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PAPERS.

33. The Courtship-habits * of the Great Crested Grebe (*Podiceps cristatus*); with an addition to the Theory of Sexual Selection. By JULIAN S. HUXLEY, B.A., Professor of Biology in the Rice Institute, Houston, Texas †.

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(Plates I. & II.‡)

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* It was not until this paper was in print that I realized that the word *Courtship* is perhaps misleading as applied to the incidents here recorded. While Courtship should, strictly speaking, denote only *ante-nuptial* behaviour, it may readily be extended to include any behaviour by which an organism of one sex seeks to "win over" one of the opposite sex. It will be seen that the behaviour of the Grebe cannot be included under this. "Love-habits" would be a better term in some ways; for the present, however, it is sufficient to point out the inadequacy of the present biological terminology.

† Communicated by the SECRETARY.

‡ For explanation of the Plates see p. 561.

PART I.

1. Introduction.

In these days the camera almost monopolizes the time and attention of those who take an interest in the life of birds. It has rendered splendid service, but I believe that it has almost exhausted its first field. At the present moment both zoology and photography would profit if naturalists for a little time would drop the camera in favour of the field-glass and the note-book. For the many who do not care about using a telescope, the prismatic binocular has more than doubled the possibilities of field-observation; and when full advantage shall have been taken of those possibilities, not only will science be the richer for a multitude of facts, but then, and only then, will the photographer, now hard-pressed for new subjects, suddenly find a number of fresh avenues opened up to him.

This second paper on the courtship-habits of British birds, like the first, will, I hope, help to show what wealth of interesting things still lie hidden in and about the breeding places of familiar birds. A good glass, a note-book, some patience, and a spare fortnight in the spring—with these I not only managed to discover many unknown facts about the Crested Grebe, but also had one of the pleasantest of holidays. "Go thou and do likewise."

I shall first give a connected account of my own and others' observations, followed by a discussion; and in a second part or appendix I shall give in detail some of the material worked up in the first part, as well as some notes on various points not connected with the main subject of the paper.

2. Appearance.

Structure first, function afterwards: I must describe something of the bird's appearance before attempting to give an account of its habits, though I shall try to be as brief as possible, since any

standard work of descriptive ornithology will give full details of the plumage and taxonomic characters. The Great Crested Grebe, then, is of course a water-bird, and essentially a diving-bird. Its tail is remarkable in being reduced to a few tiny feathers, and its legs are set as far back as possible, so as to have the position of a ship's propellers. Its body is long and approaches the cylindrical; the neck is very long and flexible, the head flat, the beak sharp, long, and powerful. In colour, the Great Crested Grebe has back and flanks of much the same smoky mottled brown as its small cousin, the Dabchick; the underparts, however, including the chin, throat, and front of the neck, are of an exquisitely pure white (furnishing the "Grebe" of commerce). The back of the neck is very dark brown.

The chief ornament of the bird, the crest from which it takes its name, is reserved for the head. In these pages I shall use the word *crest* to denote *all the erectile feathers of the head taken together*. The crest, as thus defined, consists of two parts—the *ear-tufts* (or *ears*, as for brevity's sake they may be called) and the *ruff*.

Both are composed of special narrow, elongated feathers, stiff, and formed of comparatively few barbs. Those constituting the ears are black, all of about the same length, and spring in two tufts from the top of the head, above the tympanum. The ruff is bigger and more elaborate: it consists of a broad band of feathers springing from the sides of the face and head, their free ends pointing downwards and backwards on either side of the neck. If we take the part of the head behind the eye, we find that at first the feathers are of the ordinary length, then slightly elongated (the beginning of the ruff), and then longer and longer till we get to the hinder border of the ruff. Corresponding to the increase of length there is a change in colour. The proximal (upper) part of the ruff is white, then we get to vivid chestnut, and this deepens gradually to glossy black (see any good picture of the Crested Grebe).

Both ruff and ears are extremely erectile; and as the birds make great play with them during all the actions of courtship, the various positions into which they can be put must be described.

Let us begin with the ears. These, when depressed or shut, stretch straight out backwards, continuing the line of the flat head's crown. When shut forcibly, the feathers of which they are made are close together and all parallel.

Often, however, they are not thus "at attention," but "standing at ease," to use a military metaphor: then the tufts as a whole point in the same direction, but their component feathers diverge and bristle-out a bit. This seems to be the usual and most restful condition.

Further, the tufts may be erected: and they may be erected in two ways—either *laterally* or *vertically*. When erected laterally, they stick out horizontally at right angles to the head, so that

from the sides they can scarcely be seen, as they are end-on to the eyes. When erected vertically, they seem, when viewed from the side, to be sticking straight upwards; but when they are seen from in front, it is found that they diverge from each other at a considerable angle (Pls. I. & II. figs. 4, 5, 11). During erection, the individual feathers always diverge fanwise very considerably. Thus there are four conditions of the ear-tufts to be distinguished.

They may be:—(a) *Depressed.*
(1) *Shut tight.*
(2) *At rest* (relaxed).
(b) *Erected.*
(3) *Vertically.*
(4) *Laterally.*

The ruff is more complex in its attitudes, as in its structure. During depression it, too, may be either shut tight or lying easy. When really shut, it bears from the side a curious resemblance to the gill-covers of some eel-like fish: its rounded hinder border lies along the side of the cylindrical neck, whose outlines its own scarcely overlap, either dorsally or ventrally (fig. 1). When relaxed (at rest), this resemblance disappears, for the feathers all diverge slightly, and the smooth appearance of the surface is lost.

When the ruff is erected, the feathers composing it may be made to diverge in a single plane only, the original (longitudinal-vertical) plane of the "gill-cover," or they may diverge outwards as well, making an angle with the side of the head (movement in the transverse, as well as the sagittal plane). I do not think that they are ever moved in the transverse plane alone. As a result of these movements, three chief forms can be taken on by the ruff. First there is the *curtain form*, in which motion in the vertical plane alone takes place, the ventral edge being brought forward till it makes an acute angle with the line of the chin (fig. 3), the two halves thus hanging like curtains on either side of the head. Then there is the *pear-shaped* condition (figs. 4, 11), where there is a considerable amount of forward and a moderate amount of transverse motion. The ruff in this state has its vertical height greater than its breadth (fig. 5). Owing to the transverse bristling of the feathers, the two halves of the ruff almost blend into a single whole; they can scarcely be distinguished either from the front or, still less, from behind, whereas in the curtain form they are very distinct. Finally, there is the *elliptical form*, when, added to the same amount of longitudinal motion, the greatest possible amount of transverse bristling has taken place. The ruff is now actually broader than it is high (fig. 9), and the blending of the two halves is practically complete. There are, of course, intermediate states. Instead of "full pear-shaped," you may have "half pear-shaped"; and between pear-shaped and elliptical there comes the *circular*.

The three I have named, however, are those which the bird usually adopts.

The ruff, therefore, may be:—

(a) *Depressed.*
  (1) *Shut tight* ("gill-cover").
  (2) *At rest* (relaxed).

(b) *Erected.*
  (3) *Curtain-like* (motion of feathers in one plane).
  (4) *Pear-shaped* } (motion of feathers in two planes).
  (5) *Elliptical* }

By a combination of particular positions of ruff, ears, and neck, and sometimes wings and body too, the birds can assume a number of characteristic and often-recurring *attitudes*, which are the raw materials, so to speak, of all the elaborate *habits of courtship*.

Before giving any more definitions, I will now give an outline of the Grebe's annual history, and then go on to describe some of the actual happenings that I saw, in order to give an idea of the problems to be solved. Then I shall try to define and classify the various courtship-habits, and discuss the general bearing of the facts.

3. Annual History.

This is somewhat as follows *. About the first week of February they leave the sea-coast and fly back in bands to the inland waters where they breed. They live in flocks for about three weeks, and then start pairing-up. Pairing-up lasts altogether about a fortnight, bringing us to mid-March. From this time on to the end of summer, the unit is neither the flock nor the individual, but the family, represented at first by the pair. About the beginning of April nest-building begins, and by the end of the month every nest will have eggs. The family parties live together through the summer, though apparently the cock leaves the hen to look after the young when they are half-grown (Pycraft, '11). There is usually no second brood unless the first is destroyed. At the end of September they gather into flocks again, and live thus for well over a month, finally leaving for the sea-coast in the second week of November.

The period of pairing-up itself I have unfortunately not been able to observe; the keeper tells me that there is much flying and chasing about. The part played by the "courtship" in the actual pairing-up is thus left uncertain. From analogy with other birds and with ourselves we should expect that the chasing was the expression of felt but unreasoned likes and dislikes, and that the courtship-actions were only gone through *after* the two birds had become fairly well-disposed towards each other. The courtship-

* The dates refer to the movements of the birds at Tring Reservoir, and have been given me by the head-keeper there.

actions, I am told, are at any rate to be seen immediately after pairing-up.

4. Some Descriptions.

(*a*) Let us start with the commonest of all the scenes of courtship—the one which had first attracted and puzzled me years ago, and led me to choose the Grebe as a bird to watch.

As the birds ride on the water, very little of their under-surface is usually visible; but now and then a twinkle of white is seen. This may be merely a bird rolling half over to preen its belly; but if it proceed from two birds close together, this form of courtship is almost sure to be in progress. In such a case, the glass reveals that the two birds are always a pair, cock and hen; they are facing each other, their beaks perhaps a foot, perhaps a mere couple of inches apart, their necks held up perfectly straight and elongated to a truly surprising extent. It is this holding up of the neck that shows some of the white of throat and breast. Their ears are erected vertically and their ruffs are full pear-shaped. The few little feathers that do duty for a tail are cocked up as far as they will go—that is to say, about half an inch (fig. 11).

In this attitude the birds proceed to go through a curious set ritual.

Let us describe a particular case. A pair of birds, cock and hen, that had been fishing not far apart, suddenly approached each other, raising their necks and ruffs as they did so, till by the time they had got face to face they were in the attitude I have just described. Then they both began shaking their heads at each other in a peculiar and formal-looking manner. Each bird began by waggling its head violently from side to side, some four or five times in quick succession, like a man nodding emphatic dissent. Then the quick side-to-side motion gave place to a slow one, and the beak and head were swung slowly across and back, with a seemingly vague and enquiring action, as if the bird were searching the horizon for it knew not what. The head was moved back and forth perhaps a couple of times, and then the violent shaking began again. This alternation of shaking and slow side-to-side swinging was repeated over and over again by each bird: strangely enough, the pair kept no time with each other—the violent shakings of the two neither coincided nor alternated, but each shook and swung without any apparent reference to the other's rhythm.

After six or seven repetitions of the performance another action came in. After the slow swing and before the waggling (or sometimes, I think, taking the place of the slow swinging), but not every time, the bird bent its neck right back and down as if to preen its wings, put its beak under some of the wing-feathers near the tail, raised them an inch or so, let them fall, and brought its head swiftly back into position for another of the violent shakings. This action had obviously something to do with

preening, but had an extraordinary look, as of a stereotyped and meaningless relic. The birds seemed to be performing some routine-action absent-mindedly and by mere force of association, as one may sometimes see a man wind up his watch in the day-time, just because he has been changing his waistcoat.

Finally, after each bird had given about a dozen or fifteen violent shakes, with a corresponding number of slow swings and liftings of wings in between, they veered up into the wind almost simultaneously, lowered their crests, brought their necks down, and, in a word, became normal once more both in appearance and behaviour.

One must have names for things if one is going to discuss them, as any philosopher will tell you. So I propose to call a whole performance such as that just described *a bout of shaking*; each little time of violent waggling I shall call simply *a shake*, and shall measure the length of a bout by the number of shakes in it (counting the shakes of both birds added together). Finally, the curious actions resembling preening I shall call *habit-preening*, because I believe them to have (or rather, to have had) something to do with real preening, but, in the performance as gone through to-day, to have become a mere habit, vestigial so far as its original function is concerned.

(*b*) That is one little scene: now take another.

A solitary bird, which proved to be a hen, came flying over from one reservoir to another. She alighted near one shore and began swimming slowly across towards the other, meanwhile alternating between two attitudes.

First of all she arched her neck right forward till the bill, which pointed slightly downwards, was just above the water. The ears meanwhile were scarcely erected; the ruff was thrown forward in curtain-form, and thus, since the head had been brought so far forwards and downwards, actually swept the water on either side (fig. 3). So she progressed, looking from side to side, and now and then giving a short barking call. After four or five of these calls, which represented perhaps 20 or 30 seconds of time, she put down her ruff and raised her neck nearly straight up to enlarge her circle of vision.

After some seconds of looking about her in this position, she relapsed again into the first attitude—"with neck outstretched, you fancy how." This was repeated eight or nine times, till at last a cock, thirty or forty yards away, appeared to notice the calling bird. He pricked up his neck, looked towards her for a short time, and then dived. At this she changed her whole demeanour. Up went her wings: back between them, with erected ruff and ears, went her head. A glance at fig. 7 will show her attitude. The wings were brought up, half-spread on either side of the body, with their anterior border pointing downwards. They were almost in the transverse plane, but sloped slightly backwards from the water.

In this position the beautiful white bar formed by the marginal wing-coverts, along the anterior margin of the wing, and the broad white blaze formed by the secondaries, which are quite invisible when the wings are closed, shone out vividly. The gap between the wings was filled by the head; this from the front somewhat resembled an old-fashioned picture of the sun, with the ruff rayed out considerably all round, and the ears were erected laterally so as to fit on to the top of the ruff on either side. Below the head shone the white of the puffed-out breast. The bird's whole appearance was wonderfully striking, and as unlike as possible to that of its everyday self.

All this took but an instant; directly the cock had dived she was in this attitude. As she waited for his re-appearance she turned eagerly from side to side, swinging nearly to the right-about and back again as if not to miss him. Eventually he came up, three or four feet on the far side, and facing away from her in the most amazing attitude. I could scarcely believe my eyes. He seemed to grow out of the water. First his head, the ruff nearly circular, the beak pointing down along the neck in a stiff and peculiar manner; then the neck, quite straight and vertical; then the body, straight and vertical too; until finally the whole bird, save for a few inches, was standing erect in the water, and reminding me of nothing so much as the hypnotized phantom of a rather slender Penguin.

As I say, it grew out of the water, and as it grew it gradually revolved on its long axis until at its fullest height it came to face the hen. Though all this was done with an unhurried and uniform motion, yet of course it took very little time. Then from his stiff, erect position he sank slowly on to the surface; the hen meanwhile put down her wings and raised her neck; and the pair settled down to a bout of the head-shaking. Their attitudes and actions were practically the same as those of the pair described above, but the bout only lasted about half as long. It was ended by the two birds ceasing to shake and gradually drifting apart. Finally they put down their crests and went off together to preen themselves and fish.

These actions, too, must now be named. I propose to call the attitude of the hen as she searched and called for her mate the *Dundreary-attitude*, for the two halves of the ruff in curtain-form give the bird, especially when seen from the front, a considerable resemblance to that famous personage of the drama. The attitude later assumed by the hen, with head back and wings arched, shall be the *Cat-attitude*, for the round ruff gives the bird the look of a very contented and somewhat fat cat. The cock's combined dive and emergence I shall call the *Ghost-dive*. The whole ceremony I have called the Discovery Ceremony (see p. 512).

(*c*) Now for the highest development of the courtship-actions that I have seen. The incident I am going to describe took place in the middle of the hour-and-a-half's watching the results of

which are recorded on p. 549. A pair of birds had been preening themselves and fishing, with occasional languid bouts of head-shaking. After a dive they came up not far apart and swam together with outstretched necks, which, as they neared each other, they gradually raised, beginning to shake their heads a little at the same time. The raising and the shaking progressed simultaneously, till when the birds were face to face they were in the regular "shaking" attitude and waggling their heads with a vengeance. The bout of shaking thus begun was the longest I ever saw: between them the birds shook their heads no less than 84 times, and with as much vigour at the eighty-fourth as at the first shake. There was rather a curious difference between the cock and the hen. At first neither of the birds did any of the wing-lifting, the strange parody of preening described above, and there named habit-preening. After the fifteenth shake, the hen began to give an occasional wing-lift, and these became more and more frequent on her part, until after about the sixtieth shake she was turning round and putting her beak under her wing-feathers between nearly every shake. The cock, on the other hand, did not begin this habit-preening until after the fortieth shake, and even after that only repeated the trick at rare intervals.

