions of some importance. It is closely related to the law of battle so firmly established by Darwin, but differs from it in one important particular, namely, that the struggles have their primary origin in an impulse to acquire a territory rather than in one to acquire a female. Concerning the existence of battles in animal life during the period of reproduction there are no two opinions; nowhere are they more noticeable than in the sexual life of birds, and the facts which will be found in the foregoing pages concerning them add nothing new materially, though they serve to confirm our previous knowledge of the subject, already fairly comprehensive. It is in regard to the meaning of such struggles that opinion is so divided. Is a female or a territory the primary cause of disturbance? In the life histories of eleven of the more common forms dealt with, will be found evidence, greater or less, of the disposition to secure a territory, and in most cases it will be observed that the male settles in a small area of ground, there awaits a female, and there remains so long as the young require care: and that far from remaining a passive onlooker at any intrusion he actively repels the approach of a stranger. Conflicts also occur even before the appearance of a female upon the scene. Reference is made to these initial struggles in the histories of the Willow Warbler, Wood Warbler, Blackcap and Marsh Warbler. They demand our careful consideration, since the absence of the female compels us to look elsewhere than in her direction for the primary factor in the dispute. If indeed they were of rare occurrence —a casual struggle here or there—if they bore no trace of persistent striving towards some biological end, and if they were in no way related to the movements of the male in the few acres which he has occupied as a territory, one might perhaps argue that individuals who occasionally exercised just those qualities requisite for obtaining the female when she did at length arrive would by so doing gain some slight

advantage. We should then have to regard them solely as practice for the more serious side of life. But none of these possibilities are fulfilled; the conflicts are not of the type that would justify our relegating them to the category of "play" in Professor Groos's sense of the word; they are no less intense, though admittedly less frequent in occurrence, than those which occur after the arrival of a female; they bear the impress of earnestness, and, if I interpret them aright, are directly related to invasion of territory and thus become one stage in a series of events, which follow one another in orderly sequence and make towards the goal of reproduction. In considering the determining influence of *territory* as opposed to that of *the female*, can we attach any significance to a contest between two females described in the life of the Whitethroat? Certainly not, if it were simply an accidental departure from the normal routine of female activity. But further observations show that it was no mere isolated incident, though the evidence is scarcely sufficient to admit of such behaviour being spoken of as a general accompaniment of the sexual life of birds. So long as the evidence seemed to show that a direct appeal to strength was the special prerogative of maleness, so long were we justified in regarding the possession of a female as a possible incentive; we now know however that male will fight with male, female with female, pair with pair, and that even male and female will combine to attack a single male or a single female. Here then we have a complexity of strife which is very difficult to explain if it be attributed primarily to an impulse in the male to acquire a female; and if it does not spring from the securing and defence of a territory, I know not in what direction to seek the real factor.

The working of the whole theory of breeding territory is explained in some detail in the earlier part of the life of the Reed Warbler. I have there made some attempt to show how by its assistance we can interpret, on the one hand, the singular desertion of the females by the males in the race to the breeding grounds, the equally singular banishment of

their offspring by the parents, and the numbers of unpaired individuals of both sexes. On the other, we can detect in the search for new quarters, which necessarily follows the banishment of one individual after a conflict with a rival, the inception of a movement which must ultimately lead to an extension of breeding range, and possibly form the foundation of those extensive journeys undertaken each spring for the purpose of procreation. If the struggle for territory were confined solely to the males of the same species, it would be sufficiently interesting, but it becomes more so when we recollect that the males of closely related forms contest the question of ownership with one another. Such racial strife is more frequent than one might suppose to be the case—in fact it is only within recent years that close observation has revealed how common is that which previously I deemed of rare occurrence, and it is not difficult to imagine what far-reaching effects this extension of territorial warfare may have had on the past history of bird life.

With the advent of a female in the territory of a given male we witness the commencement of the period of sexual activity, productive of such striking emotional behaviour. This emotion is expressed by movements of the wings, tail, and feathers, and by extravagant antics correlated in some instances with an extravagant use of the vocal powers. Generally speaking, each species has a definite type of response which is peculiar to all its members, but we can often observe a great similarity, or even identity, in the overt expressional movements of different species. We have the slow flapping flight; we have, without actual flight, the rapid fluttering of wings, the slow flapping of wings, the outspread motionless wings; we have the outspread tail, and the sidelong motion of the tail. All of these movements—and others might be added—characterise the emotion which accompanies the sexual instinct. A consideration of these activities led to some discussion of the theory of sexual selection and the modifications of that theory, which from

time to time have been suggested by those who have given thought to the problem. Now this theory in all its interpretations has but one end in view, namely, that the fitter individuals shall attain to reproduction; and inasmuch as the struggle for territory makes towards a similar goal, it is a matter of some difficulty to assign a place to both in the drama of bird life. Therefore when discussing the theory of breeding territory in the life of the Reed Warbler, I gave my reasons for attributing to those battles, which precede reproduction, the elimination of the weaker individuals. Frequent, however, as these struggles are, much as they appeal to our imagination, yet there is no gainsaying the fact that in each season a proportion of both males and females will escape the necessity for a struggle; and just in so far as the unfit elude its meshes the sieve may be said to be imperfect in operation. Here the advocates of an emotional test will doubtless take their stand; a second ordeal, they will say, must be all to the good, ensuring, as it will, a more complete elimination of the unfit. This second test must be complementary, not antagonistic to the first, otherwise the securing of a territory will ensure nothing; it must operate not on those wanderers with no settled home, nor on the victims of many struggles, but on the weaker members who without being challenged have become possessed of territories and thus undeservedly qualified to propagate their kind. If this be really true, it is manifest that each season there must be a certain proportion of males who, though possessing territories, are nevertheless doomed to remain without a mate. My experience does not bear this out. No single instance of a male possessing a territory and yet failing to attain to reproduction has ever come to my knowledge; and of all the objections to a second test, this is perhaps the most serious. We must therefore wait before unreservedly accepting it, until we are in possession of a body of observations serving to show that the securing of a territory does not suffice to ensure the attainment of reproduction; and such observa-

tions ought not to be carried out near the limit of the breeding range of a species, where from other causes unpaired individuals of both sexes may be of not uncommon occurrence. Are we not, however, attaching too great an importance to this imperfection in the first test? Is it not a question of average, and will not the struggle for territory over a long period of time be sufficient at least to maintain that standard of efficiency which is necessary to ensure the position of the species in the struggle for existence? I am inclined to think it will, while at the same time recognising the point as a debatable one.

That the male displays his charms before the female, and that she on her part appreciates the display and exercises a deliberate choice, was at one time deemed possible, but so many and so weighty were the objections which were raised that biologists searched about for a more reasonable interpretation. Such an one they found in the modification proposed by Professor Groos, who, fixing his attention upon the necessity for some effective means of hindering a too liberal yielding to the sexual impulse, saw in the reluctance of the female a barrier which might require all the so-called arts of courtship for its removal. Some criticisms bearing directly upon this aspect of the problem will be found in the life of the Marsh Warbler. Serious objections seem to me to stand in the way of its acceptance, but nevertheless it is the only modification of the theory which can in any way be made to correspond with the facts.

More space is devoted in the foregoing pages to emotional manifestation than to any other aspect of behaviour. Perhaps it is as well that it should be so, for we know little enough of the constitution of emotion or of the part it has to play in organic life, and only by minute observation, careful analysis, and comparison, can we hope to make any headway in the direction of a more complete understanding of the objective aspect of the subject. That each instinct has its corresponding emotion, as suggested by Dr. McDougall, seems to be true.