At the close of the bout, the pair swung parallel, but did not bring their necks down. Nor did they lower their ruffs; on the contrary, they put them up still further, from the pear-shaped form customary for shaking to the extreme elliptical, bringing down their ears meanwhile from the vertical to the lateral position, so that the whole crest now appeared like a large chestnut-and-black Elizabethan ruff. This change in the crests made me think something exciting was going to happen. Sure enough, the hen soon dived. The cock waited in the same attitude, motionless, for perhaps a quarter of a minute. Then he, too, dived. Another quarter of a minute passed. Then the hen appeared again, and a second or two later, some twenty-five yards away, the cock came up as well.

They were in a crouching position, with necks bent forward, ruffs still elliptical, and both were holding in their beaks a bunch of dark ribbony weed, which they must have pulled from the bottom. The hen looked about her eagerly when she first came up; when the cock appeared she put her head down still further and swam straight towards him at a good pace. He caught sight of her almost immediately too, and likewise lowering his head, made off to meet her. They did not slacken speed at all, and I wondered what would happen when they met. My wonder was justified: when about a yard apart they both sprang up from the water into an almost erect position, looking somewhat like the "ghostly Penguin" already described. *Sprang* is perhaps too strong a word; there was no actual leap, but a very quick rising-up of the birds. The whole process, however, was much quicker and more vigorous than the slow "growing out of the water" of the ghost-dive. In addition, the head was here not

bent down along the neck, but held slightly back, the beak horizontal, still holding the weed. Carrying on with the impetus of their motion, the two birds came actually to touch each other with their breasts. From the common fulcrum thus formed bodies and necks alike sloped slightly back—the birds would have fallen forwards had each not thus supported the other. Only the very tip of the body was in the water, and there I could see a great splashing, showing that the legs were hard at work. The appearance either bird presented to its mate had changed altogether in an instant of time. Before, they had been black and dark mottled brown: they saw each other now all brilliant white, with chestnut and black surrounding the face in a circle.

In this position they stayed for a few seconds rocking gently from side to side upon the point of their breasts; it was an ecstatic motion, as if they were swaying to the music of a dance. Then, still rocking and still in contact, they settled very gradually down on to the surface of the water; so gradually did they sink that I should think their legs must have been continuously working against their weight. All this time, too, they had been shaking their heads violently at frequent intervals, and after coming down from the erect attitude they ended the performance by what was simply an ordinary bout of rather excited shaking; the only unusual thing about it was that the birds at the beginning were still, I think, actually touching each other. The weed by this time had all disappeared: what had happened to it was very hard to make out, but I believe that some of it was thrown away, and some of it eaten by the birds while settling down from the Penguin position.

In their final bout they shook about twenty times, getting less excited towards the end; they eventually drifted apart, put their crests down, and almost at once began to pick food off the surface of the water.

Let us call the diving for water-weed and the appearing again with it in the bill the *weed-trick*; and the rapid swimming together, with the subsequent figure erect breast-to-breast, let us call the *Penguin-dance*, for here once more the general resemblance to Penguins (exceptionally graceful ones, let us admit) forced itself upon the mind.

(*d*) One last scene before we pass from mere description to the heavier task of analysis.

Sitting on the bank one day, looking out over a broad belt of low flags and rushes which here took the place of the usual *Arundo*, I saw a Grebe come swimming steadily along parallel to the bank, bending its head forward a little with each stroke, as is the bird's way in all but very leisurely swimming. I happened to look further on in the direction in which it was going, and there, twenty or thirty yards ahead of it, I saw what I took to be a dead Grebe floating on the water. The body was rather humped up; the neck was extended perfectly straight in the line of the

body, flat upon the surface of the water; the ruff and ears were depressed (fig. 8). So convinced was I that this was a dead bird that I at once began revolving plans for wading in and fetching it out directly the other bird should have passed it by. Meanwhile, I wanted to see whether the living would show any interest in the dead, and was therefore much interested to see the swimming bird swim up to the tail-end of the corpse and then a little way alongside of it, bending its head down a bit as if to examine the body. Then it came back to the tail-end, and then, to my extreme bewilderment, proceeded to scramble out of the water on to the said tail-end; there it stood for some seconds, in the customary and very ungraceful out-of-water attitude—the body nearly upright, leaning slightly forward, the neck arched back and down, with a snaky Cormorant-look about it, the ruff and ears depressed. Then it proceeded to waddle awkwardly along the body to the head end, slipping off thence into the water and gracefulness once more. Hardly had it done this when the supposed corpse lifted its head and neck, gave a sort of jump, and it, too, was swimming in the water by the other's side. It was now seen that the "corpse" had been resting its body on a half-made nest whose top was scarcely above the water, and it was this which had given it the curious hunched-up look. The two swam about together for a bit, but soon parted company without evincing any further particular interest in each other.

Both these birds had crests of very much the average size, so that it was hard to tell their sex; but I think that the "corpse" was a hen, the other bird a cock.

The meaning of this action (which I only saw this one time) remained extremely problematical to me while I was at the Reservoirs. The mystery will, however, be solved in the next section, and so let us anticipate and call the attitude of the "corpse" the *passive*, that of the bird that climbed on the "corpse's" back the *active pairing attitude*.

5. The Relations of the Sexes in the Great Crested Grebe.

(i.) The Act of Pairing.

As I say, it was especially the proceeding last described which puzzled me; and it was not till I had got home and looked up the literature, that I found a welcome paper by Selous ('01) * which exactly dovetailed into my own observations. I had been mainly concerned with the behaviour of the birds on the open water and during incubation; he had paid special attention to nest-building and pairing His observations solve the mystery that has so far surrounded the Grebes' actual pairing; by them it is now established that the attitude which so puzzled me is adopted always, and only, for the purpose of coition, and that coition takes place solely on the nest. I should

* A short summary of this paper will be found on p. 529.

perhaps have said "on *a* nest"; for the birds may build several incomplete nests or platforms before one, finally chosen to be the true nest, is finished and laid in.

From Selous's observations, the actions and ceremonies connected with coition are quite elaborate—almost of the same order of elaboration as the courtship-ceremonies, though the two rituals are completely independent and appear to have developed along quite different lines.

We have already got to know the *passive* and the *active pairing attitudes*. To complete the description of the mere attitudes, it remains to add that, before sinking down into the passive pairing attitude (which Selous calls "lying along the water"), the birds usually assume a curious fixed and rigid pose. I will quote Selous's words:—"... curling his neck over and down, with the bill pointing at the ground [weeds], perhaps six inches above it, he stood thus, fixed and rigid, for some moments (as though making a point) before sinking down and lying all along. There was no mistaking the entirely sexual character of this strange performance, the peculiar fixed rigidity full of import and expression."

We must now see how the *attitudes* are combined in the *actions* themselves.

In the first place, we have the *active pairing attitude* and the actions associated with it. These actions in pairing have been already once described, and they seem to show little variation. The bird leaps up, and comes down almost upright near the other's tail. Copulation is then attempted. Selous found it hard to decide if such an attempt was successful or not. When it seemed successful, the birds apparently uttered a louder cry than usual, and afterwards their behaviour had a satisfied look. Once, however, when the birds seemed thus satisfied, he adds: "The time occupied was extremely short, and one would hardly have thought from the position of the two birds that actual pairing had been possible." In other cases he could be fairly sure that the attempt was not successful. Whether successful or not, the act always ends in the peculiar way already described: the active bird waddles forwards along the other's body, and walks somehow over its head into the water, upon which the passive bird raises its neck, leaves the nest or platform, and swims away in normal position.

In the second place, we find that the *passive attitude* ("lying along") may take place either on the nest or platform itself, or else on the open water (but then apparently never far from the nest); the act of pairing itself, however, is possible only when the "passive" bird is lying on some firm support. In the second place, both cock and hen go into this attitude (the precise attitude which the lower bird assumes during the act of coition) indiscriminately: Selous's records give an approximately equal number of times for the two sexes.

However, before trying to draw any general conclusions, let us

take a particular case—that described by Selous on pp. 180–181 of his paper :—

About an hour earlier in the day there had been an attempt at pairing. Then, after a period of rest on the open water, the birds swam together towards the nest (which had been built the day before). When just outside the bed of reeds in which the nest was situated, the hen went into the passive attitude, on the open water. The cock came up to her, swam a few yards past her, went twice back to her and away again, then went right into the weeds and himself lay along the water in the passive attitude. While he was doing this (or immediately afterwards) the hen swam to the nest, leapt on to it, and sank down in the passive attitude once more. Upon this the cock came up to the nest, jumped on to the hen's back, and they apparently paired successfully, both birds meanwhile uttering a special shrill screaming cry.

Here are various points to be noticed. The *joint approach* of the birds to the neighbourhood of the nest is invariable when they have previously been some distance away. When one bird is sitting, or when both are already close to the nest, as when building is in progress, the case is of course different (p. 533); but in the period between nest-building and incubation they seem never to approach the nest singly.

The passive attitude on the open water close to the weeds and nest may or may not be assumed. In the three cases where this happened and Selous is absolutely sure of his facts, the bird that assumed this position was the female, and was also the leader in the procession towards the weeds. (We want to know more about this. It seems probable, from other considerations, that it is a mere coincidence for the leader to have been always the hen; but, this being granted, it is quite likely that the leading bird would be the more eager, and so would hasten to put itself into the attitude which apparently expresses readiness to pair.) In other cases the birds swam straight to the nest, and one of them ascended it and then went into the passive position.

Next, the way in which the cock swam about close to the hen while she was in the passive attitude, but still on the open water, "as though about to pair" (I quote Selous), is interesting. There must be a strong association established between the sight of the passive attitude and the desire to pair, so that the active bird shows its thoughts, so to speak, even when pairing is impossible (as when the passive bird is on the open water).

When the passive bird has gone into position on the nest, it is very nearly always the case that the active bird comes up to the passive one and examines it or swims about a bit, whether an attempt to pair is afterwards made (Selous, '01, pp. 180, 345) or not (*loc. cit.* pp. 165, 344, etc.). Sometimes the second bird is not eager, and refuses to come near at all (*e. g.*, *loc. cit.* pp. 172, 456). At other times (*loc. cit.* p. 341, and perhaps p. 181) an attempt

to pair is made, and the active bird jumps up apparently at once, without any delay. In the case observed by me the active bird seemed very definitely to examine the passive one, poking its beak down close to it; but the examination was very short, the attempt at pairing following immediately.

When the active bird is moderately eager but not quite eager enough to attempt to pair, it may swim up to the passive bird a number of times, each time make as if to spring up, and then decide not to, but swim away again.

The assumption of the passive attitude by one bird is generally, so far as I can see, used as an invitation to the other bird to pair: perhaps I should express myself rather differently, and say that it always denotes readiness to pair, and is generally used as a *primary excitant—i. e.*, it is the first sign given by either of the birds of readiness to pair. This is well brought out by incidents such as this:—Both birds are building the nest; suddenly the hen jumps up on to the nest and goes into the passive attitude, every now and then raising her neck and looking round at the cock (Selous, *op. cit.*). At other times it may be only a *secondary excitant*—a mere symbol. This may happen when one bird is sitting and the other approaches the nest; the sitting bird may then assume the passive position at each approach of the other. Here the *approach* is the primary stimulus, and the assumption of the passive attitude is called forth by it, and not by internal causes. In this second case a less degree of "sexual feeling" is presumably needed to induce the passive attitude than in the first case.

But we are going too fast. We must not omit to notice the curious action of the cock in himself copying the hen's passive attitude. This action—one bird going into the passive attitude, the other coming up and examining it, and then going off and assuming the same attitude—appears only to occur when the first bird goes into position on the open water (and not on the nest), and even then not always. It seems, however, to happen in the majority of cases (though we are perforce generalizing from very few instances). It looks as if it were a signal to the first bird that the second was ready and willing to proceed further in the matter; for the birds after this may proceed together to the nest, where the first (*loc. cit.* p. 180) or the second (*ibid.* p. 456) bird ascends the nest and assumes the passive attitude once more. In other cases, however (*ibid.* pp. 179, 454), the affair ended with the second bird's assumption of the attitude. Here it looks as if a ritual ceremony was developing out of a useful action (see below).

As regards the actual act of pairing (or its attempt, which for our present purpose comes to the same thing), *the two sexes seem here also to play interchangeable roles.* In 1900 Selous saw three attempts to pair, one apparently successful, two unsuccessful: in all three cases the active bird was the larger of the pair. In 1901 he saw two attempts, both of which he thinks were

successful: here the active bird was in both cases the smaller of the pair.

Now, if we could be sure that the 1901 pair was the same that was there in 1900, all would be well: but we cannot be sure. There was a marked difference in the pairing-behaviour of the 1900 and 1901 pairs—a difference that cannot be referred back to the fact that in 1900 the birds were building a true nest and were incubating, while in 1901 they had only got to the length of building a pairing-platform. In 1900 the smaller bird (that we have so far presumed to be the hen) was more forward in invitation, while the active pairing-position was adopted by the larger bird alone; in 1901 the case was exactly reversed. It would be, in my opinion, more remarkable that such a change of character should take place in two birds in the space of one year than that the same water should be occupied by two different pairs—albeit but a single one—in two successive years. Mr. Selous, however, writes to me that for various reasons (*e. g.*, the site of the nest, etc.) he is practically convinced that the birds were the same in both years. However, whether the pair was the same pair or not, in both years there was a marked difference in size both of body and crest between the two birds of the pair, and, if all the books are not wrong, this should be quite enough to distinguish the sexes. Sometimes, it is true, the two birds of a pair are almost exactly alike; but nowhere do I find it stated that the hen is ever larger or has a better crest than the cock. It is the part of the professional ornithologist to find out if this is ever so; till then, we must be content to say that it is extremely probable that either cock or hen can play the "active" part in copulation—what we should usually call the male part. This can be more easily imagined in birds than in almost any other animals in which copulation takes place, but even in a bird is remarkable enough. Definite attitudes of the two participating organisms have been evolved to facilitate the passage of genital products in a definite direction: and here, hey presto! although the genital products continue to pass in the same direction, yet the attitudes, developed only in relation with and accessory to this direction, are at will reversed.

This facultative reversal of pairing-position would certainly be remarkable; but even for the moment supposing that it does *not* occur in our Grebe, it would merely appear as the as yet unattained end of a process of sex-equalization which in this species has already run a considerable course. This process consists in a gradual transference of all the secondary sexual characters of the male to the female, and *vice versa*. In its general aspect it will be discussed later; here it will be sufficient to consider it in relation to the pairing actions alone.

Let us see what is without doubt common to both sexes in the Crested Grebe to-day. First of all, we find that either cock or hen may lead the way towards the pairing-platform. Secondly, either cock or hen may assume the passive pairing-position (the

position that one would naturally call *female*) on the open water. Thirdly, either cock or hen may assume this position on the nest or pairing-platform. This is important, for the pairing-platform is never ascended except for the purpose of pairing, or for this position, which we may call the beginning of, or the invitation to, pairing, and the nest only ascended for these two purposes and for incubation. Fourthly, when one bird is in the passive position, the other, be it cock or hen, may come up to it, examine it, and make as if to leap up on to it, just as it often does before an actual attempt at pairing is made. The natural end of this sequence would be that, fifthly, either cock or hen might not only make as if to ascend into the active position, but actually do so. If the text-books are right in their descriptions of the sexes in the species, then we can say that this end has been reached, and that, as far as pairing-positions go, the sexes are interchangeable. If the text-books are wrong, then our evidence is simply insufficient. Here it can only be shown that, however incredible this reversal may appear, yet it is quite certain that in the Great Crested Grebe all the preliminary steps towards it have been already taken.

Further, Selous (*loc. cit.*) places on record some remarkable facts which show that reversal of pairing-attitude does take place in tame Pigeons. Here he several times saw, immediately after the act of pairing, the "male" bird crouch, and the "female" then get into the normal male attitude. The act of pairing was then gone through a second time, but with the attitudes of the birds reversed. See also Selous '02.

We have therefore evidence that the full reversal can take place, and now only want to be certain that it has taken place in this species. In any case we can say that characters (in this case *attitudes* and *actions* only) of the female have been transferred to the male, as well as characters of the male to the female.

We must now go on to consider a very different question, which is also well brought out in the pairing-habits of the Great Crested Grebe: I mean the gradual change of a useful action into a symbol and then into a ritual: or, in other words, the change by which the same act which first subserved a definite purpose directly comes later to subserve it only indirectly (symbolically), and then not at all. The action in question here is the passive pairing-attitude, and the Grebe is interesting as showing all three stages of the process at one time—the passive attitude employed sometimes directly, sometimes symbolically, and sometimes ritually. Speaking phylogenetically, we have the following steps:—

(1) The ascent on to a nest or platform, and the assumption of the passive attitude, are necessary if pairing is to take place, and the passive bird must get into position before the active bird can even begin its part in the coition act.

(2) The ascent and the attitude are used by the passive bird as

an incentive to the active bird, as a sign of readiness to pair. The active bird may or may not respond.

(3) As a symbol, the *attitude* is obviously more important than the actual ascent on to the nest, since the attitude is used only in pairing, while the birds may ascend the nest for various purposes; and, in addition, the assumption of the attitude comes after the ascent, and is thus in time more immediately associated with the act of pairing. Thus the attitude by itself comes to be used on the open water (though always close to the nest) as a sign of readiness to pair. We may say that readiness to pair is indicated precociously—it is pushed back a step. Such processes of pushing back are very common in early ontogeny; embryologists then say that the time of appearance of the character is *cœnogenetic* (even though the character itself, as here, may be palingenetic). The phylogenetic change has here been precisely similar; the only difference is that the displacement affects a mature instead of a very early period of life.

(4) The attitude being now sometimes a mere symbol can be, and is, employed by either the active or the passive bird. In fact, when one bird employs it thus symbolically, the other usually responds by immediately repeating this symbolic use.

(5) From useful symbolism to mere ritual is the last step—one that has taken place often enough in various human affairs. It appears that these actions and attitudes, once symbolic of certain states of mind and leading up to certain definite ends, lose their active symbolism and become ends in themselves. When I say that they lose their active symbolism, I mean that they are now not so much associated with readiness to pair as with the vague idea of pairing in general. Thus associated with pleasurable and exciting emotions, they may become the channels through which these emotions can express themselves, and so change from purposeful stimuli to further action into merely pleasurable self-exhausting processes (see below). It is at least hard to see how to explain such happenings as that described on p. 534, (*c*) 6, where first one bird and then the other goes into the passive position on the open water, after which there is simply a resumption of feeding or preening.

Another general point worth noticing is this:—In the case of this Grebe the male has even less possibility of enforcing his desires than the majority of birds. In a few birds the male is not so helpless. The ordinary Barndoor Cock, for instance, is often rather forcible in his methods. In the Wild Duck (*Anas boschas* L.) the drakes often kill the ducks by continued treading*. Somewhat similar forcible pairing is recorded of the Mute Swan (*Cygnus olor*). In such species it is by no means necessary for the race that the act of pairing should be particularly pleasant to the female. In most birds, however, the female has the upper hand: she can always prevent the cock

* Huxley, Biol. Centralbl. 1912.

from pairing with her, by simply running or flying away (*cf.* the Redshank, Huxley, '12$_1$). In our Grebe we are a step further still: not only must the female (or the passive bird, if we want to be precise; but this is, for the present, complicating the issue unnecessarily) be willing to pair, but she must also take the first steps—must ascend a nest or platform and assume a special position—before the cock can think of pairing. Here, therefore, supposing that the functions of the sexes had not been almost equally distributed, it would have been necessary for the hen to have had a strong impulse towards pairing; it might be that she was impelled directly by a violent physiological stimulus, or more indirectly by association, through the act being extremely pleasurable.

The phylogenetic course of events is hard to disentangle; we might suppose it to have been somewhat as follows:—

(1) Owing to the need of a firm support for pairing, it became necessary, as above set forth, for the female to take the initiative in the act of pairing, by assuming a special position.

(2) The male had thus no means of expressing his readiness to pair [whereas in most monogamous birds it is the male, as one would expect, who takes the initiative: *cf.* the Warblers (Howard, '13), the Redshank (Huxley, '12$_1$), etc.].

(3) Meanwhile, quite independently, a process, or tendency—call it what you will—had shown itself, by which the characters of one sex might be or tended to be transferred to the other, and *vice versa*.

(4) This was seized upon by Selection (we cannot as yet speak less metaphorically) and employed to supply the present want; the pairing attitude of the female was transferred to the male, to give him, too, a means of expressing his readiness to pair—to enable him, should he wish it, as well as the hen, to take the first step towards the performance of the act of copulation by the pair.

(5) As so often occurs, the process did not stop precisely at the desired spot (we still speak in metaphors, for brevity's sake); with the female pairing-attitude was transferred the female pairing-instinct, and so came about the complete or nearly complete facultative reversal of the pairing habits.

This naturally does not pretend to be more than a possible scheme; but it is worth while setting out such a scheme, merely to show how this "reversal of the sexes" could have come about.

(ii.) Courtship.

I have started with the subject of coition, because the first thing I want to make clear about the courtship-actions is their total lack of connection with the act of pairing itself—a notable fact, in which the Grebe differs radically, of course, from many other birds, especially those in which the sexes differ in appearance, *e. g.* the Bustard or the Peacock, but also some in which the sexes look alike, *e. g.* the Redshank.

In relation to this, no doubt, is the fact that pairing only takes place on the nest, and that the nest is hidden away among the reeds, while the courtship actions are, I believe, always gone through out on the open water. This, in itself, would not be conclusive evidence of total separation of the two sets of actions, for the performance out in the open might be followed directly by a return to the reeds and subsequent pairing. But there are two further facts which make it conclusive. In the first place, one of the reservoirs at Tring is completely bare of reeds, and consequently of Grebes' nests too. It is, however, the richest in fish, and numbers of Grebes fly over to it from the other reservoirs every day, and at all hours of the day, to feed. Now, in spite of the absence of reeds, and so of nests, and so of the possibility of pairing, the birds interrupt their fishing, or sleeping, or preening, to go through the ritual of courtship just as often on this reservoir as on any of the others. That is point number one.

Point number two goes still further.

I frequently kept individual pairs under observation for a considerable length of time, and then, if I watched long enough, always found that one set of courtship-activities would in point of fact be followed by a pretty long interval of resting or fishing, and that then this time spent in every-day affairs would be again succeeded by another series of courtship-actions—a proof that these actions are what we may call *self-exhausting* and not *excitatory*. The best record, because the longest, was on this same reedless reservoir. I had one pair under observation for an hour and forty minutes (section 10, record 11). During that time they had six simple bouts of shaking, and also two prodigious long bouts, followed each time by the diving for weed and then the strange Penguin-dance. And between all these elaborate displays of sexual emotion, no sign (or possibility) of pairing—nothing but swimming, resting, preening, and feeding.

I was thus—much against my preconceived ideas—driven to think of all the complicated postures and evolutions of courtship in the Grebes as being merely *an expression of emotion*.

The particular form of expression used is no doubt determined—predetermined—by the arrangement and innervation of certain structures which the birds possess: but the impulse to use the muscles and nerves is an emotional one—during courtship there must be in the mind of the bird an excitement, a definite feeling of emotion. Let us, to satisfy the physiologists, try to put it in terms of nerve-currents. One member of a pair is continually seeing its mate at its side. This, in its present physiological condition, stimulates certain tracts of its brain, charging them up and up until they are in a state of considerable tension (mental accompaniment:—state of diffused emotional excitement). Finally, the tension reaches the critical point, and a discharge follows. This discharge flows down hereditarily-determined paths, and actuates the muscles concerned in courtship (mental accompaniment:—violent and special emotion, quickly dissipating

itself with a sense of "something accomplished, something done.")

This merely indicates the possible material mechanism; of the actual, we know next to nothing. However, by comparing the actions of the birds with our own in circumstances as similar as possible, we can deduce the bird's emotions with much more probability of accuracy than we can possibly have about their nervous processes: that is to say, we can interpret the facts psychologically better than we can physiologically. I shall therefore (without begging any questions whatever) interpret processes of cause and effect in terms of mind whenever it suits my purpose so to do—which, as I just said, will be more often than not.

Let us take the parallel from human affairs. Far be it from me to go into the matter with a heavy hand: let us merely look at a few familiar facts in an unfamiliar biological light. The "courtship-actions" of man are mostly predetermined by heredity: any young couple that you like to take will be pretty certain to "express their emotion" by holding each other's hands, by putting their arms round each other's waists, or by kissing each other; and of this last action kissing on the mouth is the "highest development." Let us merely notice that these actions are not perhaps exactly parallel with what we find in the Grebe—that they are altogether more fluid, less fixed, and that they are sometimes less self-exhausting and more excitatory in character: on the whole, however, they are not very different. Moreover, in their case we know a great deal about the accompanying emotions, either from our own experience or from what others tell us. To take only the most specialized form of human courtship-actions, the kiss; although we know that it may act as an excitant (*cf.* Dante's famous lines on Paola and Francesca) yet the accompanying emotion is in itself quite special, different from all others, and the emotional process is usually something *an und für sich*, expressing itself in the action, and exhausting itself in the process with a feeling of inevitability. In the memory, however, it leaves its trace, and as it were desires to repeat itself, but only when the emotional tension shall again have risen (think of Plato's epigram to Agathon: or the lovers in Richard Feverel; or Romeo and Juliet). That will suffice to show what I mean by a self-exhausting expression of emotion. Such a process would be one that to the doer of it feels at the time almost inevitable, though he can only do it at certain moments. At other times, determined by his general mental state (*cf.* section 10, record 1), the action, however pleasant to recollection, is not "spontaneously" possible, and if performed is forced or at least not fully pleasurable. When normally executed, the action is accompanied by violent and pleasurable emotion, which usually dies down, or changes, into a quite different feeling, one of satisfaction, meanwhile leaving its mark in the memory. Its recollection then acts as a partial stimulus, so that next time it is a little more easily performed.

This will, in the first place, show how difficult, and almost inevitably futile, it is to try and deal with the emotional essence of things by the methods of "ordinary biology"; I think, however, that it will serve to explain what I mean by a self-exhausting expression of emotion, and will give the point of view from which to look at the facts of the Grebe's courtship: let us now go on to examine the facts themselves more systematically. I will take the different forms of courtship-action one by one, describe their usual occurrence and their relation to other actions, and then mention the most important variations or exceptions that I have seen.

The various attitudes already described are combined into definite *actions* or *ceremonies*.

(*a*) The simplest form of courtship-action is the *bout of shaking*, of which I have described a typical example. As already seen, shaking may take place either before or after other courtship-actions, but in perhaps the majority of cases it is not thus a link in a chain of processes, but a single self-originating and self-exhausting process. It varies a certain amount in intensity and in length, and also in the amount of habit-preening that takes place. Of this there may be none, or, towards the end of a bout, there may sometimes be more preens than shakes. The bouts seem, to the casual onlooker, to start themselves—in reality, I think, each bird excites the other. One gently shakes its head under the force of rising emotional tension; the other bird had not quite got to that stage, but the sight of its mate shaking acts as a stimulus, and it too pricks up its head a little and gives a shake. This reacts on the first bird, and so the excitement is mutually increased and the process fulfils itself—a very good example of "crowd-psychology," and also a good example of an epigenetic process *.

There is one well-marked variation of this form of courtship which seems to denote a higher level of excitement; it is especially common when a third bird has intruded into the domestic harmony of the pair and has been driven off (section 5, iv.).

Here the beaks are pointed somewhat downwards, the neck brought a little forward instead of vertical, the whole head brought forward and curved over, and the ruff erected more than usual (fig. 6). This attitude is almost always confined to the beginning of a bout, the birds sooner or later relapsing into the ordinary position.

The bout of shaking is not only the commonest form of courtship-action, but it also forms part of all the other more elaborate forms. It always ends the series of actions, and often begins them as well. It is as it were the foundation on which they are built, and was probably (if I may express a mere opinion) the earliest to appear in phylogeny.

The other ceremonies of courtship are all formed by the

* See also p. 544, where one bird won't shake, and the other wants to.

combination, in various arrangements, of the shaking-bout, the Dundreary, the Cat, the Ghost-dive, the weed-trick, and the Penguin-dance; in addition, they may be slightly modified by jealousy.

They can be divided into two groups: (1) those in which the Cat-position plays a prominent part, and (2) those into which weed-carrying enters. Let us consider them in this order.

The Cat-position forms a part of two quite distinct ceremonies, which, simply for the sake of ready reference, I shall call the *Ceremony of Discovery* and *the Display*. The first of these is gone through, as far as I can make out, when the two birds of a pair find and rejoin each other after being separated for some time. The second always occurs in the middle of a bout of shaking; on such occasions I presume that the shaking has not been "self-exhausting," but that the emotional excitement that accompanies it has reached a slightly higher level than usual, with the result that it overflows into a new nervous channel, and so expresses itself in this new way.

(b) *The Ceremony of Discovery.*—A typical case has already been described (p. 497). I should interpret the facts thus:—The two birds of a pair have become separated—perhaps they have gone off fishing in different directions, or one has been on the nest and the other has not stayed near by. They wish to rejoin each other. To this end the bird that is searching puts itself into a special attitude, which is probably adapted for uttering the special cry only heard on such occasions, and cruises about, alternating its signal-calls with moments of looking about it. On hearing the call, several neighbouring birds will usually prick up their necks and look about them; but I believe that it is usually only the searching bird's true mate who takes any further interest (this would doubtless depend on the emotional state of the neighbouring birds). Once this discovery of the missing mate has been made, a special ceremony takes place to celebrate the event. This ceremony is a peculiar one, and is practically confined to these occasions of discovery; very possibly the memory of the ceremony and its excitement adds to the eagerness felt by one bird of a pair to rejoin the other. The ceremony itself usually consists in this—the bird has been discovered dives, upon which the searcher puts itself into what I have called the Cat-attitude, a bizarre but beautiful position obviously recalling the elaborate displays of many other birds. In this attitude the searcher waits, almost always in a state of great excitement, as shown by its turning itself hither and thither, from side to side. It is stimulated to this excitement by the diving bird: first of all, as the dive is very shallow, the diver's approach is marked by a swift ripple of the surface; and then, when the diver at length appears, it is in a shape as unlike that of everyday life as is the "Cat-position" of the searcher—albeit the two are at opposite poles of the Grebe's capabilities. Sometimes the diver emerges when only

a few feet from the searcher. This is merely to reconnoitre his position; head and neck alone appear, the crest not erected, and are swiftly withdrawn again. The final appearance takes place almost always beyond the searcher, and the bird emerges with its back to the other, facing it only as, revolving on its axis, it settles down. The performance always ends with a bout of shaking.

Although in my "typical" cases the searcher has always been the female, yet the male may also search for his mate in the same way. I have watched an obvious cock in the regular Dundreary (search) attitude for a long time; only on this occasion no mate responded to the call. Further watching is necessary to see whether it is merely an accident that my searchers have usually been hens, or whether my observations represent reality. (It may possibly be connected with the fact that the hens seem to spend more time on the nest than the cocks; but this is mere conjecture.)

(c) *The Display Ceremony* is quite different. The birds are already together, and the display is simply a form of excitement similar to the bouts of shaking. In typical cases the pair will be indulging in a bout of shaking; suddenly one of them flies off a few yards and puts itself into the full Cat-position, showing its circular ruff and white-striped wings to its mate. There is no diving, however, and, after some seconds' display, the birds swim together and there is another bout of shaking; after this they simply swim off, or separate, or feed. Either cock or hen may go into the Cat-attitude. In one case the first bout of shaking had been preceded by a "flirtation" (p. 521) on the part of the cock.

To show how one ceremony may blend into another, I adduce the following instance:—There was a regular Discovery Ceremony, the hen calling to the cock, but with this difference, that they swam together, shook, and the hen flapped off and went into the Cat-position, and that only then did the cock remember, so to speak, to do the ghost-dive (p. 498). Another mixed "ceremony," this time more closely related to pure display, is related on p. 547.

(*d*) Finally comes the ceremony of the *Penguin-dance*. I have little to add to the description already given (p. 499). Twice, curiously enough, a single pair was seen to perform the dance twice in a morning. This might imply that some special physiological state, probably of high excitement, was necessary for the act, for I only saw it on two other occasions, and Selous only saw it once.