The sexual and parental instinct and the instinct of pugnacity all have their corresponding emotion, which is supposed to have a definite part to play in furthering the life of the individual. I do not for a moment deny that such a supposition may be correct, but there are many facts which are at variance first with this and then with that interpretation, if we are to regard the correlation of *this* instinctive performance with *that* emotional expression as definitely fixed and exclusive of cross-correlation, and very much that we do not in the least understand. For instance, there is the interpretation placed upon the emotion which accompanies the parental instinct. Many species, when their nest or young are interfered with, perform in a manner which, without an undue stretching of the imagination, might be regarded as a simulation of helplessness, and their behaviour thus appears to be purposive. Instances are given in the life of the Lesser Whitethroat and some remarks added which, though they do not carry us much further towards a solution, serve to show the difficulties in the path of interpretation. One might go on discussing this particular aspect of behaviour interminably. Here I will only draw attention to one feature of all emotional manifestation, namely, the similarity in the type and intensity of the response at different emotional periods. I am fully aware that in using the term "similarity" I lay myself open to criticism, on the ground that our perceptual powers are too feeble to differentiate between such subtle manifestations. But while I am quite prepared to admit the dulness of our perceptual powers when compared with those of the lower animals, I nevertheless hesitate to attribute the observed similarity wholly to this fact; in other words, I believe that it is really there and has to be reckoned with. Professor Lloyd Morgan holds that the differentiation of emotion from a common base is a more fruitful conception than the mode of synthesis proposed by Dr. McDougall. Similarity, on his view, becomes more explicable; for if it can be shown that there is a strong probability of some specific type of behaviour serving a double or a treble purpose, so much

the more reason is there for its survival. The reactions that we meet with in bird life may thus be said to have been developed firstly as a means for arousing the requisite amount of pairing hunger in the female, secondly as a warning to intruders, and thirdly as a protection for the helpless offspring. Clearly everything centres round the strength of the probability in each case.

Emotional behaviour as a whole is so intricate that it is difficult to lay hold on anything very definite, but observation discloses one fact at least which seems to be of some importance and which is referred to in the life of the Marsh Warbler, namely, that the visible manifestations are uniformly strong or uniformly weak in the same species at different emotional periods. An example will make my meaning clearer. The Blackcap exhibits many peculiar antics and assumes many peculiar attitudes during the period of sexual activity and again when it has young. The Willow Warbler assumes one peculiar attitude during sexual activity and again, though in a minor degree, when its nest or young are intruded upon. Now the sexual behaviour of these two species is widely divergent; the one bird is intensely demonstrative, no limit being placed apparently upon the antics it can and does perform, the other has only one definite performance which really calls for remark. Great however as the difference is between them, it need not trouble us here, since a certain amount of latitude is permissible in the application of the utility hypothesis to the behaviour at this special time; let us therefore grant that in each case it serves its purpose equally well in its own particular sphere—arouses, that is to say, the pairing hunger of the respective females. Our difficulty arises in regard to the behaviour when the parental instinct is uppermost; for it is then no longer a question of calling forth a response in this female or in that, but of influencing the behaviour of an intruder. A certain definite standard of response is consequently necessary in the case of both species, since a very definite part has to be played, and this standard must have been gradually evolved by

selection, and adjusted to this particular end. That the so-called delusion of the intruder may be complete, the response must be sufficiently intense, yet it must not exceed the point beyond which it might easily become prejudicial; the same measure of latitude which we gave to the interpretation of the sexual behaviour cannot well therefore be permitted. Now one might conceivably suppose that the response of the Blackcap would be of sufficient intensity to attract attention to itself and preserve the young from molestation, but that of the Willow Warbler is so weak that it is difficult to believe that it can answer this purpose. We might extend the number of such cases indefinitely; we can find examples wherein the emotional manifestation, when the parental instinct is dominant, ranges from almost zero up to remarkable extravagance, and yet trace a similar relation to the sexual response as that in the illustration which we have taken.

In the history of the Marsh Warbler some comparisons were made between the specific types of reaction in closely related forms which enabled us to form some idea of the complexity of the subject. Some species display their emotions far more intensely than others; some respond vigorously on the slightest provocation; others require a stimulus of a more prolonged kind to produce the customary reaction, whilst in a third class the point of motor release seems never to be reached. Why should the expressional movement visible to an external observer be marked in A and not in B? We have no answer to this question; we know nothing beyond the mere fact that it is so. But such differences must appeal to anyone who compares the behaviour of one family with that of another, or, better still, of one closely related species with that of another. Now instinct and emotion are believed to be two manifestations of one and the same process. Must we then say, just because the observed response varies in different species, that the emotion varies too, and can we link up the strength of the instinct with the intensity of the emotion with which it corresponds?

It is difficult to do this until we know in the first place what guides the response into certain definite channels. There may even be other factors which might contribute towards the result we see. A suggestion was put forward in the life of the Blackcap that the temporary separation of the sexes, which occurs in the case of many migrants, might lead to an intensification of the response when the crucial moment did at length arrive; and moreover, that it was almost possible to trace a distinct gradation in the visible manifestations, commencing with the species that pair for life and culminating with those which are necessarily separated at the commencement of the period of sexual activity. A considerable body of observations taken from the lives of many species would be required to show whether this suggestion has sufficient foundation of fact. Our comparisons, it may be remembered, showed that the reactions may be alike, or unlike, or differ only in degree. No one could tell whether the bird he were observing was a Grasshopper Warbler or a Savi's Warbler, if he were to judge by attitude alone at a time of sexual excitement; no one on the other hand could mistake a Willow Warbler for a Chiff-chaff under similar circumstances, though he might possibly confuse a Willow Warbler with a Wood Warbler; and so we might draw up a list of closely related forms showing similar irregularities of behaviour. Of the remainder of our more common Warblers, the Blackcap can be distinguished from the Garden Warbler, the Whitethroat from the Lesser Whitethroat, and the Reed Warbler from the Marsh Warbler. The last two species are well worthy of attention, so remarkably alike are they in appearance, and yet so far apart in their power of song and in emotional manifestation. Well may we be excused some feeling of disappointment with our feeble efforts at interpretation. That the difference in the attitudes they assume is one of degree only can be seen by comparing the corresponding plates in the lives of the two species, wherein the wings are represented as partially and fully expanded.

One more question may be raised with regard to emotional behaviour. Does every individual of a species respond similarly under similar circumstances throughout the whole of its breeding range? Beyond the fact that I have never seen Marsh Warblers in this country expand their wings so fully as those in Holland, I have no evidence bearing upon this point. Yet more wonderful facts are to be found in nature than a variation in the intensity of the reactions in different geographical races; for only if the reactions have a use, and if that use bears some direct relation to the particular degree in which they are executed, should we expect to find them oscillating round a common mean.

Closely connected with, but a separate aspect of this emotional behaviour is the peculiar habit, common to the males of certain species, of picking up and carrying decayed vegetation of some description whilst they are following the female during sexual emotion. We may regard this habit as a stepping-stone to the next important stage in the period of reproduction, the building of the nest. A reference to the plates in the lives of the Grasshopper Warbler, Savi's Warbler, Lesser Whitethroat, and Blackcap will convey some idea of the appearance of the respective males during this peculiar performance. The habit may form part of the sexual life of most species, but whether it be so or not it is evident that the disposition to secure and carry something is much more strongly implanted in the males of some species than in those of others. One would be surprised to find a male Grasshopper Warbler or Savi's Warbler that failed, when the proper moment arrived, to search for, pick up, and carry a piece of vegetation of some description—a decayed leaf of the hazel, oak, bramble, &c., or of the common reed, as the case may be—and equally surprised to find a male Willow Warbler, Chiff-chaff or Wood Warbler that behaved in this way. Here again all attempts at interpretation are rendered difficult by the absence of anything universal. The male Whitethroat builds nests even before a female has arrived, and this,

as Professor Groos says in referring to a similar habit of the Wren, is only one step further in the same direction. Is the habit confined to those males only which share the task of constructing the nest with the female? We must know this before we can hope to reach any definite conclusion, and I have not sufficient data to go upon. But if it were so, we need hardly, one would think, regard the habit as a detached and inexplicable incident in the sexual life of the bird, but as a genuine step on the part of the male towards building the nest.