The performance can only be gone through when both are equally excited; for instance, once (p. 547) after a bout of shaking the cock dived and fetched weed from the bottom. The hen, however, was not stimulated to do so too, and when he came up he found no answering stimulus, and so dropped the weed as he swam towards his mate.

There is no reason for supposing even this elaborate ceremony to have any direct relation whatever with coition. It is a form

of excitement and enjoyment, seemingly as thrilling to the birds as it is to the watcher, but, like all the other courtship-actions, self-exhausting.

Very interesting "incomplete stages in development" of this ceremony were seen in one pair of birds, ranging from simple diving to the complete ceremony (see below).

(e) *Other Courtship Ceremonies.*

(1) *Back-to-back Ceremony.*

There are considerable individual variations in the courtship-activities of the Grebe, and I have seen occurrences which may well be interpreted as rudiments of new ceremonies. In one pair, for instance (section 10, record 12), the birds almost always went into a formal back to back, or rather tail to tail, attitude after each bout of shaking.

(2) *Diving Ceremony.*

Other actions seem to stand in some relation to the more highly-developed ceremonies. For instance (pp. 545, 552), simple diving, either by one or both birds, without any fetching of weed from the bottom, is introduced as part of the courtship between the two bouts of shaking.

(3) *Weed-trick Ceremony.*

In still other cases, the weed-trick is gone through and is followed immediately by a bout of shaking. In both pairs in which this was seen, one bird alone brought weed, although in one pair (not in the other) both had previously dived. I am inclined to believe (but more observations are needed) that two distinct ceremonies are here involved: first, the fetching and offering of weed by one bird, usually the cock, to its mate; and, secondly, a typically "mutual" ceremony involving simultaneous diving of both birds of a pair: and on to this latter the "penguin dance" has been grafted.

The offering of weed is strongly reminiscent of occurrences in the sex-differentiated, non-mutual courtships of other birds, such as the Warblers, where the cock often carries leaves or twigs in his mouth during sexual ecstasy (Howard). It seems to me probable that, since diving is necessary for weed-fetching, the one has come to be associated with the other, and the two ceremonies have come to be mixed up: in the extreme case on one side there is no mutual ceremony—only an offering of weed by one bird to the other; at the other extreme we have the complete penguin dance as described on p. 499, where both cock and hen bring up weed; and as intermediates we have mutual diving (p. 552) and mutual diving where the cock alone brings up weed (p. 552, end).

Taken all in all, the courtship is chiefly *mutual* and *self-exhausting*: the *excitatory, secondary-sexual* forms of courtship such as weed-offering or pure display serve not as excitants to

coition, as in most birds, but as excitants to some further act of courtship; and this is always a mutual and also a self-exhausting one. The excitants to coition are of a very special nature, and are symbols, rather than mere general excitants.

Habit-Preening. (See p. 497.)

This is very frequent, occurring in about half the bouts of shaking seen. The more excitement, the less preening, seems to be the rule; long bouts may sometimes degenerate into practically undiluted preening, the head simply being brought more or less up, but not shaken, between the "preens." It is always the hind end of the wings, I believe, which is raised and let fall by the beak.

In some way there must be a strong association between preening and head-shaking in the Grebe, for solitary birds who were really preening themselves I have several times seen raise their heads, slightly bristle their crests, and give a rudimentary shake. Why or how the association has taken place is more difficult to say. I certainly believe that the action I call habit-preening has been derived from true preening, and has been ceremonialized in the process of becoming part of a courtship-action. For the present we must leave it at that.

"Habit-Shaking."

That for some reason there is a very real association between shaking and preening is shown by the following facts. When actively engaged in real preening of themselves, the birds are often seen to lift their heads, give a rudimentary shake or two (without erecting ears or ruff) and then go back to business. This is generally seen when the bird is engaged in preening its hinder parts. We have observed it in autumn as well as in spring, and so it presumably takes place the year round; there is thus obviously a real association between the preening and the shaking, and the shaking is not a mere release of simpler sexual energy.

This is exactly the converse of what I have called "habit-preening," and may therefore appropriately be styled "habit-shaking."

There is thus a single association with a two-fold result. How it can possibly have arisen, or what purpose it can serve, remains to me at present an absolute mystery. I leave it as a puzzle to future bird-watchers and comparative psychologists.

Fighting between Cocks.

I saw very little of this beyond mere hostile expression (p. 521). Once, however, I saw two birds actually grappling: one was struggling half-submerged, while the other was more or less on top of it, and had hold of the feathers of the back of its opponent's head. After some considerable splashing and struggling, they separated and swam apart.

In birds which pair up early and remain "married" for the season, like the Grebe, one would, of course, not expect to find any of the regular combats seen in other species. It would be interesting to see whether there is more fighting in February, during the actual process of pairing-up.

The question must now be put—"What for?" What is the good of all these divings and posturings, these actions of courtship, these "expressions of emotion"? To what end are colours and structures developed solely to be used in them, and what return is got for the time and energy spent in carrying them out? They are common to both sexes, and so have nothing to do with any form of true sexual selection; they are self-exhausting processes, not leading up to or connected with coition, and so cannot be sexual excitants in the ordinary sense of the term.

It must be, however, that they fulfil some function; and I believe I know what this function is. I believe that the courtship ceremonies serve to keep the two birds of a pair together, and to keep them constant to each other.

The Great Crested Grebe is a species in which the two sexes play nearly equal parts in all activities concerned with the family. The cock shares equally in nest-building, nearly equally in incubation and early care of the young (it is only later that the young pass into the care of a single parent, probably the female, see Pycraft, '11). Thus, from the point of view of the species, it is obviously of importance that there should be a form of "marriage"—a constancy, at least for the season—between the members of a pair. The same result—marriage—is observable in such a species as man; but in man the main cause is a division of labour between male and female, whereas in the Grebe the sexes have been made as similar as possible. It would seem that the Grebes' family affairs had simply required more labour to be spent on them, and that Evolution had happened to go along the simple path of increasing the quantity of labour, by bringing the male in to do female's work, instead of improving the quality by adopting the principle of specialization.

Birds have obviously got to a pitch where their psychological states play an important part in their lives. Thus, if a method is to be devised for keeping two birds together, provision will have to be made for an interplay of consciousness or emotion between them. It would be biologically enough if they could both quite blindly, and separately, attend to the common object—nest, eggs, or young; but with brains like theirs there is bound to be a considerable amount of mental action and reaction between them. All birds express their feelings partly by voice, and very largely by motions of neck, wings, and tail; and not only this, but the expression can be, and is, employed as a form of language. This being so, we have here a basis on which can be reared various emotional methods of keeping birds of a pair together. As always, selection of accidental variations has led to very diverse results; so that we see this "emotional companionship" playing a

part in many apparently very different actions of birds. Herring-Gulls sit or stand close beside each other for hours together, occasionally rousing themselves to a joint ceremony of shaking their necks. As the Snipe drums overhead, there is often a call from the marsh below. Many birds when paired are always calling to each other, and probably singing birds sing partly to their mate; Dabchicks have a special spring note, usually given as a duet. As a very simple case, I have seen a pair of Blue Tits very recently paired up who, although feeding, were perpetually calling to each other and at frequent intervals coming close up side by side; it was perfectly obvious that they simply took pleasure in each other's presence, like the engaged couple that they were.

We have thus the following train of reasoning. Many birds must be kept in pairs during the breeding-season. This may be partly effected by the instincts of the separate birds—the instinct to build a nest, to sit on eggs, to feed young; and partly by instincts which only can find play when the two birds are together. These latter are often very emotional, and the courtship habits of the Grebe afford a very specialized example of this emotional bond between members of a pair.

If my contention is correct, it is clear that many actions and structures solely used in courtship are of use to the species, and not only to one sex of the species; these therefore must be maintained by Natural as opposed to Sexual Selection.

(iii.) Nest-building.

I rely almost entirely on the observations of Selous ('01, and see my Summary, section 8).

Materials.—Selous' nest was made mainly of dark ribbony weed, fetched from the bottom. Some surface-weed was also used. Besides this, such objects as water-lily stalks and large water-logged sticks are occasionally employed, the latter seeming to help anchor the nest. To steady the nest still further, the weeds are often woven among the stems of growing water-plants. As with other birds, the materials vary with the situation. In Arundo-beds the nest is very largely made of bits of reed-stem, though always with some weed; while elsewhere no reed is used at all.

Time, etc.—The main bulk of the nest appears to be built very quickly—in a few hours, in fact. This main portion is always built in the early morning (as with many other birds), and while on one day there may be no nest to be seen, by the next it may be nearly completed. In this very active building both cock and hen often take part simultaneously; they work very hard, averaging between them more than two cargoes of weed every minute, and going on for half an hour or an hour at a time without stopping.

After one nest has been built, another may be started (and

nearly finished) next day at no great distance. In the case noted by Selous, during the building of each nest the cock built himself a platform or rudimentary nest close to the bank and not far from the nest that was in progress. In the construction of this the hen did not share.

Functions of Nest.

There seem to be at least three kinds of nests—the true nests, the pairing platforms, and the cock's platforms.

(1) The true nests are bulky structures, rising well out of the water. A single pair of birds may build more than one. In one of these the eggs are finally laid. It is not known whether a pair always build more than one (probably not), nor whether, if more than one is built, it is always the last that is chosen to receive the eggs.

(2) The pairing platform (one seen by Selous and one by me) is a sodden, messy-looking structure, apparently much trodden down, and practically flush with the surface of the water. It seems to be used only as affording the necessary support for the action of pairing, and is apparently built some time before the true nest, *e. g.* Selous ('01, p. 339 *et seqq*) watched a pair for three weeks and saw no nest except a single platform, which was used exclusively for pairing (and pairing actions). It is distinctly improbable (from the appearance of all true nests that I have examined) that such a platform would be built up and turned into a true nest, though no evidence on this point is forthcoming.

What is certain, however, is that pairing need not always take place on such a platform, since Selous saw it occur on a true nest, and one which had probably one egg already in it. It appears to me likely that such platforms are built early in the season, when only copulation (or the preliminaries thereto), and not incubation, is in progress. Then, later, true nests are necessary to lay the eggs in, and once these are built copulation can take place in them just as well as on the platforms—*i. e.* the platforms are only temporary expedients, rendered necessary by the birds' pairing habits, and would thus phylogenetically appear to be degenerate nests.

(3) The platforms of the cock. These, too, are imperfect structures, and are probably also degenerate nests. In the case observed by Selous they were built close to the bank by the cock alone, during the construction of a true nest close by. When built, they were used (by the cock alone) as resting-places where he sat or, more frequently, stood.

Their true purpose is hard to see. It cannot be that the cock needs a resting-place more than the hen (unless—merely to state a case!—we suppose that in the month of May both sexes need

to rest on some firm support more than at other times, and that the hen incubates more than the cock, so that he has to build himself an extra resting-place). Possibly such platforms have something to do with receiving the young after hatching, and are built precociously. But this is mere guesswork—further watching must reveal their secret. Mr. Selous, in a letter to me, says he thinks now that the platform is due to an aberration of the nest-building instinct in the male. From Selous' own records, however, it is clear that the male certainly uses it to rest on.

Differences in building of the different kinds of nest.

The bulk of the true nest is built by both birds together in a very short time. After that, it seems to be casually added to during the time of incubation. This is useful, for the nest would otherwise get gradually pressed down into the water. It also tends to lose its slightly cupped form, and to remedy this the sitting bird may often be seen to pick bits of weed from the inside or the outside of the nest and lay them on the rim.

The cargoes of weed brought during incubation are often very small compared with those brought during the first building of the nest, and the whole action seems often to have rather the stamp of a habit about it—"I am going to the nest, so perhaps I had better bring a weed or two along."

During the main building, one bird sometimes sits on the nest for a short time; during this period one bird might also lie along the nest in the passive pairing position, as an invitation to the other to pair. But apparently pairing and pairing-actions are gone through more often when the bulk of the nest is finished, or when a platform alone exists—nest-construction thus appearing to use up most of the emotional energy of the birds.

The cock's platform.—It would be interesting to know if this is always made during the construction of the main nest, or if sometimes the cock set about it in cold blood, before or after the true nest was finished. It is quite possible that the cock and the hen stimulate each other to active nest-building as they do to courtship activities (p. 511), and that while they are in this excited state, and only then, some of the nest-building energy is, in the cock, diverted to his platform.

The pairing platform.—This (only one recorded case) was already built when Selous first noticed it. Only small pieces of weed were added to it, and usually "in a very perfunctory manner" (Selous, '01, p. 342). After one bird had unsuccessfully invited the other to pair, it often "manipulated the weeds a little with its bill" before coming off the platform.

We thus badly want to know about the building of the pairing platform; and also whether, during its construction, the cock builds a platform for himself, as he does during the building of the true nest.

Share of the sexes in nest-building.

The only data are based on the actions of a single pair—that observed by Selous in 1900; we must not, therefore, generalize too far. However, certain things emerge clearly. Both sexes work vigorously at the nest. During nest-building, the cock builds a platform by and for himself not far from the nest. In this particular pair the cock seemed slightly more active in nest-building, though the hen was more skilful. This may be, and probably is, merely an individual trait. As far as the building of the true nest goes, both sexes seem to be at least as similar as they are, for example, in appearance and in courtship habits. The mysterious platforms of the cock remain as one of the few truly secondary sexual characters of the species.

Psychology.

It seems probable that the same sort of psychological mechanism holds here as in courtship. Fetching weeds from the bottom and piling them in a heap is an instinctive act affording pleasure or relief. Although it is much easier to imagine a bird deriving pleasure from solitary nest-building than from solitary courtship action, yet here, too, it seems as if the cock and hen are mutually stimulated to activity. This is, at all events, an eminently useful trait, for it ensures that the nest shall be quickly built, that the pair shall keep together, that they shall build one nest at a time (instead of two, perhaps widely separated ones), and so forth.

That it is pleasurable may be further inferred from the fact that when the fever is upon them the birds may build two large nests in two successive days (Selous, *loc. cit*). This may seem wasteful, but here, as in so much else, Nature indulges in a considerable reserve—better too much than too little. This is the case with reserves of food, our own appetites, the number of times which most animals pair, the number of unpaired males in polygamous species and in Bees, etc., etc. Here, perhaps, the reserve is indirect rather than direct; it may not even be any advantage to have built two nests instead of one, but it may well be an advantage to have such a strong nest-building instinct that two or more nests happen to result, instead of one.

Finally, again, as in the courtship, association plays its part. What has once been done with pleasure, is done again easily as a habit. So when a bird is near the finished nest, and especially when the birds are there together, weeds are often added, but almost always in a more or less perfunctory way.

Why, after one bird has unsuccessfully invited its mate to pair on the platform, it should often dive and bring weed to the platform, I do not fully see. We can only say that diving and weed

are connected by separate and perhaps roundabout mental paths with nest-building, courtship, and pairing; and that what we know is only an outline of the birds' behaviour.

(iv.) Relations of different pairs to each other.

(Fuller details are given in Part II.)

The Great Crested Grebe, as we have already seen, pairs up very early in the season. What is the relation of the pairs of birds to one another?

As a general rule, the two birds of a pair seem to take very little notice of the rest of their species. Occasionally, however, there is some contact. There may be jealousy on the part of one bird, and this jealousy may, in any particular case, be merely precautionary, or actually justified by flirtatious behaviour on the part of the other bird of the pair; or there may be hostility between members of one pair and members of another.

Simple hostility is the rarer of the two: the only reason I can discover for it is the trespassing of one or both birds of a strange pair upon the "territory" of another (p. 558). In its symptoms there is nothing very remarkable: the birds go into the threatening Dundreary-attitude, often "barking" angrily at each other; finally, one may fly or dive at the other and drive it away, but often the very mild form of hostility involved in staying quite still, assuming the threatening attitude, and barking at the enemy (who is also doing the same) is all that happens.

It is much more interesting, however, to find in these birds what we had best call flirtation, as an accompaniment to their monogamy. The whole thing is very human: when one member of the pair is rather excited and the other is either lethargic or far away, there is no channel for the relief of its excitement. If a bird of opposite sex is in the neighbourhood, however, this would provide the desired relief, and the result is that the "temptation" is often too strong, and a bout of shaking ensues between two birds who are not mated. I have never actually seen such flirtations go beyond a bout of shaking; there is no reason that they should not, except that, as far as I could see, the birds did not seem to be used to each other, so to speak, and so their excitement often cooled down very quickly.

If the rightful mate sees what is going on, it is always roused to action, however lethargic it may have been before. It drives the odd bird away (often by a subaqueous attack with the beak) and then almost always has a strong bout of shaking with its mate. Thus all the anger of jealousy is directed against the usurper, not against the mate—which again is distinctly human! The "erring spouse" is always equally ready to shake with his mate as with the *tertium quid*—and often more so.

Here, again, the sexes are qualitatively alike—either will take

the initiative in flirtation, although from my records the cock seems to do so rather oftener than the hen.

Where there is a simple pleasurable ceremony, for whose performance two birds are necessary, it would seem quite natural that flirtation would occur. If the ceremony is an advantageous one, flirtation represents an overshooting of the mark by Natural Selection—a slight disharmony. "Adultery" I would think very improbable in this species, since the act of pairing is connected with a nest, built jointly by the pair, in a definite spot of their own territory.

(v.) Other Activities.

Incubation.

It appears that both sexes sit, but that probably the hen sits for a much longer time. Mr. A. T. A. Ritchie informs me that when there is a punt near the nest and the hen does not want to return to the eggs, the cock will often drive her to her duties.

Care of the Young.

After the young birds are hatched, both parents attend on them for some time; but later in the season, when the young are half-grown, the observations of Mr. W. P. Pycraft (Pycraft, '11) make it certain that only a single bird, probably the hen, looks after the brood.

Thus here there is no complete and qualitative division between the sexes, except in this last particular.

There is, however, rather more of a quantitative division than usual.

6. Discussion.

There are various considerable difficulties concerned with the courtship-structures and actions of the Great Crested Grebe. In the first place, it is clear, from what has been said, that in this bird there is no sexual selection in the ordinary sense of the word; the crest and the courtship-actions are almost identically developed in cock and hen alike.

On the other hand, the crest is only fully developed in the breeding-season, thus resembling true secondary sexual characters; and, as I have pointed out (Huxley, '12_2) it is used only in courtship, so that if not "secondary," it is at least "sexual." Further, the crest is smaller (though but slightly) in the female than in the male, a fact which it is, at first sight, simplest to explain by assuming that the crest was acquired by the cock as a secondary sexual character, and has now been almost completely transferred to the hen (*cf.* similar transference, complete or incomplete, in Lycænid and other butterflies (Weismann), Reindeer, mammæ of mammals, colours of many birds). We will revert to this point.

The courtship *actions*, however, can scarcely be explained by transference. The Penguin-dance, for instance, can never have been anything but a joint ceremony, equally shared by both sexes. Furthermore, even in the Dabchick, although it (and it alone in the subfamily) lacks all courtship-structures on the head, there is a *joint* courtship-action—the two birds come face to face, stretch up their necks, and emit the well-known cry. This being so, it is fairly clear that the ancestral courtship-actions of the Grebes were not in the nature of a display by one sex, but were joint actions of the pair. There is nothing especially remarkable in this. The display-courtships are, on the whole, more striking, and so have been more frequently described; but (to draw on my own limited experience) Razorbills and Herring-Gulls have very well-marked joint courtship-actions, although the actions are associated with no special structures whatever, and Selous has described other such actions in Swans, Divers, Guillemots, Fulmars, and other species.

I should put forward the theory that the courtship-habits of birds are based upon at least two totally different foundations: in the first place the actions gone through by males alone, apparently as the direct result of sexual eagerness (*solitary actions*), and, in the second place, the actions gone through by male and female together, and perhaps often (though by no means always) connected or associated with nest-building (*combined actions*). Primitively in neither case would there be any special structure or colour associated with the action. For solitary actions this is well seen in the dowdy Warblers, so fully described by Eliot Howard; here the cocks resemble the hens, but go through elaborate droopings of wings and fannings of tail, with bristlings of feathers on throat and crown. Later, Sexual Selection has stepped in, and naturally enough has taken what was already given, and added to it. The same instinctively-displayed parts—wings and tail, throat and crown—are the parts which are especially singled out for the development, first of special colours (Finches, Woodpeckers), then of special colours and structures combined (Turkey, Argus Pheasant, Blackcock, etc.). In combined actions a similar process has been gone through. In the Herring-Gull and Razorbill we have the instinctive actions pure and simple—a direct outcome of nervous excitement. Then, again, something has stepped in and used what was thus provided, and we get combined actions displaying colour (coloured mouths of Fulmar Petrels, Selous), and finally colour and structure, as in the Grebe. The members of the Heron tribe in general, and the Egrets in particular, have also ornamental structures common to both sexes; it would be very interesting to know the course of courtship in these birds. Pycraft ('13) figures a mutual display executed by the Kagu.

The question now arises, How have such colours and structures arisen? By Sexual Selection followed by transference, or by

some other process? Such other process can easily be imagined, and I feel confident that it has played a considerable part. We may call it *Double* or, better, *Mutual Sexual Selection* (*Mutual Selection* for short). Where combined courtship-actions exist, and a variation in the direction of bright colour or strange structure occurred, it would make the actions more exciting and enjoyable, and those birds which showed the new variation best would pair up first and peg out their "territories" for nesting before the others could get mates. The level would tend to be raised generation by generation. Mutual Selection is in a way a blend between Sexual and Natural Selection. The structures and actions arising under it have their immediate origin in the preferences of individual birds, not in anything outside the species, and in their immediate function they are entirely confined to the courtship. On the other hand, the mutual courtship itself, the activities of both birds taken together, may be of use to the species as a whole, in keeping the sexes together when necessary. Then the indirect function of all the shaking-bouts and displays of the Grebe is a function of use to the species, and besides the direct origin there is added an indirect origin under the pressure of Natural Selection.

Mutual Selection has a certain similarity with assortative mating, but is by no means the same thing. Like true Sexual Selection, it encourages an ever higher level in the development of a character, once variation has given it a basis to start from. In the Grebe the line of variation encouraged by Mutual Selection has been the tendency to produce ruffs and tufts of feathers on the head, and to go through actions involving, besides the use of these structures, diving and sporting with water-weed.

The question in the Grebe is complicated, as noted above, by the slightly less developed crest of the hen; this, however, might easily be accounted for by differences in the metabolism of cock and hen. The Discovery and (especially) the Display Ceremonies are also rather stumbling-blocks in the way of an explanation by Mutual Selection; they seem so very like the Displays of solitary courtship. However, even here the second bird plays a part, which in the Discovery Ceremony is at least as important as that of the displaying birds.

What is quite clear, however, is that, even supposing (what to me personally appears very doubtful) that ordinary Sexual Selection has "produced" the structures and the cat-position (we must know more about the habits of other species of the genus to decide this), yet it has gone hand-in-hand with a process of Mutual Sexual Selection as regards the majority of the actions. These actions (like the display of the Peacock, but unlike that of the Warblers) are much too elaborate and much too specialized to be considered as the immediate outcome of any form of physiological excitement. They obviously have a long and complicated evolution behind them, and, as they can only

be performed by the two birds together, there is nothing to account for them as they now stand but some such process as I have just sketched under the name of Mutual Selection

Then there comes the question of the facultative reversal of the act of pairing (or, possibly, only of preliminary pairing-attitudes). The other cases noted by Selous (Pigeon and Moorhen) differ in that the male crouched to the female directly after the act of pairing, who at once proceeded to play the male's part. In the Grebe there was always a long interval before the "reversal of instinct" took place.

In all, however, it is very difficult to see how to account for it, except on the assumption that there has been a reciprocal "transference" of pairing-instincts. This transference may be apparent or real. It is apparent if we believe that the units for such sexual characters are equally present in the germ-plasm of both sexes, and that the characters themselves do not appear in the other sex (or only appear as rudiments) as a result of the great primary sex-difference.

If the transference is real, then one must assume that the zygotic constitution of the two sexes is different in regard to secondary as well as primary differences, but that there is a constant tendency—depending on some as yet unknown process—to transfer such characters to the opposite sex. (Hybridization experiments, where the female of a species can transmit to her male hybrid offspring the secondary sexual characters of her own species, indicate that the first method is the true one.) How else than in one of these two ways can we explain transference in both directions? This is seen, for example, in man, where a male organ, the moustache, appears rudimentarily in the female, and female organs, the mammæ, appear rudimentarily in the male: in abnormal cases, besides, the transference may be complete, the organs being completely developed in the wrong sex. Such moustached women and men with breasts again support the idea that the transference is not a real transference, but consists in the removal of an inhibition only.

(I would not trouble to mention the theory that these appearances of characters of one sex in the other are due to descent from a hermaphrodite ancestor, were it not actually the case that Metchnikoff has advanced it. It is enough to point out that if this were so, the primitive mammal must have been a hermaphro lite.)

To us it makes little odds whether there is inhibition alone or transference followed by inhibition. In both cases the character will be in antagonism with the inhibitor: supposing that there is no longer any need to inhibit a character of one sex in the other, then on Darwinian and Weismannian principles the inhibiting "force" will atrophy, and the character, remaining as strong as ever, will appear equally in both sexes.

Apply this to the present case. Birds are for the most part

so constructed that impregnation would take place equally well whether the sexes are in normal or reversed position: that is to say, there is no necessity for keeping to the customary position—and accordingly "reciprocal transference" of the pairing attitudes (whether the transference be apparent or real) may, and quite probably will, take place. If so, then in one of our Grebes the instincts and reflexes for the pairing-actions proper to its sex co-exist side by side with those for the pairing-actions proper to the other sex. It is also obvious, first, that both cannot be gratified simultaneously; and, secondly, that these two very different sets of actions must be associated with two very different sets of emotional states. The bird may "feel female" or it may "feel male," and according to its feelings, so will it tend to act. But, as we saw before, in discussing the pairing-attitudes, it appears that, owing to the difficulty of coition in the Grebe, the "female" (passive) pairing-attitude has become a mere symbol of readiness to pair. Thus Natural Selection has come in to assist the slow process of transference (at any rate, so far as pairing-attitudes are concerned), and since whatever involves them will probably involve coition itself as well, we have an additional reason for believing that actual reversal of pairing does take place, as Selous supposes, in the Grebe.

At any rate, there can be no doubt about the reversal in the Pigeon and Moorhen. The sudden reversal that here takes place is rather different, but may be explained somewhat as follows:—Here, too, both active and passive instincts are now represented in either sex. A bird is in a state of sexual excitement; this excitement releases itself in the performance of, say, the male part in the act of pairing. The excitement is not always completely exhausted by the act, and, if so, the act is repeated (just as the shaking-bouts of the Grebes are continued for a longer or shorter time, according to the degree of what we may call courtship-excitement). But supposing that general sexual excitement arouses both the male and female emotional states, then the performance of the act once in the male attitude will only exhaust the feeling of "male excitement," leaving the "female feeling" still a-tingle. The result will be, first, an inducement to repeat the act and, secondly, an inducement to repeat it with attitudes reversed.

Thus such immediate reversal is more or less an accident of heredity, while the Grebe's reversal is an accident aided by the usefulness of the transferred actions, which thus bring the accident within the sway of Natural Selection.

This treatment of the question is of necessity sadly speculative, but it is our duty at least to try to construct a coherent mechanism of theory to explain the isolated facts of observation.

Finally, a word as to terminology. I have already pointed out (Huxley, '12$_2$) that the phrase *secondary sexual* cannot be applied to the Grebes' ruff and ears or to their courtship-actions, because

this term always implies a difference between the two sexes, and yet the crest of the Grebe has a sort of secondary sexual look about it—unreflectingly, one would at once write it down as such. This is due to our incomplete classification. We begin by separating out *sexual* characters from all others—these being characters that are different in the two sexes. We divide them into *primary*, *accessory*, and *secondary*. The mammæ of mammals (with the exception of man) have nothing to do with courtship or mating, yet they are usually included under the same heading as the tail of the Peacock, while the Grebes' courtship-structures would be left out in the cold.

Besides the mere criterion of difference in the two sexes, we must have some other criterion—a criterion of use.

It is naturally impossible to draw up any completed classification that will satisfy every case. To do so would be beyond the powers even of a Herbert Spencer—and not of much use when done.

It is enough to point out, first, that our group of Secondary Sexual Characters is a bit of an *omnium gatherum*. Some of them, as the mimicry of the female *Papilio*, or the brown colour of the female Pheasant, are protective, of use to the individual and to her offspring. Others, such as the mammæ of mammals, are of use only to the offspring; others, like the sexual differences in the beak of the Huia, where male and female hunt in couples, one splitting open the wood, the other picking out the hidden grubs, have arisen by a division of labour, and are of use to the couple as a couple. One might go on, but it would be unprofitable.

In the second place, we must recognize as a fact that the existence of individuals of separate sexes with wills of their own has led to the development of what we call courtship—simply a process in which a series of actions is carried out as the outcome of an emotional state based on sexual excitement. All courtship is based on sexual excitement, and characters connected with courtship merit a separate name of their own. This name lies ready to hand in Poulton's term *epigamic*; we must, however, remember that the literal meaning of the term must not be pressed, for in many cases the courtship ceremonies do not lead, directly or indirectly, to the act of pairing. Let us rather turn it the other way about, and, defining an *epigamic character* as one that is used in courtship, go on to define *courtship* as a series of actions based immediately or remotely upon sexual excitement, and, to make ourselves clear, we must add that sexual excitement is not merely sexual desire, but that whole emotional state into which a member of one sex may be thrown by a member of the other. The necessity for the distinction is obvious, if we think of the conditions in Man. Sexual excitement, of course, includes mere sexual desire, and also includes the fighting of males among each other as a result of sexual desire.

If we want a tabular statement, we can draw up something like the following *:—

(A) *Characters different in the two sexes.*
(*Sexual characters*).
(1) *Primary.* Of the gametes and gonads.
(2) *Accessory.* Concerned with the union of the gametes.
[Copulatory organs, pairing attitudes, sexual desire.]
(3) *Secondary.* All others.
(*a*) Developed through Natural Selection.
[Huia beak; mammæ; marsupium; incubation by ♀ alone in birds, &c.]
(*b*) Capable of being developed through Sexual Selection.
[Horns of deer; tail of Peacock, &c.]
(B) *Characters similar in the two sexes.*
(1) Capable of being developed through Mutual Selection.
[Grebes' courtship and crest; Herring-Gull's courtship, &c.]
(2) All other characters.

Epigamic.
(Courtship characters, i.e. *all* characters concerned with the *relations of the sexes*, excepting those connected immediately with coition.)

It might perhaps be better, as has been suggested to me, to restrict the term *Secondary Sexual* to 3*b*, and employ *Sex-limited* where I have employed *secondary sexual*. For one thing, however, this would conflict with Darwinian use; also, I am at present more concerned to show the necessity for new thinking than for new terminology, which will be more suitable in a more general and definitive paper.

I will conclude by hoping that anyone who has the opportunity will observe the habits of the Crested Grebe during the time of pairing-up in early spring; the full courtship of the Dabchick would also be of very great interest. In the near future, I hope to publish a more general paper upon Mutual Selection, so that any notes sent to me on this subject will be gratefully received and acknowledged.

For some further discussion, I refer the reader to the Postscript (p. 559).

PART II.

7. Locality, Methods, etc.

Through the kindness of the Hon. Walter Rothschild, I was given a permit to watch, and a punt to watch from, at the Tring Reservoirs. These consist of four large sheets of water in the eastern corner of Hertfordshire. Two have dense beds of reeds

* Simple sexual *desire*, if we adopt this scheme, we may call an *accessory* sexual emotion. Sexual *excitement* includes this, and all the *epigamic* sexual emotions as well. Pairing attitudes are accessory sexual attitudes. Let it, by the way, never be forgotten that *emotions* and *attitudes* are just as much *characters* as are *colours* or *structures*.

(chiefly *Arundo phragmites*) along one shore, affording cover for the nests of the Grebes, while the banks of the other two are bare. One of these latter is, however, very rich in fish, and a number of Grebes come over every day to feed on it. There, of course, they are nowhere near their nests, and this is of some importance in connection with the meaning of their courtship-actions.

As there were thirty pairs or more on the water, I was never at a loss for "material." In fact, it was often very hard for my pencil to keep up with the birds' actions.