We come now to the actual construction of the nest. Nothing in nature is perhaps more wonderful than these delicate pieces of architecture, adapted with such a wealth and diversity of form to their surroundings. In some species the work of construction is shared by both sexes, in others the female is responsible for the greater part, if not for the whole. So industrious is the male Whitethroat that he may build one or more nests even before a female has arrived, a peculiarity to which I have referred, and which no doubt he shares with other species. What is the meaning of such exceptional industry? In the opinion of Professor Groos, it must be included in the category of "play," but, as the history of the Whitethroat shows, such nests may be structurally complete and ultimately made use of for the purpose of reproduction. The females of the Willow Warbler and Garden Warbler sometimes build one or more partial nests before the final structure is commenced. We can trace the reason of this in some instances. The Willow Warbler that built four nests deserted the first, I believe, because of constant persecution by the adjoining male. Some, however, say that these loosely ordered platforms represent the initial attempts of young birds, just as the Reed Warbler's nest woven to three reeds instead of more might be attributed to a similar lack of experience. Could a few strands of decayed vegetation laid crosswise here and there afford the necessary data for experience? And when we here speak of experience,

what exactly do we mean? That the initial efforts of the young bird to rear its offspring are doomed to failure? Hardly, one would think, if the preservation of the race is to be secured. The nest has a very definite biological end to serve; it matters not whether it is a little more or a little less highly elaborated; what matters is that it should be sufficiently stable to fulfil the requirements of incubation and ensure the safety of the offspring. Those individuals that failed in the first attempt, even though their failure was tempered by success on subsequent occasions, could have no chance with others in whom the instinct was perfect from birth, and must have long since been eliminated. Moreover no increase of skill begotten of experience, which would lead to a greater perfection of detail, a more highly elaborated production over and above that which was necessary for success, could benefit the offspring. One finds nests, it is true, which seem to bear traces of imperfect workmanship, but they have generally followed the destruction of a first attempt and are built therefore hurriedly to receive the eggs already overdue; yet even they, unfinished though they may be in workmanship, meet the biological end of nest building. I do not deny the existence of nests ill adapted to their surroundings. A change of environment is all that is required to supply the conditions necessary for the appearance of individual variations in constructive ability, some of which will disappear, while others more in harmony with their surroundings will remain; and I have given my reasons in the history of the Marsh Warbler for believing that such a change of environment is actually in progress at the present time in the case of that particular species. There, as a reference to the illustrations will show, we have different types of nests which seem to bear the stamp of varying degrees of constructive skill, and all will perhaps in the future become modified before the evolution is complete, since they appear to be either too flimsy or too robust.

Others regard the passing on of experience by the elder to

the younger as a possible explanation of the art of nest building. Tradition in connection with this particular aspect of behaviour does not appeal to me as a satisfactory solution, for we cannot, as I pointed out when discussing the nest building instinct of the Reed Warbler, assume that a young male and a young female never mate together; and even granting that such an assumption were in some cases correct, there is a still greater difficulty to be overcome in the fact that the females of certain species—the Willow Warbler, Wood Warbler and Reed Warbler for instance—are alone responsible for the work of construction. If then this wonderful art is neither begotten of experience nor is the outcome of tradition, how is it to be explained? I cannot explain how it is done; we seem forced to fall back on inherited instinct. I believe that the young bird is as perfectly equipped with the mechanism necessary to produce these beautiful pieces of architecture as many insects which are provided with the mechanism necessary for the performance of a complicated series of activities once and once only in their lives.

Regarding as a whole the species whose lives have been dealt with in this work, we find that there is no one rule which summarizes the behaviour of the sexes as to the care of their offspring. The males of one species share the burden equally with their mates, the males of another take little part in the rearing of their family. It is the males of the three smaller species, the Willow Warbler, Wood Warbler and Chiff-chaff, who for some reason are not called upon to work so diligently as their mates, and these three build dome-shaped nests. Can we establish any relation between the behaviour of the male and the specific type of structure that has been evolved? It is difficult to do so with the life histories of a few species only to draw upon. But if there is one fact that the behaviour of the female, and in some cases of the male, does really seem to show, it is the necessity for constant brooding when the young have just left the egg. We can understand the immense importance of warmth; we need

only handle and examine these fragile organisms in order to realize how prejudicial prolonged exposure must be to them. So that even if we could not verify it by direct observation, we should still have general reasons for believing that much of the parents' time would be passed in brooding. Since warmth and consequently freedom from exposure are of such vital importance, does it seem unreasonable to suggest that the covered nest would contribute towards that end, and by freeing the parents of part of their task give rise to the habit we observe in the case of some males? We require evidence from the lives of many species, whose young are nidicolous and whose nests are protected, to show whether there is really such a modification of behaviour as is here suggested. If a covered nest does afford protection to the young and thus allow greater freedom to the parents, it is clear that they will have more time to seek the necessary food and will therefore be in a position to rear a larger number of offspring; I have not, however, had sufficient time to investigate the matter closely. Some facts relating to brooding will be found in the lives of the Willow Warbler, Chiff-chaff, Whitethroat, Reed Warbler and Marsh Warbler.

The methods adopted for feeding the young and for ensuring the cleanliness of the nest involve a complicated series of activities showing wonderful nicety of adaptation, and suggest to my mind that the behaviour is purely instinctive. All the species dealt with are very much alike in the treatment of their offspring. I see no reason why a Garden Warbler should not rear Whitethroats, or a Whitethroat Blackcaps, as successfully as their respective progeny. In fact, experiment proves that such really is the case, for I have placed eggs of the Whitethroat in a nest of the Garden Warbler and have seen the young successfully reared. Some particular aspects of the parental instinct are discussed in the histories of the Whitethroat, Reed Warbler and Marsh Warbler. The normal routine of tending the young is as follows: the parent arrives at the nest with food and sometimes feeds one, more often two,

occasionally three, but the first one as a rule receives the larger share of food and ejects the *fæces*, which are thereupon swallowed by the parent or carried away and dropped some distance from the nest. Does the parent bird remember which of its young it fed at the last visit, or is the process in this respect a haphazard one? My interpretation is simple enough though not altogether free from the possibility of criticism; it relieves the parent of all responsibility but at the same time leaves nothing to chance. I regard the sensation of hunger as the guiding factor. According to the strength of this sensation the young bird is active in stretching up its neck and in struggling towards its parent, and on the average the more active individual is the one that secures the food. There is therefore no need for the parent to remember to which of its offspring it attended on the last occasion; its business is to place the food in the nearest open throat; the rest is done for it. But, it may be said, is not hesitation shown by the parents as they stand upon the side of the nest and contemplate their offspring before finally parting with the *larvæ* they are carrying? Certainly, I reply; but is not their behaviour related to that of their offspring? Do they not hesitate only because the young hesitate also as the time draws nigh for sleep and response is therefore weak? I think we can explain it thus: we must regard the parents and offspring not as separate units, but as a biologically determined whole within which the sequence of activities forms a complete circle. The young bird that is hungry is the more active in stretching up its neck and thus has a greater chance of securing food. Having received it, it proceeds to eject the *fæces*, which are carried away by the parent. Hunger being temporarily appeased, it lies in the bottom of the nest taking but little heed of the parent returning with a fresh supply, and though it may open its mouth, yet the persistent striving towards some end is manifestly absent; digestion however proceeds apace, the hunger sensation once more asserts itself, response becomes increasingly active, and in time it receives a further supply.

This in outline is what seems to be the normal routine. There are plenty of deviations from the rule and plenty of variations of procedure; the same bird may be fed by both parents in quick succession, or by one parent again and again until well-nigh exhausted by the abundance of food showered upon it.

Numerous references have been made to the method which has been evolved for ensuring the complete removal of the excrement and thereby the cleanliness of the nest. The importance of cleanliness is alluded to in the life of the Whitethroat and it is unnecessary to discuss the matter further; attention may nevertheless be directed to the method by which this end is secured.

We must remember that cleanliness is only brought about by correlated behaviour on the part of parent and offspring. The usual procedure is as follows: the parent delivers food to one of the nestlings and then waits for it to eject the *fæces;* if it fails to do so the parent sometimes touches the anus with its bill, which seems to have the effect of stimulating the nerves which control defæcation; the *fæces* are then carried away and dropped some distance from the nest or swallowed. Yet this correlated behaviour on the part of parent and offspring, wonderful though it is, would not be sufficient to ensure complete cleanliness without the contributory physiological factor, *i.e.*, the membranous sac or envelope in which the *fæces* are enclosed and which facilitates the act of removal. But is ease of removal alone sufficient to account for this wonderful contrivance? Ease of removal implies economy in time, and time is everything. That the young in the early stages of growth should sleep as much as possible, should be kept as warm as possible, and should run no risk of prolonged exposure is imperative if the species is to maintain its position. This biological end is furthered by the specialized activities of the parents, whose behaviour shows how admirably racial preparation has fitted them for the task. All their movements, or all her movements as the case may be, are delicately adapted to contribute to the main parental function of supplying

the necessary food, affording protection from cold and from enemies, and attending to the sanitation of the nest as efficiently and rapidly as possible. If then the *fæces*, instead of being enclosed in this envelope, were ejected in smaller pieces, as is occasionally done even now, what would be the result? Some part of the parents' duty must perforce be neglected; either the young must receive insufficient nourishment, or the nest must become contaminated, or the nestlings must suffer from exposure. The lessening as far as possible of the risk which thus threatens the fragile offspring is, I believe, the biological end for which this envelope has been evolved. But no matter how perfect the system which has been organically built up, the species will not benefit unless the parents, either by the aid of their intelligence, or through acquired experience, or by instinct, are able to take advantage of the special facility for removal which is thus afforded them. I believe that their ability to do so is due to racial preparation. The experiments with small leaves placed in the nest, referred to in the life of the Whitethroat, seem to point to an impulse of considerable strength to remove anything of a foreign nature. For if in place of instinct we fall back upon intelligence, ought we to find leaves carefully picked up and carried away and even efforts made, not without some success, to swallow them? Should we not rather anticipate some small measure of discrimination? The leaf experiments however do not constitute conclusive evidence in favour of something congenital as opposed to something acquired through experience; let us therefore consider the position of a young bird carrying out its parental functions for the first time. How is it to gain its experience? Only, I suppose, by trial and error. But during the process of learning by trial and error what is to happen to the offspring? They must be the sufferers; it is upon them that the initial blunders of an inexperienced parent will recoil, and it is upon them that the future of the race must depend.

How can we account for the parallel development of the

envelope in the young and the instinct to remove in the parent? By the slow accumulation of two sets of entirely separate but mutually dependent accidental variations, with nothing but elimination to determine the direction of accumulation, or by the sudden appearance of a physiological development in the young bird, *plus* the sudden appearance of the corresponding instinct in the parent? In a case of this description Professor Lloyd Morgan's theory* of the survival of coincident variations is helpful as showing how the acquired modification can determine the survival of congenital variations in the direction of increased accommodation without biological transmission. At first small pieces of the excrement may have been occasionally swallowed for food; but supposing a small amount of intelligence had then been brought to bear upon the situation, leading to removal of part *plus* the occasional swallowing of part, there would have been a distinct gain to those individuals in whom such modification presented itself. Acquired accommodation would in this case have

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* The theory of the survival of coincident variations is by no means easy to grasp. It may therefore be of some help if I quote, from a private communication, Professor Lloyd Morgan's own statement of his case. He writes thus: "The essential feature of this suggestion may be put as follows: Let M be a modification of instinctive behaviour, such modification being intelligently acquired as the outcome of individual experience; and let V be a variation of the hereditary tendency to the instinctive behaviour thus susceptible of modification. Now a change of V in the direction of better adaptation, if it have in itself survival value, will be inbred through natural selection. But in itself it may not reach a value which determines survival instead of elimination. Since, however, acquired modifications of behaviour are themselves factors in survival, the organism in which there is a combination of favourable variation and favourable modification will stand the best chance. A variation too slight to be selected, if it stood alone, survives when it is supported by an intelligent modification in a like favourable direction. Hence, though the acquired modification may not itself be directly inherited, it none the less acts as foster-nurse to coincident variation, *i.e.*, those in a like favourable direction. In like manner, where intelligence is lacking, coincident non-adaptive variations will stand the greater chance of elimination. In symbolic terms + M coincident with + V makes for survival; while − M coincident with − V makes for elimination. The + V in the survivors is inherited. The − V is bred out of the race."

had a double effect; it would not only have fostered the survival of congenital variation of behaviour in the direction of removal, but also the congenital variation in the direction of an efficient covering which would contribute towards ease of removal.

Some discussion of the vocal powers will be found in the histories of the Willow Warbler, Blackcap, Lesser Whitethroat and Marsh Warbler, more especially with regard to the utility of song, the power of imitation, the variation in different districts, and so forth; and now when one comes to gather up the threads, the mystery of it all deepens and hope of interpretation wanes. For what is the use of song? To evoke the pairing hunger of the female as Prof. Lloyd Morgan suggests? It may be so, yet the facts at our disposal are not of the kind to carry conviction. The same considerations which led to our questioning the correctness of Professor Groos' theory in regard to emotional manifestation are relevant here also. I made a suggestion in the life of the Willow Warbler and discussed it again in that of the Marsh Warbler. Briefly it was as follows: a male must have some means of proclaiming to the females the fact that it is in possession of a territory and ready to reproduce, and this it can accomplish through the medium of those special sounds emitted at this particular season. Such sounds are therefore not only directly related to but are an integral part of the law of territory; and since on the average it will be the more vigorous males that will secure territory and attain to reproduction a gradual augmentation in the power of producing sounds ought to follow. The facts which were used in support of this view will be found principally in the life of the Willow Warbler. It must not, however, be supposed that this suggestion explains, or attempts to explain, why a Land-Rail, for instance, should produce such raucous sounds and a Marsh Warbler such beautiful ones; it does not touch the question of the origin of the sound nor claim to show why this or that voice should have been framed in just this or that particular fashion; but

neither, I think, does any other interpretation. It simply starts with the assumption of "one voice, one value," and shows how the sounds produced, whether harsh, monotonous or beautiful, may each in their own particular fashion possess a similar meaning. So much for its use.

We must now refer briefly to the question often asked as to whether a young bird learns to sing or whether it sings instinctively through racial preparation, as a duckling swims instinctively when placed in water. Is song, that is to say, a matter of tradition—handed down from parent to offspring—or is it a matter of congenital endowment? There are facts placed on record—and I believe perfectly authentic facts—which seem to show that tradition may play a larger part than it is sometimes given credit for. Young birds reared in confinement away from their own species, but in company with other songsters, are said to reproduce only those notes which they have been accustomed to hear. I have all along combated the view that the young bird sings true to type just because it has predominant opportunities of hearing its parents' notes, and despite the facts here alluded to, I still think that each species has a definite congenital song. When is the young bird supposed to learn its song—whilst in the nest or during the winter months? The former, one would suppose, would be the more susceptible period, yet that is precisely the time when the voices of many songsters are heard the less frequently, if indeed they have not ceased altogether. The Grasshopper Warbler, after a period of comparative silence, only recommences to sing when its young have left the nest; the Nightingale becomes well-nigh silent when the time comes for the exercise of parental care; the Marsh Warbler's song grows more and more feeble at a corresponding time, and so on. If therefore song is an individual acquirement, a matter of imitation, what is there to prevent the young from assimilating the notes of the more vociferous individuals of other species in the vicinity of their nest? Nothing, I imagine, so long as we exclude the

congenital factor. What then is the meaning of the evidence derived from birds in captivity? An answer to this question may perhaps be found in the power of imitation so highly developed in many species. This remarkable power is referred to in the lives of the Blackcap and Reed Warbler, more fully in that of the Marsh Warbler, and some idea of the nature and extent of the development can be gained by studying the lists of voices and songs imitated. It is apparently so simple a matter for certain species to reproduce alien strains that one may well ask how a definite type could have been evolved in the absence of any instinctive basis. I should not demur to song being spoken of as a matter of imitation, though founded on an instinctive basis, if by this is meant that a stimulus of an appropriate kind is necessary to set it agoing, but we should not be then justified in speaking of song as having been learnt by imitation. The power of imitation and the true song must be two separate manifestations of one process; may not the absence of the true song in the case of birds reared in captivity be due to an absence of the appropriate stimulus, just as in the absence of appropriate stimuli other hereditary co-ordinations refuse to respond, the alien cries being the stimulus to the power of imitation which must also be founded on a congenital basis.