Some of the watching was done concealed in the boathouses, and some from a screened punt, but the major part from the bank. This is in many ways the most useful. With good instruments* (in this case Goerz-Trieder binoculars $\times 12$ and a telescope $\times 30$) every action can be easily followed, the birds are not scared, the field of view is uninterrupted, and it is far easier to follow the actions of the same pair of birds for a long period of time.

This, as I say, is best for discovering the general course of events; but just as the microscopist must for certain details supplement his low-power lens with an immersion objective, so here, watching at close quarters must be adopted in order to work out the exact meaning of each separate bit of behaviour. Only when the general course of events has been roughly traced and some hypothesis, however vague, framed concerning it in the watcher's mind, can the fine shades of behaviour have any meaning for him. It is impossible to notice or record everything, and only when some general idea has been gained can the value of any fact be properly appreciated. It is on this account that I would say, always begin by distant watching; otherwise you will not be able to see the wood for the trees.

My brother, Mr. N. T. Huxley, spent much time watching, and several of the incidents here recorded are from his notes. His help was most valuable, and I wish to acknowledge it here. To Mr. James Street, Head Keeper at the Tring Reservoirs, I am indebted for much information, and for his help in arranging hiding-places, etc.

8. Abstract of Selous's Work.

I venture to append a short abstract which I had to make of Selous's diary notes for my own use, in hopes that others may find it useful too.

* A simple apparatus, which makes the task of simultaneous note-taking and observation very much easier, may be constructed as follows:—On to a folding camera tripod is screwed a ball-and-socket camera-holder (special telescope-holders can, I believe, be purchased); the field-glasses are clamped, by means of a long screw and nut, between two leather-lined pieces of wood, and the lower piece of wood can be screwed on to the platform of the ball-and-socket. Both for stationary and moving objects the fatigue of observation is enormously lessened by this means; in addition, one or both hands are left free, and so notes can be taken while watching—a necessity, almost, for reliable work.

The place of observation was a single large sheet of water. In 1900 he watched, fairly continuously, from April 27th to May 25th, except for a break of nine days (May 8th to 17th). At first there was but a single pair of Grebes. A nest was built, probably shortly before May 3rd. On May 3rd the birds paired (or attempted to pair) on the nest. A single egg was laid by May 3rd, a second before May 8th; then came a gap, and on the 17th the nest was destroyed by a boy. There was now a third bird, an odd male, on the lake. The hen "flirted" with him, but the "right" cock drove him away: and, although he stayed till the 22nd, he apparently remained alone and disconsolate all the time. In a single day (May 20th) the pair built a good portion of a second nest. This they continued to build during the 21st, the cock meanwhile building (by himself) a rudimentary nest or platform close to the bank. On the 22nd they were building another (third) nest in the reeds, the cock again building a (second) platform by the bank. On the 23rd there was an unsuccessful, and later a successful, attempt at pairing on the nest. On the 28th the nest seemed abandoned; however, when Selous returned, towards the end of July, there were two nearly full-grown young.

In 1901 he watched for a good part of April, then nearly continuously from April 22nd to May 14th, and then off and on till nearly the end of May. There was again a single pair on the water, and he believes these to have been the same birds as were there the year before. Before he started watching they had made a kind of nest, but a very poor one—a mere sodden heap of weeds scarcely showing above the surface and not at first sight to be easily distinguished from the growing weeds about it. This appears to have been only a pairing-platform. On the 25th they paired on this platform. On May 2nd they executed a regular weed-trick and Penguin-dance, and, some time afterwards, paired again on the platform. As time went on they grew less and less interesting, and it finally grew clear that they were not going to lay. On June 12th, when Selous visited the place after a fortnight's absence, there was no sign of the birds—they had gone for good.

That is the bald diary; now for the birds' behaviour. Under different headings I will summarize the actions of the "1900 pair," and the "1901 pair." (In passing, be it remarked that Selous has no proof that the birds he saw in 1901 were really the same as those of 1900. He says:—"As they were the one and only pair on the same sheet of water, and as the nest was in approximately the same place, I assume and feel personally quite certain that they were." However, there are certain definite differences in behaviour in 1900 and 1901, which make it at least possible that they were not the same pair.)

Nest-building.

(*a*) 1900.—Both birds may help in building the nest, usually diving to fetch weeds from the bottom, but sometimes gathering

them from the surface. The mass of weeds brought up by the bird may be very large—a good deal larger than the bird's head, indeed, with streamers trailing beyond the tail. One bird (usually the male) might bring weed to the nest while the other was incubating; when this was so, the sitting bird would generally arrange the weeds with its beak, though sometimes both would arrange the weed together. Weed was added to the nest for at least five days after the first egg was laid.

In the building of the second nest, he saw one morning the cock build a few minutes alone; then both cock and hen build together very hard for about forty-five minutes (74 cargoes in forty minutes); then the hen build a little by herself. The cock, meanwhile, after a short rest, began building a platform, acting precisely as when building the true nest. After fetching 28 cargoes he stopped and rested. The next morning the same great activity was visible; but now the birds were building a third (true) nest. In fifty minutes (including a pause) they brought 100 cargoes of weed, the last 10 or so being brought by the cock alone. This time the cock did not at first desert the nest altogether in favour of his platform, but every now and then diverted a cargo of weed to his own private platform-use. After a rest, however, he reversed his former behaviour; he now began working systematically at the platform, but occasionally took a cargo to the nest. Sometimes he seemed to hesitate between the nest and the platform. The next day there was a little more building, mainly by the cock, and after this no more records.

As to the part played in nest-building by cock and hen respectively, Selous says in regard to this pair:—"The interest taken by the male in the nest has been very marked throughout, more so even—in appearance, at any rate—than that of the female, though in the actual building of it she has been yet more efficient than he" (*l. c.* p. 179). Although he never carried quite so large a cargo as the hen sometimes did, yet his average was as good as hers, and when he swam with his burden to the nest he went much faster.

Sometimes the cock would pass his cargo of weeds to the hen, who (if she did not drop it) would put it on the nest. He never saw this action reversed, nor did he even see the hen help in the building of the cock's platform, or building one for herself alone. The hen alone brought large sticks to the nest (however, the cock was seen to bring a stick to his platform).

In the only recorded case where a nest was watched during incubation (Selous, *l. c.* pp. 161–170), the cock alone brought weeds to the nest, though the hen might arrange what he brought. This is probably of no importance. (The bulk of the nest was presumably built beforehand by both birds together.)

(*b*) 1901.—This year the only "nest" seen by Selous seems to have been a mere pairing-platform, the actual building of which was not observed. Occasionally the birds would add to it, but in a very perfunctory-looking way, and never more than a few bits of weed at a time.

Courtship-Actions.

Selous observed numerous *bouts of shaking*, which he refers to in various ways: *e. g.*, "They front each other in the water, and, with their snaky necks reared up, *tâter* a little with the beak, or make little tosses of their heads in the air" (*loc. cit.* p. 341). He has not, however, attended accurately to the positions of ruff and ears. All that can be said is that his pair (or two pairs) of birds certainly went through the ceremony of shaking, and apparently in just the same way as the many pairs seen by me. As far as I can judge (though judging is difficult) they did not shake quite so often. The important thing to notice, however, is that they did shake, even when they were quite alone on the water. That either jealousy or choice of mates should be the immediate cause, or purpose, of the action is thus absolutely excluded.

On p. 457 he says:—"They front each other with reared necks in the way often alluded to; then, without *tâter*-ing, each throws up the head several times into the air, at the same time opening and closing the long, slender bill." He obviously considers this as being different from the usual ceremony, and adds that he has seen the same action several times, though less pronounced. I think it probable, if not certain, that his eye was here simply caught by a somewhat more pronounced shake than usual, the process referred to as *tâter*-ing being then what I should call a bout of languid shaking; but in the absence of further details one cannot be sure.

A possible but rather rudimentary *display ceremony* is perhaps indicated on Selous's p. 340:—"Once, too, the male flies suddenly some way off over the water."

Then on p. 343 is described a very fine weed-trick and Penguin-dance. It started with a bout of shaking; then the hen dived and came up with a small piece of weed which she apparently dropped. Just before or just after the hen came up (probably before, to judge from my experience), the cock dived too, and brought up a large bunch of weed. They came face to face, and "all at once both leaped entirely upright in the water." The hen took hold of the dangling end of the weed which the cock was carrying, and then they "*chassé*d," "with little waddling steps" from side to side (in the case seen by me, the birds *rotated* slightly back and fro on their axis and did not actually move from side to side. I think Selous is mistaken: such an action as he describes would be impossible on open water). Finally they sank down again, the weed was dropped, and "the male sets off, full of intention, to the nest on the opposite shore." After some time the act of pairing was gone through. This is important as showing that this elaborate courtship-action may sometimes lead more or less directly to pairing, *i. e.* may act (more or less) as an excitant.

Finally, I must just refer to two more scenes. (1) (p. 163):—

"When just in front of each other one dives and brings up some weed, which they both discuss in the friendliest manner, pulling it about, and perhaps eating a little." (2) (p. 340):—"Once one of them—I think the male—comes up with something in his bill, which he dabbles about on the surface and seems to sport with, the other coming close up and appearing to take an interest." This something Selous thinks was a bunch of weed. These actions may bear some relation to the weed-trick, and at all events, even if the main purpose was feeding, the common participation of the two birds denotes that some sexual flavour attached to the act. More light is needed on the habit. (It is, perhaps, connected with the arranging of the weeds on the nest by both birds together, as described on Selous's p. 162.)

Relations of the pair with other birds of the same species.

For some days a solitary male appeared on the water where the single pair was living. The hen of the pair apparently * indulged in a little flirtation with the odd cock—a bout of shaking. This roused the jealousy of the rightful husband, who approached in the usual threatening "Dumdreary" attitude, and dived to attack the third bird from below the surface, repeating the diving attack a second time. Later the rightful couple were together and apparently bore down purposefully upon the odd male. The hen rested, while the cock drove his rival away by the attacking dive, and then returned, to go through an "excited" bout of shaking with his mate; first, however, "he swims about for a little, with the head still lowered, and in a proud sort of way."

Thus, as far as jealousy is concerned, Selous's observations are in agreement with mine.

Pairing-Actions.

The most important of Selous's observations are concerned with nest-building and pairing; indeed, the full sequence of the pairing-actions seems to have been witnessed by his eyes alone. I have already given a general account of his observations and the deductions to be drawn from them. Here I have simply tabulated some of his detailed descriptions.

1900.

(a) *One bird on the nest.*

(1) *May 3rd.* The hen was on the nest; the cock swam up and attempted to pair. There is no record of the hen previously "going" into the passive position, but as this was at the very beginning of Selous's observations, he may well not have grasped its significance.

* I say *apparently*, for Selous is not quite certain as to the birds' identity. This description, however, agrees excellently with my observations.

(2) *May 3rd.* After this attempt the hen continued to sit; the cock returned at intervals, and at one of his returns Selous noticed the hen assume the passive position. (Here there is again, perhaps, an error of omission. See the next entry.)

(3) *May 4th.* The hen was sitting; the cock approached at least seven times, and at each approach the hen went into the passive position. In these last two cases (2 and 3) the cock paid no particular attention to the hen, save for the mere fact of his approaching the nest.

(b) *Both birds close to the nest.*

(4) *May 21st.* The birds were resting after having built most of a second true nest; they then began building again, and after about a quarter of an hour the hen jumped up on to the nest and assumed the passive position. The cock made no response. She soon came off, and the building went on.

(5) *May 22nd.* Almost exactly the same scene as (4) on the previous day.

(c) *Both birds approach the nest together from a distance.*

(6) *May 23rd.* (Not recorded which bird led the way.) The hen assumed the passive attitude on the water; when she stopped the cock did the same, but remained in the attitude longer.

(7) *May 23rd.* After (6) there was a pause of about forty minutes, during some of which the cock (alone) added to the nest; he then ascended the nest and assumed the passive attitude. The hen came up several times, and each time acted as if about to leap up into the active attitude. Meanwhile the cock rose once or twice and then sank down again into the passive attitude. Finally he gave it up and took to the water.

(8) *May 23rd.* After (7) there was a pause of a few minutes, during which the birds separated and went quite far afield. Then the hen ascended the nest and assumed the passive attitude. The cock came up, behaved just as the hen had done before (in 7), but finally leaped up, and there was an attempt to pair.

[I have put (6), (7) and (8) together because each one seems to lead up to the next. If we were to separate them strictly, (7) should be under heading (b), for the birds remained fairly close to the nest all the time between (6) and (7).]

(9) *May 23rd.* Nearly an hour later. This has been already described (p. 503). The hen incited the cock by lying along the water; the cock responded by also going into the passive attitude; the hen ascended the nest and assumed the passive attitude, and the cock then attempted to pair.

Thus, in 1900, the three actual attempts at pairing were made

by the cock. Of the "incitations to pair" (when one bird goes into the passive attitude), seven were made by the hen and one by the cock. In the case of this one, the cock ascended the nest directly; as to the hen, on two occasions she was already on the nest, on three she ascended the nest directly, and on two she assumed the attitude on the open water.

1901. (Only a pairing-platform available.)

(a) *One bird sitting.* (No instances, because the birds apparently do not sit on the pairing-platform.)

(b) *Both birds near the platform.* No record. (There are two doubtful records where he first notices the birds already at the bed of weeds where the platform is, but here probably he had simply not noticed their previous approach.)

(c) *Both birds approach the platform together from a distance.* (Fifteen records, counting the two doubtful ones.)

(i.) One bird swims straight to the platform, ascends, and assumes the passive attitude.

This was seen ten times; once it was done by the hen, the other nine times by the cock.

(ii.) One bird assumes the passive attitude on the water near the platform.

This was observed five times; twice it was the female, once the male, and twice the sex was doubtful. (Here, therefore, there is not the preponderance of incitations by the male that was seen in (i.)).

On April 25th the hen assumed the passive attitude, and nothing further happened (immediately).

On May 11th the hen went into the passive attitude, upon which the cock followed suit by going into the attitude too. Some time afterwards the scene was repeated, but with the parts played by the sexes reversed (*cf.* 1900 (6) & (9), above).

This passive attitude, adopted successively by both birds on the water, might or might not lead to one of them ascending the platform and there assuming the passive attitude.

Very often an incitation might have no immediate result, but after a short pause further pairing-actions might be gone through. I will quote a couple of Selous's records for whole mornings.

April 25th.

(α) (There have already been several approaches to the neighbourhood of the nest, and several bouts of shaking.) The hen goes into the passive attitude near the nest; but there is no result, and both swim away.

(β) "Very soon afterwards" they return, and the cock goes straight to the platform, where he assumes the passive

attitude. The hen very shortly jumps up, and pairing takes place.

(γ) A little later they again approach the platform, and the cock again goes into the passive attitude upon it. The hen, however, takes no notice, and the cock comes off.

(δ) He follows her, they both turn, and he repeats his previous action—again without result. He then comes off, and fetching a piece of weed, lays it on the nest. The female comes up, and they lay a few bits of weed on the nest together, but very perfunctorily.

May 11*th*.

(α) Not long after a bout of shaking, they swim together to the weeds. The hen assumes the passive attitude on the water. The cock approaches, "appearing interested" (*cf.* p. 501), but suddenly turns round and also assumes the passive position (but not so pronouncedly), in such a way that the two are tail to tail. Both then rise up, the cock presses past the hen, and goes into the passive position on the nest. The hen makes but a slight response, and the cock, after adding a piece of weed to the nest, swims off in company with his mate.

(β) After less than half an hour they swim towards the platform, the cock leading. The cock goes into the passive attitude, and is imitated by the hen when she arrives. There is, however, no further result, and the pair swim off in company.

(γ) After about forty minutes they again swim towards the platform; the cock is far ahead, and on reaching the platform he ascends it and assumes the passive attitude. On this, however, the hen apparently becomes coy, for she suddenly turns and swims off; but when the cock follows her, she turns and swims eagerly to him—a pretty piece of psychology.

With this I have summarised the most important of Selous's facts. Others will be found under the separate headings.

9. Further details regarding the Relations of the Sexes.

(i.) Shaking.

The typical bout of shaking is of ten or a dozen shakes, the crest erected in a definite way, the necks stretched straight up to their fullest extent, the two birds facing each other at a distance of a few inches only.

It is usually initiated by the birds swimming towards each other at a moderate pace, meanwhile gradually raising their crests and necks, and giving a repeated double call rather resembling that up-and-down call of the Snipe as he sits in the marsh.

At the beginning of a bout the attitude often seems to express an extra degree of excitement, but especially so after a "flirtation"; the ruff is a little more circular, the ears pressed forward to their limit, and the neck curved over a little at the top, so that the heads and beaks are pointing somewhat downwards; this attitude never lasts long, and soon subsides into the ordinary one, in which the birds give somewhat the alert impression of a couple of smooth-haired Fox-terriers. As a general rule, habit-preening does not begin until after a few shakes, and usually gets a little more frequent as the bout goes on.

Usually, the bout is closed by the two birds simply drifting slowly apart, and gradually lowering their crests, or else one or both of them may turn sharp up into the wind with a more sudden closure of the crest.

In the longest bout seen the pair gave 84 shakes, while in the shortest seen (which is also the shortest possible) each bird only gave a single shake.

Often there are somewhat abortive bouts, without enthusiasm on the part of either bird; these do not last long, never for more than seven or eight shakes, and the crests and necks are often not erected to their proper position. There are degrees of excitement. In the lowest the neck is in the graceful curve of the ordinary swimming position, the ruff is relaxed, and the ears are scarcely half-raised. In the next stage, the ears are fully raised: then, the ruffs are slightly expanded as well: then, the neck is raised more and more: and finally both ruff and neck come to their typical extension.

A certain frame of mind is necessary for shaking, and sometimes even the expressed desire of the other bird to shake cannot arouse this state (see p. 544); for still further details the reader is referred to section 10.

(ii.) **Nest building.**

There is one curious habit connected with nest-building about the significance of which I am not at all sure: this is the trampling down of the nest. Lying in a punt in the reeds I have heard this trampling, first on one side, then on the other—squelch, squelch, squelch,—sounds of some creature trampling heavily with alternate feet on something sodden.

This is the water-birds treading down their nests. The Grebe does it, and, I believe, the Coot, and possibly other birds as well. The one occasion where I saw it well is worth recording, partly on this account and partly for another reason, as will shortly be seen. A pair had been fishing and resting; the cock then stayed perfectly still, not very far from the nest, for some minutes, and the hen went off and fished. The cock moved slowly towards the nest, and was there joined by the hen; after a short time the hen got on to the nest, there, in the usual ungainly upright position, stamped heavily twelve or fourteen times on the sodden weeds, and then settled down into a sitting position She

remained thus for about two minutes, then got off, apparently put a few bits of weed on the nest, and swam off with the cock, who for his part had remained quite quiet all the time. When I went to inspect the nest later in the day, I found that there were no eggs, and that it seemed to be a mere pairing-platform—old, sodden, low, and covered with excreta.

This is thus the only case on record where a bird has ascended the pairing-platform or nest except for the purpose of incubation or to go into the passive pairing-attitude.

The cock of course uses his special platform to rest on, so it is possible that the pairing-platform is used by the hen as a corresponding resting-place. Or, in amplification of what I have already suggested (p. 518), that when the true nest is built the hen incubates longer and so uses that as a resting-place, the cock has his platform, and both sexes use the pairing-platform.

A third possibility (but not a very likely one) is that the sitting on the nest (platform) in this case was in reality only the first step towards assuming the passive attitude, but that the bird's sexual excitement was not high enough to complete the action.

Most probably this, like many other bits of behaviour, was an "accidental" and useless release of energy, rendered possible by the mechanism of the bird's mind.

(iii.) Details of the Relations of Different Pairs to each other.

I have thought it worth while to go into this at some length, in order to show how extremely complicated the birds' mental states are, and how like may at a moment's notice be turned into dislike. We will consider the relations of a pair with an odd bird in the neighbourhood.

Let us for brevity's sake call the three birds X, Y, and "Y." "Y" is the intruder, whom we also call *the odd bird*; X and Y are the pair, or *the paired birds*, cock and hen; Y is of the same sex as "Y," X of the opposite sex. This will serve when we want general formulæ. In particular cases, where the sexes have been accurately observed, we can employ a similar formula, *e.g.* ♂, ♀, "♀," or ♂, ♀, "♂," according as the odd bird is a cock or hen; or we can simply say "Y"="♂" or "♀" as the case may be.

Now for our general statements:—

1. The disposition of X towards "Y" may be (*a*) well-disposed—in other words, X may be at the moment flirtatiously inclined in general.
   (*b*) Indifferent. Then X does nothing in particular, and Y drives "Y" away.
   (*c*) Hostile. Then X helps Y drive "Y" away;

but the actual initiative, the first step towards a "flirtation," may be taken (i.) by X, (ii.) by "Y."

2. The disposition of Y towards "Y"; this is always more or less hostile, but there are variations (*a*) in the time at which the hostility is first shown, and (*b*) in the way in which it is shown.

(*a*) *Time.* Y becomes hostile

(i.) on passing near "Y," although "Y" has been quite inactive;
(ii.) on passing near "Y," but only after "Y" has first gone into the hostile Dundreary attitude;
(iii.) only when X (its mate) makes as if to approach "Y";
(iv.) only when its mate actually begins to shake with "Y";
(v.) only after its mate has shaken for some time with "Y."

(*b*) *Method.*

Y may (i.) simply swim at "Y";
(ii.) assume the hostile attitude and swim towards "Y";
(iii.) fly at "Y" along the surface of the water;
(iv.) dive and endeavour to come at "Y" with the beak from below the surface.

In addition, these actions may be gone through in succession; if so, they are always gone through in this order, except that (iii.) and (iv.) may be reversed.

3. The disposition of "Y."

"Y" may be (*a*) simply indifferent to the presence of the pair;
(*b*) hostile to the pair;
(*c*) eager to "flirt" with X.

Here again the initiative may be taken (i.) by X, (ii.) by "Y."

Combinations of these pretty well exhaust the possibilities; here I shall give an idea of the most usual happenings.

When the two birds of a pair are swimming along together, and they pass close to a third bird, X usually takes no notice, and Y goes into the Dundreary attitude while passing "Y," sometimes swimming a little towards "Y." The odd bird, "Y," may be, and usually is, entirely indifferent to the pair, though it may adopt a threatening (Dundreary) attitude as a response to the similar threat of Y; and I once saw "Y" take the initiative in threatening.

On the other hand, I have never seen any sign of a flirtation between X and the odd bird in these circumstances.

That X should be willing or desirous to flirt with "Y," it seems necessary that its mate should either be absent or fairly distant, or, if close at hand, lethargic (see section 10, record 1), or unwilling to perform any courtship-actions. When a flirtation does ensue, "Y" may have taken the initiative, by swimming close up, calling, or going into the searching Dundreary attitude; or X may have taken the initiative by swimming up to a

perfectly innocent "Y." The former, from my records, seems to be more usual (as one would expect: it is more probable that a lone bird will be more eager to "shake" than one whose mate is near at hand).

One interesting fact emerges from table A (p. 542): in seven out of eight cases where there was a flirtation and I could be sure of the sexes, "Y" was a female, while of the cases where X was indifferent or hostile to "Y," "Y" was female in about half the number.

This is probably not merely chance; I believe that here the male Grebe possesses a little more of the normal characteristics of males.

I have several records where "Y" is very threatening from the first; here the pair always seem to make common cause against the intruder. I do not see how these cases can have anything to do with a desire of "Y" to shake, etc., nor is there in the behaviour of the pair any sign of jealousy. There seems to be only hostility, and I am disposed to think that in all such cases the pair has been trespassing on another's territory (see p. 558).

Y may drive "Y" right off, or content itself with going into the threatening attitude. "Y" is always driven off if Y sees a flirtation going on; but when the pair are simply swimming past the odd bird, Y contents itself with going into the threatening attitude (in one doubtful case only was "Y" driven away); here we have association at work. In cases where "Y" hangs about, it may be driven off by Y even though no flirtation takes place.

If Y wishes to drive "Y" off, it usually dives. Sometimes "Y" is completely taken by surprise, and, as it flies off, its place is at once taken by the jealous one. Presumably Y's beak sometimes actually comes into play, which must be very unpleasant for "Y." At other times "Y" sees Y dive, and is off at once.

The mere presence of an odd bird is not sufficient stimulus to induce a bout of shaking between the pair. Shaking is usual (though not invariable) after a flirtation and subsequent driving away of "Y."

When a bout of shaking does take place after flirtation, it always seems to begin in the *forward position*. This position in its full development I have never seen except after an odd bird has been driven away, so that we have here an interesting example of a definite form of courtship-action used exclusively under the influence of jealousy.

Let us close with one or two interesting cases—actual happenings. Here is one:—

1. The cock of a pair, saw an odd bird (? sex) near by, and drove it off, by flying at it, spluttering along the water. He then came back towards his mate, and from his attitude I thought

he was going to shake with her. However, he then saw another odd bird (? sex) not far off, and, his pecker presumably being up, went off and drove it away too. After this he came back, and a short but vigorous bout of shaking ensued. I do not suppose he would have driven the second bird off if he had not been roused by the first.

2. Then a second:—An odd cock was seen "in a very threatening attitude," some twenty yards away from a pair. They got close together, the cock going into a fairly good threatening attitude: they then swam, the cock leading, towards the intruder, but suddenly turned tail; however, they soon faced round again, and waited a bit. "Y" was now only about ten yards off. Then the pair swam a little away (this is very odd) and then all three dived; as a result, "Y" was driven a short distance away, and the pair made as if to shake, but did not. "Y" approached again, and the same scene was re-enacted almost identically (most ludicrous to watch, it was!); finally came several long dives on the part of all three birds, and "Y" was driven right off. Strange to say, no shaking followed.

Here, in face of an obviously hostile third bird, the pair united at once in common action (*cf.* Selous, in the case of Ring-Dotterel).

3. Once I saw the odd bird approach "like a dolphin"—progressing for the most part subaqueously, but now and then lifting first head and then back out of the water, only to disappear again. What this may mean I do not know.

4. In one case where there had been a flirtatious shake ("Y" = ♀), the rightful hen came up, and instead of at once driving "Y" away, started shaking, so that for a short time there was a *parti à trois*. She then drove "Y" off, and then returned and had a long shake with X. This I have only seen once.

5. Once where "Y" (a hen) had called, X swam almost up to her, but at the last moment was seized with a "fit of repentance," returned to his mate, and shook with her. Perhaps it was not repentance at all; perhaps on seeing her mate go off towards "Y," the hen gave some sign that she was ready to shake, or rather that she was roused enough to shake. This would be all the cock wanted, and, seeing this, he came back. This is only a possible explanation, but it at least has its parallels in our own affairs.

6. A variation on the above was given by the same cock a little earlier; this time he had actually shaken a bit with "Y", but on seeing his mate approaching, he suddenly turned on "Y" and drove her off. The rightful hen did not trouble herself further; but there was, curiously enough, no shaking on the part of the pair.

7. An odd bird approached; Y (? sex) swam towards it. Both went into the threatening attitude and remained perfectly motionless, looking very fierce at each other at a distance of only

five or six feet, calling ("barking") the while. At length Y came up with a loud trumpet call, there was a great flying of all three, "Y" was driven off, and the pair had a short bout of shaking.

This is something like 2—hostility evinced from the start by "Y," the pair acting together against the intruder.

8. I only once saw two pairs come into conflict; and unfortunately could not make out much. There was much diving, and, finally, two birds went off together; the other two had a short bout of shaking.

Finally come the two cases where apparently two "odd birds" meet.

9. In one I saw a short bout of shaking. Then the cock went off in the search (Dundreary) attitude; the hen, though quite close, took no notice, and the cock finally went right off. I am almost sure it was this same hen who later shook with another cock.

10. In the other (p. 546), a cock came flying over, settled near a hen, and they had a short bout of shaking. Then the cock dived; the hen still kept her ruff up expectantly, but the cock came up a long way off, swimming away from her, and she put it down; and so the scene ended.

In both these cases it is pretty clear that the birds were not a pair, but that, finding themselves together, they tried a bout of shaking. This, however, was somehow not satisfactory—it was not what they were accustomed to; and they parted. Both times one bird (as it happened, the male) was obviously searching for his mate, and it may be that this "prepossession" led to the flirtation being quickly broken off.

TABLE A.

Disposition of X to "Y."

	Sex of "Y."		
	♂	♀	?
(*a*) X flirtatiously disposed to "Y"	1	7*	1
(*b*) X indifferent to "Y"	4	3	2
(*c*) X hostile to "Y"	1	2	2

* In two of the seven cases, X (♂) later became hostile to "Y" when his own mate approached, and in a third case he was almost entirely indifferent to "Y."

TABLE B.

Disposition of "Y" to the pair.

Figures in brackets include doubtful possibilities.

	Sex of "Y."		
	♂	♀	?
A.—X and Y (the pair) swimming together in a definite direction.			
(*a*) "Y" (*the odd bird*) *threatening*:			
(i.) "Y" takes the initiative	...	...	1
(ii.) "Y" does not take the initiative	1	...	...
(*b*) "Y" *flirtatious*	...	...	...
(*c*) "Y" *indifferent*	1	5	...
B.—X and Y fishing, resting, etc.—not swimming.			
(*a*) "Y" *threatening*:			
(i.) "Y" takes the initiative	1 (2)	...	0 (1)
(ii.) "Y" does not take the initiative	...	...	...
(iii.) Doubtful	...	...	0 (1)
(*b*) "Y" *flirtations*:			
(i.) "Y" takes the initiative	0 (1)	3	1 (2)
(ii.) "Y" does not take the initiative	...	2	...
(iii.) Doubtful	1 (2)	2	1 (2)
(*c*) "Y" *indifferent*	2	...	...

10. RECORDS FROM MY NOTES.

Here follow a number of actual incidents which may be of service to any future observers. Among other things, they show very clearly the individual differences between different pairs.

I have numbered these scenes, and append here a little index showing where descriptions of various courtship activities may be found:—

Courtship-action.	Scene.
Bout of shaking	1–12, 15.
Display ceremony	4, 7.
Discovery ceremony	1, 4, 10.
Diving alone	3, 5, 12.
Weed-trick	2, 6, 12.
Complete Penguin-dance	8, 11, 12.
Flirtation	7, 12, 14, 15.
Hostility to birds of other pairs	8, 9, 11–15.

1. April 10. 4.8–4.40 p.m.

A pair, ♂ and ♀ easily distinguishable.

When I first saw them they were indulging in a typical shake of moderate length, ended by one turning away from the other. After this for about 17 minutes they moved slowly in one direction, the hen always leading the way. When not swimming she did some fairly vigorous preening. Sometimes she was 30 or 40 yards ahead of her mate, but when she got as far away as this, she always swam back and joined the cock. (Pleasure merely in each other's presence, and dislike of being separated, is marked in many monogamous birds.) He spent most of the time with his head under his wing, but now and then woke up, looked about him, and gave some rapid strokes towards the hen; occasionally he did a little preening. Not only was the hen more active and awake than the cock; she was also more emotionally inclined. She kept on coming close up to him and shaking her head slightly, trying obviously to stimulate him to respond. The first time she did this (4.13) the cock just raised his head from under his wing, gave a couple of scarcely-visible shakes, without extending his neck, and relapsed into somnolence; while to her later advances he responded not at all. She was very restless; would swim up, give two or three shakes, swim a few yards off, turn, come back, swim off again, and so on, maybe three or four times in quick succession, then she would make up her mind and swim steadily off, only to come back again after a few minutes' interval. This she did four times. By 4.26, after 17 minutes of this, she began to think of feeding, for she dived twice. Her previous emotional state had, however, not quite died down, for she then came back right up to the cock, though this time without any actual shaking. At 4.32 she went right off, and began fishing a good eighty yards away. At 4.35 she caught a big fish, swallowed it, and went on diving. The cock meanwhile rested and preened himself, and at 4.40 I lost sight of both.

This well illustrates the way in which the physiological and emotional states of individual birds vary from hour to hour. That the male was capable of normal excitement is shown by his shaking in the usual way at 4.8. This exhausted his emotional fires for the time being, but left the hen still with a good deal of pent-up excitement. It seems (as one would expect) to be "no fun" to shake all by oneself, and so her potential energy had to be released through other channels, giving as a result the quarter of an hour's restlessness.