The more one reflects upon this problem of vocal imitation the more difficult it becomes to estimate its true value from the biological standpoint. Dr. Thorndike regards the phenomena presented by imitative birds as a specialization removed from the general course of mental development. Others think that it has a special part to play in the sexual process, and while dissenting from this view—my reasons for doing so will be found in the discussion of the subject in the life of the Marsh Warbler—I should be the first to admit the incompleteness of our knowledge in regard to the whole matter.

The variation in different districts is referred to in the history of the Lesser Whitethroat, and the suggestion is there

put forward that climate may exercise some influence upon the vocal muscles irrespective of natural selection, and thereby contribute towards the differences we discern. The problem is a difficult one and recent observation adds to the complexity. One wants to know whether it is an isolated phenomenon, removed from the general course of evolution, or whether it is linked with other physiological differences which we cannot yet fully determine, though we are beginning perhaps to understand them in part. As our knowledge of local races increases, so the importance of this vocal variation looms large in our field of inquiry. We cannot altogether disregard it. For even if it could be shown that varying climates could exercise differential effects on the vocal muscles, there would still remain plenty of matter for debate. Is there such a thing in song as a definite ancestral type? And if not, at what period in the life of the individual is the voice fashioned? This is the crux of the whole matter. I have suggested climate and I still hold to it as a directing influence, because, if we regard the facts presented as a whole, we find one feature which arrests our attention and may almost be spoken of as universal, namely, an alteration of the pitch in different districts; the farther we travel west—I am speaking of Europe—the more we observe the phenomena in districts dominated by the Atlantic, the lower we find the pitch becomes. If every individual of the same species and in the same locality presented this peculiarity in a similar degree, the matter would be more simple. But this is not the case. Two Chaffinches will utter their spring call side by side in Donegal, both in a lower pitch than one is accustomed to hear in the Midland counties of England, but the one so very much lower as to make the possibility of recognition by other members of the same species in other localities somewhat remote. With the meagre facts at our disposal it would be unwise to attempt to arrive at any decision. The phenomenon is probably part of the larger problem of local races, but whether the delicate adjustments which these slight differences imply are due

to some external influence, or to internal variations of the nervous system of definite or indefinite origin, we cannot say.

On more than one occasion, I have appealed to natural selection as a probable explanation of the method by which some particular piece of adaptation has been built up. One of the criticisms to which this theory is sometimes subjected is that we ought to be able to observe it in operation providing it were of such universal application. Much depends upon how much we expect to see. We cannot of course hope, within the short space of a human lifetime, to witness the completion of a process, to see some great change accomplished by virtue of some specific inherited disposition; but because we cannot be present while the whole wall is being built we are not thereby debarred from seeing some of the bricks laid. Wherever we find failure—failure to escape the dangers attendant on migration, failure to secure food under normal conditions, failure to attain the goal of reproduction—there we have elimination with the corresponding brick laid in the development of some characteristic which is of survival value. Take as an example the nesting instinct of the Reed Warbler. These birds weave their nests to three, four, five, six or seven reeds; two would clearly be insufficient to hold the nest; three do not always afford the necessary security, the majority are therefore woven to more. We can observe that a nest woven to three reeds is liable to bring disaster to the offspring, though perhaps not often, and we can infer that if it were woven to two that danger would be increased. Now it is more simple to find two reeds conveniently placed than to find three, more simple to find three than four. If then the number of reeds made use of were a matter of small moment, why should the number of nests woven to more than three be in so large a preponderance? What determines individual behaviour in this respect? Does the same individual make use of two reeds one year and fail, but five reeds the next and succeed? Or do some individuals always lay the foundations of their nest more securely than others? Since experience as

a factor cannot well be admitted, we must fall back upon racial preparation of some description; and if this be granted, then in the elimination which threatens the offspring of the careless worker we observe the process at work. Another example is afforded by a comparison of the Reed Warbler and Marsh Warbler. The peculiarly close relationship between the two birds has been referred to at some length, and judging by external characters only we may freely admit the possibility of no intermediate forms ever having arisen, but the differences of behaviour indicate something in the structure of the nervous system which we cannot explain at the present time in terms of any known theory. Here we are concerned with that particular aspect of behaviour which centres round the building of the nest. I have given my reasons for believing that at some earlier period the Marsh Warbler dwelt amongst reeds; to-day its environment is different from that of the Reed Warbler, and no one type of nest seems yet to have been evolved which adequately meets the present conditions of existence. Variation meets us in many directions, nests on the one hand needlessly secure, and on the other so ill adapted to their surroundings that disaster is liable to befall the offspring. Unless therefore I am interpreting the facts wrongly, we have here presented to us a process of elimination leading to a gradual development in a definite direction.

While firmly convinced of the importance of natural selection, I am not one of those who regard it as the exclusive means of organic process, nor do I hold the doctrine of utility as absolute. Far from it. Why should it be necessary to attempt to express whole series of phenomena relating to specific behaviour in such terms? And are there not besides many facts in nature which almost compel us to look elsewhere for an explanation? Though it may be impossible to demonstrate by actual observation the negative value of any particular piece of behaviour, I nevertheless believe that a comparison of certain peculiarities of closely related forms almost yields the evidence we require. The Willow Warbler

and Chiff-chaff, for instance, are closely related, live under the influence of a similar environment, require similar food and construct similar nests, yet the former builds upon the ground, the latter in some suitable undergrowth a foot or so above it. Can we then say that the ground leads to success in the one case but brings disaster in the other? Surely not when we bear in mind the identity of the conditions of existence of the two species. Or again, of the numberless channels into which sexual behaviour has been guided, can we say that each has some definite value attached to it? Can we even say that it is strictly correlated with something which has utility? Granting for the moment that emotional manifestation *does* play a part, granting that attitudes and antics create on the whole a more effective pairing situation, that beautiful plumage adds to the effect and that song contributes to an increased emotional tone—granting all of this, can anyone seriously suggest that wings raised a little more or a little less, slowly flapped or quickly fluttered, partially or fully expanded, a tail waved with a sidelong or an up-and-down motion, a song produced as the bird ascends or descends in the air, and a host of other trifling but specific forms of behaviour, depend for their usefulness on being cast in just this or that particular mould. If the life behaviour as a whole has utility, does it follow that every detail is independently useful?

In much of the behaviour which centres round the securing and defence of a territory, the building of a nest, and the care of the young, wherein a psychical accompaniment seems to be required as a contributory factor, one cannot help being impressed with the difficulties of evolutionary interpretation in terms of fluctuating variation or mutation only. How can we appeal to the slow accumulation of fluctuating variations only in a case where a definite organic structure in A depends for its success on a definite psychical factor in B? How can we appeal to variations of definite origin in explanation of the guidance of behaviour which is accommodating the organism to new and changed conditions of existence? How can we

appeal to the biological transmission of acquired modification with little or no evidence to go upon? It is here that Professor Lloyd Morgan's principle of the "survival of co-incident variations" comes to our aid; and to one who sees—needlessly perhaps—in the psychological aspect of the evolution of behaviour difficulties of interpretation on any known naturalistic hypothesis, acquired modification as the foster-parent of congenital variation seems to be a step in the right direction. I believe it to be an important principle, removing as it does in some measure the difficulties which surround the survival value of incipient variations.

TABLE OF MEASUREMENTS.

Name	Total Length	Length of Wing	Length of Tail	Length of Tarsus	Length of Culmen
	mm.	mm.	mm.	mm.	mm.
1 Common Whitethroat ...	145	68—75	66	21	12
2 Lesser Whitethroat ...	124	64—66	55	20	11·5
3 Orphean Warbler ...	160	79—84	66—70	23—25	16
4 Blackcap	150	70—78	65	21	10
5 Garden Warbler ...	144	80	55—60	21	12·5
6 Barred Warbler ...	153	85—90	71	24	16·5
7 Subalpine Warbler ...	127	58—61	54	20	11·5
8 Dartford Warbler ...	130	50—53	60—68	18—19	9·5—11
9 Yellow-browed Warbler	102	51—60	38—42	18	7·5
10 Pallas's Willow Warbler	95	48—53	37—42	18	7
11 Greenish Willow Warbler	102	57—65	44—48	17·5	10·5
12 Chiff-chaff	118	55—60	44—52	17—20	10
13 Siberian Chiff-chaff ...	124	55—63	47—54	21	8
14 Willow Warbler ...	110	66—71	50—65	19	10·5
15 Wood Warbler	120	73—78	50	17·5	10
16 Rufous Warbler ...	165	86—89	70—75	27·5	19
17 Radde's Bush Warbler...	127	60—65	56	21·5	12·5
18 Icterine Warbler ...	136	75·5—82	55—60	21—22	15
19 Melodious Warbler ...	130	70	58	22	15
20 Reed Warbler	132	65—70	56	20·5	15
21 Marsh Warbler ...	135	70	54	22	14
22 Great Reed Warbler ...	195	90—100	78	28—30	22
23 Sedge Warbler	130	66— 70	51—56	19—22	15
24 Aquatic Warbler ...	118	65	50	20	11
25 Grasshopper Warbler ...	127	64—66	54	20	12
26 Savi's Warbler	145	65—72	60	21—22	15—17

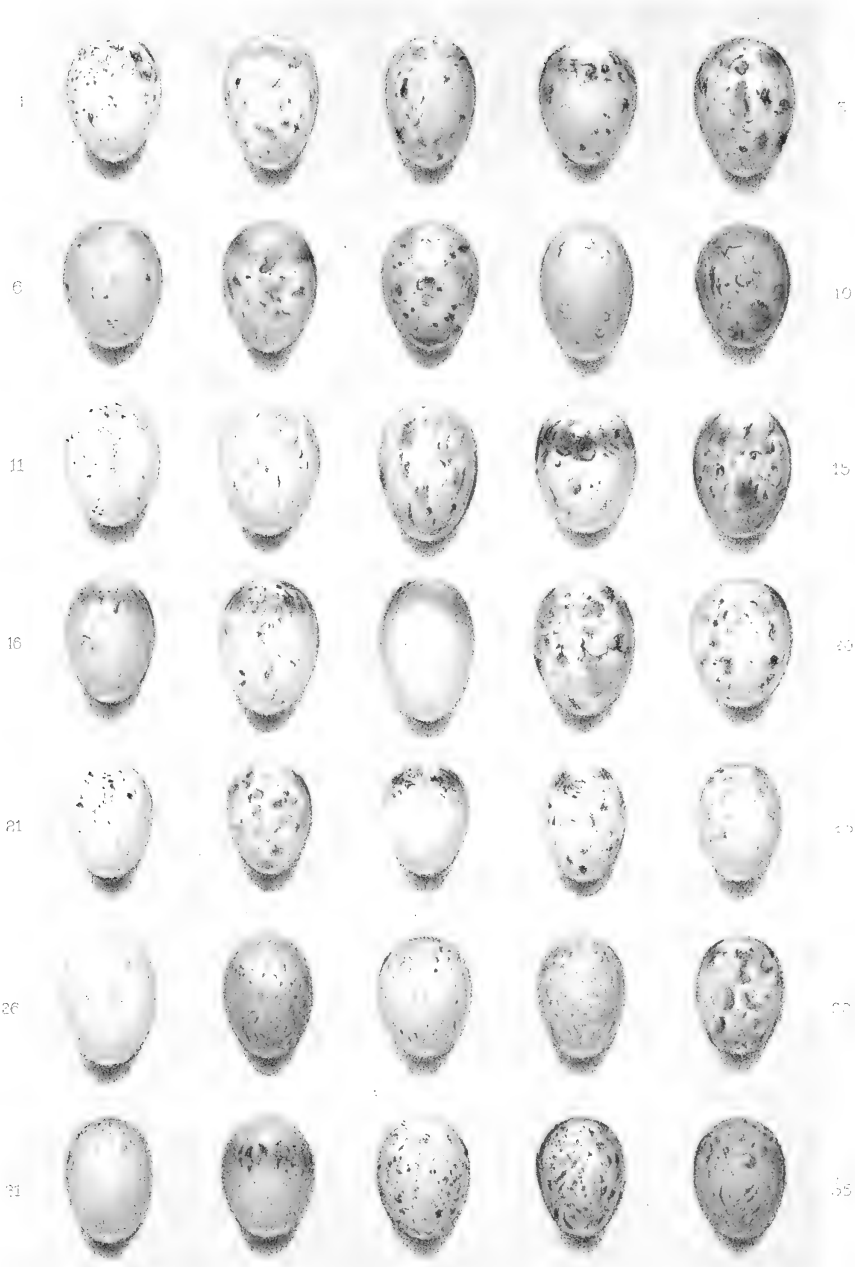
EGGS OF BRITISH WARBLERS, Pl. I.

1.	Aquatic Warbler ...	North Germany...	12 June, 1900	National Collection.
2.	,, ,, ...	Zana, Algeria ...	June, 1857 ...	,, ,,
3.	,, ,, ...	North Germany...	10 June, 1895	,, ,,
4.	,, ,, ...	Germany ...	26 May, 1901	,, ,,
5.	,, ,, ...	North Germany...	10 June, 1895	,, ,,
6.	,, ,, ...	Pomerania ...	27 May, 1886	,, ,,
7.	Sedge Warbler ...	Yorkshire ...	26 ,, 1872	,, ,,
8.	,, ,, ...	Holland	15 ,, 1876	,, ,,
9.	,, ,, ...	Berkshire ...	9 June, 1849	,, ,,
10.	,, ,, ...	Surrey	... ...	,, ,,
11.	,, ,, ...	Norfolk	22 June, 1876	,, ,,
12.	,, ,, ...	Yorkshire ...	26 May, 1872	,, ,,
13.	Reed-Warbler ...	Cambridge ...	10 June, 1856	,, ,,
14.	,, ,, ...	Norfolk	25 ,, 1877	,, ,,
15.	,, ,, ...	France	... ...	,, ,,
16.	,, ,, ...	Cambridge ...	... ...	,, ,,
17.	,, ,, ...	France	(?) July, 1896	,, ,,
18.	,, ,, ...	Cheshire... ...	1870	,, ,,
19.	Marsh-Warbler ...	Holland	... ...	,, ,,
20.	,, ,, ...	Germany ...	9 June, 1878	,, ,,
21.	,, ,, ...	,, ...	... ...	,, ,,
22.	,, ,, ...	Spain	10 June, 1873	,, ,,
23.	,, ,, ...	Holstein ...	... ...	,, ,,
24.	,, ,, ...	Spain	16 June, 1874	,, ,,
25.	Great Reed-Warbler	Germany ...	... ...	,, ,,
26.	,, ,,	Spain	18 May, 1868	,, ,,
27.	,, ,,	Algeria	11 June, 1857	,, ,,
28.	,, ,,	,, ...	6 ,, 1857	,, ,,
29.	,, ,,	,, ...	15 ,, 1857	,, ,,
30.	,, ,,	,, ...	(?) ,, 1857	,, ,,
31.	,, ,,	Holland	(?) 1875	,, ,,
32.	,, ,,	France	(?)	,, ,,
33.	,, ,,	Pomerania ...	(?)	,, ,,
34.	,, ,,	Algeria	(?) June, 1856	,, ,,

[1] *See* F. C. R. Jourdain, *Ibis*, 1913, p. 522. Although ascribed by Tristram to *A. aquaticus*, there is scarcely any doubt that these eggs are really those of the Reed-Warbler (*Acrocephalus streperus*).

EGGS OF BRITISH WARBLERS, Pl. II.

1.	Savi's Warbler ...	Hungary... ...	... ...	Mr. H. E. Howard's Collection.
2.	,, ,, ...	Algeria	1857	National Collection.
3.	,, ,, ...	Hungary... ...	... ...	,, ,,
4.	,, ,, ...	,, ...	29 May, 1899	Mr. F. C. Selous's Collection.
5.	,, ,, ...	Holland	2 June, 1859	National Collection.
6.	,, ,, ...	,, ...	20 ,, 1856	,, ,,
7.	Grasshopper Warbler	Norfolk	24 ,, 1906	Mr. J. M. Goodall's Collection.
8.	,, ,,	Sussex	12 May, 1881	National Collection.
9.	,, ,,	Moscow	5 June, (?)	,, ,,
10.	,, ,,	Northumberland	20 May, 1867	,, ,,
11.	,, ,,	,,	17 ,, 1872	,, ,,
12.	,, ,,	Co. Waterford ...	31 ,, 1888	,, ,,
13.	,, ,,	Northumberland	14 ,, 1867	,, ,,
14.	,, ,,	Norfolk	1854	,, ,,
15.	,, ,,	Durham	13 May, 1854	,, ,,
16.	,, ,,	Norfolk	1854	,, ,,
17.	,, ,,	Surrey	(?)	,, ,,
18.	,, ,,	Middlesex ...	1856	,, ,,
19.	Chiff-chaff	North Germany	30 June, 1881	,, ,,
20.	,, ...	,, ,,	10 ,, 1871	,, ,,
21.	,, ...	France	... ...	,, ,,
22.	,, ...	,, ...	... ...	,,
23.	,, ...	,, ...	2 April, 1878	,, ,,
24.	,, ...	North Germany	27 May, 1873	,, ,,
25.	Willow Warbler ...	Surrey	20 ,, 1902	Mr. F. C. Selous's Collection.
26.	,, ,, ...	Norfolk	16 ,, 1878	National Collection.
27.	,, ,, ...	Surrey	1862	,, ,,
31.	,, ,, ...	Essex	15 ,, 1862	,, ,,
32.	,, ,, ...	Norfolk	3 June, 1877	,, ,,
28.	Wood Warbler ...	France	(?)	,, ,,
29.	,, ,, ...	North Germany	6 June, 1879	,, ,,
30.	,, ,, ...	Cambridge ...	(?)	,, ,,
36.	,, ,, ...	North Germany	1 June, 1874	,, ,,
37.	,, ,, ...	Finchley... ...	(?)	,, ,,
33.	Melodious Warbler...	Algeria	27 May, 1857	,, ,,
34.	Icterine Warbler ...	Holland	1855	,, ,,
35.	,, ,, ...	North Germany	... ...	,, ,,
38.	Dartford Warbler ...	Surrey	6 June, 1866	,, ,,
39.	,, ,, ...	,, ...	(?) ,, 1860	,, ,,
40.	,, ,, ...	Tunisia	(?)	,, ,,
41.	,, ,, ...	Malaga, S. Spain	(?)	Mr. A. W. Johnson's Collection.
42.	,, ,, ...	Surrey	(?)	National Collection.
43.	,, ,, ...	,, ...	(?) June, 1862	,, ,,
44.	,, ,, ...	,, ...	(?) ,, 1860	,, ,,



H. GRÖNVOLD PINXT. C. HODGES & SON, LITH.

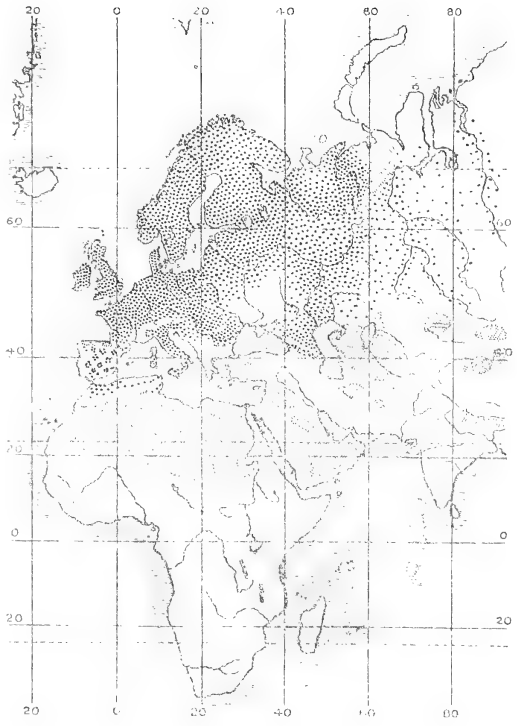
EGGS OF BRITISH WARBLERS. PL. III.

1-10 BLACKCAP. 11-20 GARDEN-W. 21-25 LESSER WHITETHROAT.
26-35 WHITETHROAT.

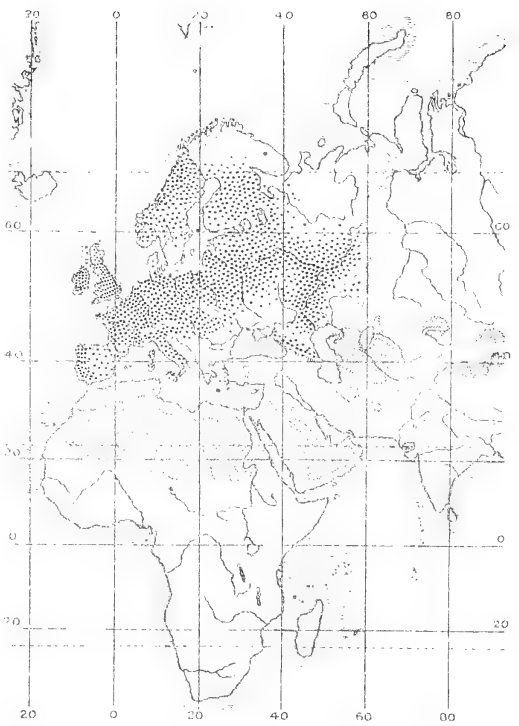
PUBLISHED BY R.H. PORTER.

EGGS OF BRITISH WARBLERS, Pl. III.

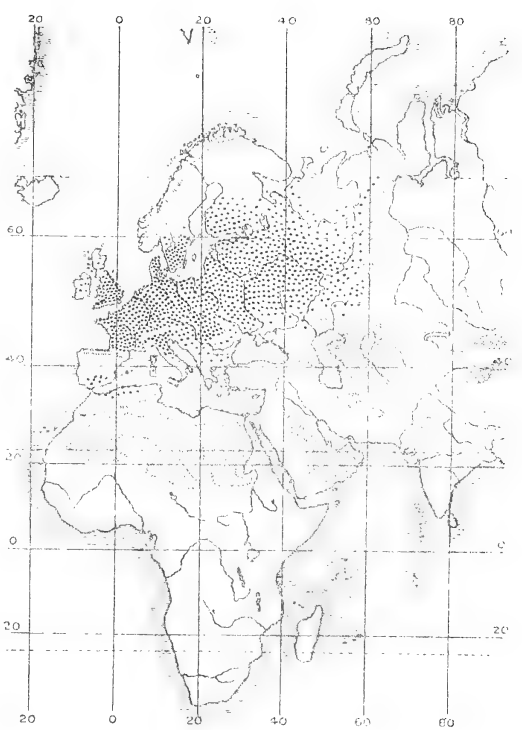
1.	Blackcap	Tenerife	19 March, 1889	National Collection.
2.	,, ...	Pomerania ...	8 June, 1875	,, ,,
3.	,, ...	Hampshire ...	(?) May, 1878	,, ,,
4.	,, ...	Surrey ...	(?)	,, ,,
5.	,, ...	Normandy ...	1 May, 1867	,, ,,
6.	,, ...	Alton, Hampshire	(?) June, 1862	,, ,,
7.	,, ...	Surrey ...	(?)	,, ,,
8.	,, ...	Pomerania ...	10 June, 1879	,, ,,
9.	,, ...	,, ...	4 ,, 1872	,, ,,
10.	,, ...	Middlesex ...	11 Aug., 1869	,, ,,
11.	Garden Warbler ...	Derbyshire ...	May, 1910	Rev. F. C. R. Jourdain's Collection.
12.	,, ,, ...	Norfolk	4 Aug., 1862	National Collection
13.	,, ,, ...	Perthshire ...	(?)	,, ,,
14.	,, ,, ...	Norfolk	(?)	,, ,,
15.	,, ,, ...	Holland	28 May, 1876	,, ,,
16.	,, ,, ...	Surrey	12 June, 1879	,, ,,
17.	,, ,, ...	N. Germany ...	12 June, (?)	,, ,,
18.	,, ,, ...	,, ...	May, 1880	Rev. F. C. R. Jourdain's Collection.
19.	,, ,, ...	Derbyshire ...	28 May, 1912	,, ,,
20.	,, ,, ...	,, ...	2 June, 1901	,, ,,
21.	Lesser Whitethroat...	England ...	(?)	,, ,,
22.	,, ,, ...	Surrey ...	(?) May, 1860	,, ,,
23.	,, ,, ...	Parnassus ...	16 May, 1873	,, ,,
24.	,, ,, ...	Hampstead ...	(?) 1856	,, ,,
25.	,, ,, ...	Norfolk ...	23 May, 1856	,, ,,
26.	Common Whitethroat	Norfolk	31 May, 1875	,, ,,
27.	,, ,,	Buckinghamshire	No date ...	,, ,,
28.	,, ,,	Inverness ...	1 June, 1871	,, ,,
29.	,, ,,	Holland	28 May, 1876	,, ,,
30.	,, ,,	Epping	(?) 1885	,, ,,
31.	,, ,,	England	No date ...	,, ,,
32.	,, ,,	Worcestershire ...	23 June, 1907	Mr. G. E. Lodge's Collection.
33.	,, ,,	Surrey	No date ...	National Collection.
34.	,, ,,	Leicestershire ...	27 May, 1906	Rev. F. C. R. Jourdain's Collection.
35.	,, ,,	Hampshire ...	(?) June, 1860	National Collection.



WILLOW-WARBLER



CHIFF-CHAFF.



WOOD-WARBLER.

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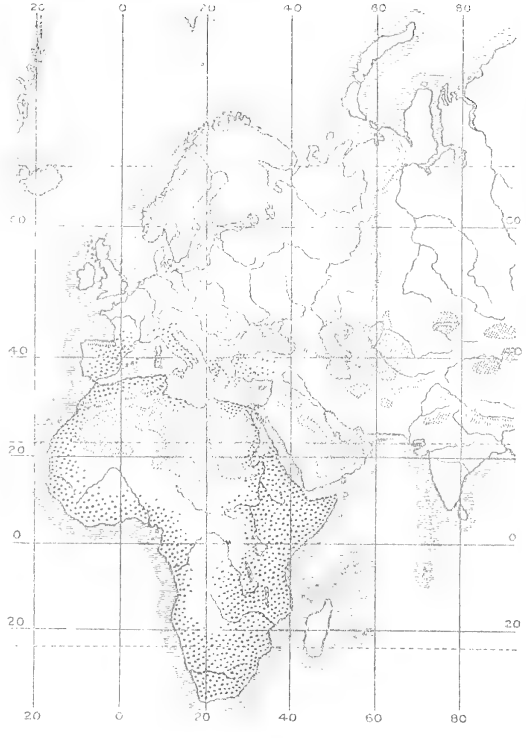
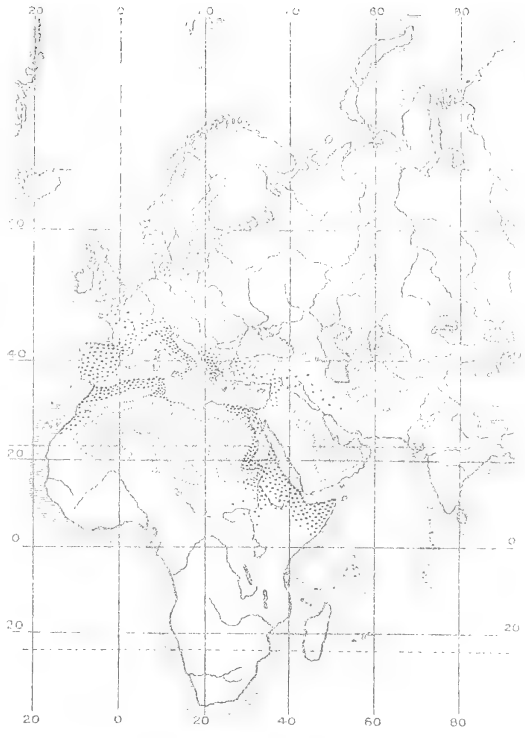
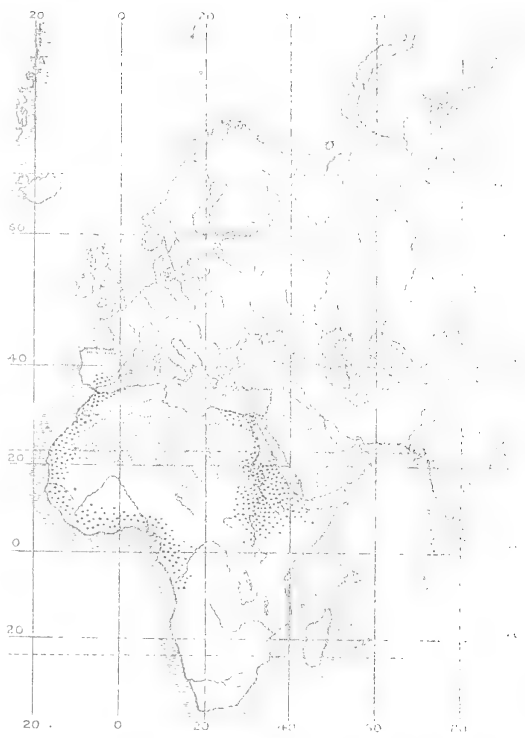


WILLOW-WARBLER.



CHIFF-CHAFF.



WOOD WARBLER.

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INDEX.

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THE BRITISH WARBLERS

A HISTORY WITH PROBLEMS OF THEIR LIVES

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

VOL. I

With 17 Coloured and 30 Photogravure Plates and 4 Maps

London

R. H. PORTER

7, PRINCES STREET, CAVENDISH SQUARE, W.

1907—1914

MEÆ CONJUGI DILECTISSIMÆ CUI DEBENTUR OPERIS
INCEPTIO INSPIRATIOQUE, DEDICATUS EST HIC LIBER.

PREFACE.

When first it occurred to me to record certain facts which I had observed in regard to the behaviour of some of the Warblers, my intention was to include only those species whose habits and instincts I felt I could discuss with some authority as a result of systematic and prolonged study. But it soon became evident that the inclusion of a number of species which, during migration, rest for a while on some of the most inhospitable parts of our shores might be desirable, and I therefore decided that a coloured figure of these rarer species, together with a description of their plumage and a short account of their distribution, should form a part of this work. Opinion will probably be divided as to the wisdom of this decision; some will no doubt think that their inclusion adds little to the value whilst certainly contributing largely to the expense.

It is inevitable that one's views become modified or even altered in the course of time, and during the progress of this work, which has extended over a period of some seven or eight years, I have from time to time been conscious of the fact that I was departing to some extent from views expressed, perhaps too strongly, at the commencement. I must therefore plead for some indulgence and ask that the various life histories shall be read in the order in which they appeared.

It only remains for me to acknowledge my indebtedness to those who have so kindly given their assistance. Professor Goeldi, M. Buturlin, Dr. Otto Herman, Count Salvadori, Mr. H. F. Witherby and Mr. Collingwood Ingram have supplied me with valuable information concerning geographical distribution, and in this respect also the Rev. F. C. R. Jourdain

has been kind enough to give me the benefit of his wide experience in the case of many species. I must especially thank Professor Lloyd Morgan, Mr. W. P. Pycraft and Mr. G. E. Lodge for many valuable criticisms and suggestions, Mr. E. W. Hopewell for his great care in revising the proof-sheets, and Mr. H. Grönvold for the infinite pains he has taken in carrying out my wishes.

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ERRATA.

xi. p. 2, line 3. The specimen obtained at Suleskerry Lighthouse has been proved to be an example of *P. borealis*.

xx. p. 3, line 32. The winter range does not extend south of Zanzibar.

xxi. p. 20, line 11. For "former" read "first-named."

xxi. p. 14, line 15. For "That bird" read "The Whitethroat."

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COLLATION OF LETTERPRESS.

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