At 4.43 a bird which is recorded as "♂, probably the same as that lost sight of at 4.40," went into the regular Cat-position, and its mate appeared in the usual way, rising erect closely from below the surface. (Discovery Ceremony.) If they were the same pair, it is obvious that the half-hour's rest had restored to the cock all his emotional energy, and the variation in emotional states is still more clearly brought out.

2. April 11. 1.50–2.30 p.m.

A pair: ♂ and ♀ rather hard to distinguish.

1.50. I just saw the end of a shake.

1.51–2.0. They swam about vaguely, occasionally diving.

2.1. I was watching one (sex?) when suddenly the other came into the field of view, carrying in its beak a big bunch (bigger a good deal than its own head) of dark, ribbony weed, which must have just been fetched from the bottom. The bird was swimming fast and rather low, in the ordinary position adopted when approaching its mate with weeds. It came right up to its mate, and the pair shook (without habit-preening) for 10 seconds or so. Then (I am practically, but not absolutely, sure) the weedless bird took some of the weed, and shaking began again. This lasted a still shorter time—"then" (I quote from my notes) "both birds turned head to wind—and lo, their ruffs were down, and there was no weed in their mouths!" They then swam off together.

2.3–2.10. Lost to sight behind reeds.

2.11. Out again. They turned to face each other, and then shook five or six times. To start with, strange to say, their necks were right down in the normal swimming position. As they shook, they gradually raised them till they were half pear-shaped. They then stayed motionless for about 20 seconds, then shook twice, and swam slowly apart.

2.12–2.27. For fifteen minutes, as near as may be, they did absolutely nothing—merely drifting and swimming aimlessly about.

2.27. One preened itself; and then they faced each other, shook 7 or 8 times, turned up wind, and swam off into the reeds.

3. April 11. 5 p.m.

I caught a pair in the middle of a bout of shaking. There were 7 or 8 shakes, with an occasional habit-preen, and then they swam apart, but with their necks still straight up and crests erected. One stayed nearly stationary; when the other had got some fifteen yards away, the stationary one dived. It came up close to the other, and shaking began again, much as before. After seven shakes they stopped and went off together, only gradually letting necks and crests subside to their ordinary positions. It must have then been feeding-time, for they took three long dives across to "Fish Corner" and began fishing.

This scene is unusual, for diving as a part of courtship-ritual is usually associated either with the cat-position or with the weed-fetching. The slow subsidence of neck and crest after shaking is also not common.

4. April 12. 8.20 a.m. A pair.

After drifting about for 5 minutes or so, they began shaking. They shook 10 or 12 times, with habit-preening; they then put

their ruffs down, and drifted slowly apart. When they were separated by about twenty yards the cock dived and came up close to the hen, upon which the pair began shaking once more. After a very few shakes they stopped, the cock put his crest down and swam off at a moderate pace; the hen, however, stayed where she was and kept her crest up. When the male was about forty yards off, he went into the cat-position: on looking at the hen, I saw that she had done the same, with wings fairly well arched. The cock had at first scarcely arched his wings, but when the hen went into position, up went his wings to the full for an instant. It was but an instant, for then he dived; "a ripple was seen coming quickly towards the hen along the surface of the water (most exciting!)"; when it had nearly reached her, the cock appeared, slowly erecting himself out of the water in the usual way. He seemed to be facing her all the time. He settled down, and a very long shake began. There was no habit-preening for the first ten or a dozen shakes, nor very much at any time. Eventually they drifted apart, put their ruffs down, and did nothing in particular for the five minutes or so I went on watching.

This shows again that courtship-diving may take place apart from the cat-position or from weed-fetching; and also that, although the cat-position seems usually to be employed as a stimulus to induce a bird of the opposite sex to do the Penguin-dive, yet the diving bird, too, may go into the same attitude before it dives.

5. April 12. 8.50 a.m.

A cock flew over from another reservoir and alighted near a hen. In under a quarter of a minute they had begun shaking. They only shook seven or eight times, with habit-preening, and then drifted apart. Soon the cock dived; the hen kept her ruff up, but the cock had dived away from her, and appeared a long way off. On seeing this, the hen lowered her crest.

This seems to show that when one bird dives, and dives deep so as to produce no ripple on the surface, the other is left in a state of suspense which is exciting enough to make it keep its crest up.

Whether the two birds were a paired couple or not could only have been proved by further watching; but I should say that they probably were not a pair, but that their close proximity and the absence of their real mates excited them. The emotion found expression in the usual actions, but then the strangeness of the hen proved unsatisfactory to the cock.

6. April 16. a.m. A pair.

I caught them shaking. After 6 or 7 shakes they separated; when they were some way apart, the hen went into a feeble cat-

attitude. The cock dived, and came up five or six yards off with a fair-sized bunch of weeds in his mouth. Strange to say, he was in something very like the normal swimming attitude, though his ruff was fairly well erected. On seeing him the hen to my surprise put her crest down, turned, and swam away, and the cock could do nothing but drop his weed, lower his crest, too, and swim after her. Nothing particular happened in the subsequent five or ten minutes.

Here, when the emotional excitement reached a certain pitch, the hen had a sudden attack of "coyness" (*cf.* similar behaviour in the female Redshank, Huxley, 12_1, p. 651).

7. April 16. 1.30 p.m.

I caught a pair shaking. Suddenly, and for no apparent reason, the hen flew off, flapping along the water. I followed her, but she simply settled in an ordinary attitude. However, on looking back at the cock again, I found him engaged in shaking with another hen. The first hen, therefore, must have been a casual acquaintance, who departed hastily on seeing the rightful mate coming up. The rightful pair shook 4 or 5 times (*without any habit-preening*), and *then on a sudden the cock* flew a few yards off, and put himself into the best cat-attitude I have seen. He turned round, first one way and then the other, just as the Peacock does when in display, and then, gradually un-arching his wings and raising his neck, swam back to begin shaking once more with his mate. This time they shook about ten times; habit-preening began about halfway through, and at the same time the ruffs were half lowered. Then they both dived nearly simultaneously, and I saw them no more (they must have made a very long dive and got into the reeds).

This is a very good example of the pure Display ceremony (see p. 513), here induced by the extra excitement of the previous "flirtation."

8. April 17. 1.30 p.m. A pair.

I saw a pair shaking; they went on for a very long time (no notes as to habit-preening), and finally one (sex?) dived. As it did so, I saw the other convert its crest into an "Elizabethan ruff"; after a few seconds it too dived. Both came up with weed in their mouths, fairly close to each other, and the usual Penguin-dance was gone through, followed by a short bout of shaking. They then put their crests down, and swam off together. To progress faster, they took three long dives, *each time going under* almost simultaneously. After the third dive they came up close to a single bird (sex?), which at once went into the Dundreary-attitude. Then all three dived in quick succession, and after some time two, which I presume to have been the original pair, came up close together, and at once began to shake, starting in the excited forward position. After that I lost sight of them.

9. April 17. 2.25–3.5 p.m.

2.25. A pair were swimming about fairly close to each other, resting and preening by turns.

2.28. The hen three times went into the Dundreary-attitude with short intervals between.

2.35. After resting for some minutes, she barked five times in succession, and relapsed into the resting position, never, however, shutting her eyes.

2.44. One bird swam off out of sight; the other barked several times. After a little bit the first one came back into view, and they both began preening themselves.

2.50. Suddenly a third bird (sex ?) came swimming towards them, and when about thirty yards off went into the Dundreary-attitude, at the same time giving five long, loud, rolling barks. At once both birds of the pair put themselves into the same attitude, and faced round on the third Grebe, uttering at the same time a series of short, low, and quickly-repeated barks. The intruder changed its course a few points and went off towards the reeds; directly it was out of the way, the pair "got up and shook." The shaking, however, only lasted for a short time, and they then relapsed into their previous state of preening and swimming about.

2.55. After they had swum out of sight and back again, I saw one of them (sex ?) go to one side in Dundreary-attitude, calling repeatedly, and on looking further afield discovered the reason for this in the shape of an intruding single bird (sex ?) (probably not the previous intruder) who was approaching in the same position and uttering the same cry, about thirty yards away. This single bird then dived and came up not six feet away from the other. They were now in an attitude I had never seen before—best described as the most hostile possible form of the "Dundreary," differing from the typical form chiefly in that the heads were not quite so low down. For some time they stayed thus facing each other, still, or moving a little forwards as if to attack, and then at once thinking better of it, and all the time giving the low, quick bark. Finally the second bird of the pair came up, giving a loud grinding trumpet-call, and then all of a sudden there was a great flying of all the three at each other, and at the end of it one bird went off, and two (undoubtedly the original pair) were left together; they at once approached and shook; the shaking, however, only went on for a short time, and then, after a few minutes' preening, I lost them.

Here, twice over, it is obvious that the presence of a third bird has screwed excitement to the shaking-point; the remarkable thing in both cases is, that the bouts of shaking thus induced should last so short a time, whereas on another occasion (April 16, 1.30 p.m.) a similarly-induced bout ended very differently.

10. April 17. p.m.

A single bird (I think a hen) was swimming about, gave the double-trumpet twice or thrice, and then looked about. Another bird, some forty yards off, noticed the call and turned, and they swam quite slowly towards each other. When they had reached each other, they began shaking, very excitedly at first. After six or seven shakes, the hen suddenly turned straight away from the cock, and flew or spluttered some eight yards away. She then put herself into a fine cat-attitude, and began turning from side to side—all this without uttering any call. The cock watched her thus for several seconds, and then dived and swam just below the surface, making a ripple, and as this approached her, the hen drew her head down ever lower on her breast. When four or five feet off, the cock put his head and neck out—apparently to see where he was, for he disappeared again at once. When he finally appeared it was three feet beyond the hen, and he was facing away from her as he "grew out of the water" into the customary ghostly Penguin; he turned to face the hen as he subsided, and finally shook with her. This bout was only a short one, however, and after it they swam some distance apart. After a minute or so the hen gave two double-trumpets, but then relapsed into the state, from which the cock had never emerged, of doing nothing in particular, and in this state some minutes later I left them.

This differs from the typical Discovery ceremony in two points: (1) the birds do not usually swim together thus, but one dives at once, (2) the cock does not generally wait and watch the hen's display ("cat-attitude") before making his "ghost-dive."

11. April 18. 10.40 a.m. to 12.17 p.m. A pair.

10.40. I saw a pair close together, the cock and hen easily distinguishable.

10.45. They preened close together for some time.

10.48. They swam off together and got close inshore.

10.52. Both dived once or twice, I think for fish.

After preening themselves for a bit (10.56–10.59) they began diving again near the bank, and the cock caught a small fish.

11.0. They came up close together and began shaking; but they only gave three or four shakes, and their ruffs were scarcely half expanded.

11.2. Again after a dive they came up close together, and again had a bout of shaking. This time they shook 10 or 12 times, and their ruffs were well up; there was no habit-preening.

11.8. After some minutes' swimming about further out from the bank, occasionally picking up things from the surface of the water, they swam together with outstretched necks (the forward swimming-attitude), the hen swimming much the faster. As they approached, and while their necks were still stretched forward, they began to shake, but

they never put their ruffs properly up, and after five or six shakes, during which the necks were gradually raised, but not to their full height, the shaking degenerated into habit-preening, and this into real preening.

11.10. They swam off and began diving again near the bank. After the second dive they came up only about three yards apart, and both shook their heads three or four times; the shaking was not very vigorous, and "had not much reference to the other bird"—*i. e.* they did not come and face each other in the customary way. They then swam out from the bank. As they passed a solitary hen some way off, the hen of the pair, who was between her cock and the single bird, went into the Dundreary-attitude. From 11.12–11.22 they swam about, picked things off the surface, fished, and took long "progressive" dives, ending up near the opposite bank of the reservoir.

11.23–11.28. After a dive they came up fairly close together, and swam towards each other with outstretched necks, which they gradually raised as they neared each other, beginning to shake their heads at the same time. A prodigious bout of shaking ensued, and was followed by diving for weed, swimming together, beautiful penguin-actions, and final bout of shaking. The whole thing has been already described in detail in section 4 *c*, p. 499. Here suffice it to say that the hen began habit-preening before the cock, and once begun, practised it more than he. She too dived first, came up first, and had more weed in her mouth.

11.29–11.39. They swam back towards where I first saw them, often picking things off the surface. A solitary cock was close to the line of route, and our cock went into the Dundreary-attitude as he passed the odd bird.

11.40. They dived. The cock came up first, and gave a couple of shakes "to himself" (*cf.* 11.10). Then the hen came up, and they shook together four or five times, but without raising their crests at all, or their necks to their full extent; they then went on fishing near the bank.

11.49. They stopped fishing; the hen began preening. The cock swam towards her from some thirty yards off. She came a little way to meet him, and they shook seven times with their ruffs half-up. The bout ended in habit-preening.

11.56. After swimming about and preening they had another shake. This again was a very long one, like that at 11.23 (I did not count the number of shakes, as I was more intent trying to make out various details of attitude); indeed it was almost a precise replica of this previous long one, and had the same sequel—a fine "Penguin-dance". The only differences I could see were that their ruffs were not quite so "sun-like" before diving, that both brought up plenty of weed, that I am almost sure a good deal of the weed was

eaten, and that the final bout of shaking was less than half as long.

12.0–12.15. The birds now swim about, preen themselves, dive, and pick things off the surface. The cock is now more active in searching for food than the hen, while previously the reverse had been true. At 12.8 they passed another bird (sex ?). My hen went close up to it, then swam rather rapidly away, then close up again. However, nothing happens, and neither bird goes into the Dundreary-attitude.

12.15. They pass near a single bird, which I think is a hen—the cock, who was leading, took no notice of it; but the hen went into the straight-necked (or angry) Dundreary-attitude and, without giving any call, swam at the third bird. The solitary one turned, swam away, and finally flew some fifteen yards off, upon which my hen turned, assumed a normal attitude, and swam back towards her mate. No shaking or other expression of emotion, however, took place.

12.17. They began fishing close inshore.

12.18. I took my eyes off them, and when I looked back could no longer be sure of them among the several birds along the shore.

My notes on this pair I have given in full because I had them under continuous observation for a considerable time (over an hour and a half). Their behaviour is of interest in various ways. In the first place, we see how, in this pair at least, outbursts of violent emotional actions alternate with calm periods during which the birds rest or feed, occasionally indulging in a short and rather languid bout of shaking. When passing near a third bird, one of the pair usually went into the threatening attitude (Dundreary). In every case I could be sure about, the bird that did this was of the same sex as the third or single bird. The pair had marked idiosyncrasies of its own, both as regards what it did do and what it did not do: and besides this, both cock and hen had tricks of their own in performing the courtship-actions, which I think were certainly permanent and not due to changeable physiological states.

All this took place on the reedless reservoir, where there are no nests, and consequently far away from the scene of actual pairing. Physiologically, therefore, the "courtship" and the act of pairing are entirely detached from each other.

12. April 18. 2.30 p.m.

A pair shook about forty times, with habit-preening. At the end they turned their backs on one another, still shaking and habit-preening—to themselves, as it were,—but gradually letting their crests sink. When about twenty yards apart they turned, swam slowly together, and shook a little, but without raising their crests. Then for about a quarter of an hour they stayed quietly facing each other, preening themselves. After this there was a short bout of shaking, then a rest, then another bout of some thirty

shakes. This, like the long first bout, was followed by their turning their backs on each other and shaking "to themselves"—a couple of shakes and 6 or 7 "habit-preens." This time, however, instead of turning, both dived suddenly and simultaneously; they emerged about forty yards apart, swam rapidly in the forward swimming-attitude towards each other, and shook about fifteen times. After a couple more short bouts, one of them (sex ?) drove off a third bird which had been following at a little distance, then came back and shook with its mate. Another short bout with ruff down, and then they rested for some time, waking up once to give four languid shakes. A solitary hen suddenly called some way off; my cock roused himself and advanced towards her. She first retired, but then came towards him, and they began to shake. This did not last long, however, for the cock's rightful mate dived and came up between the two that were shaking. She drove the stranger away, and then came back and had a bout of twenty shakes or so with her mate. After a time of resting they had a longish bout—some twenty-five shakes—and as before turned back to back. This time the procedure was again altered. When 20 or 25 yards away, the cock dived; the hen waited for him, with her ruff down. He appeared after nearly half a minute, with some weed in his bill, a little closer to the hen. He approached, but dropped the weed before getting to her, and they only indulged in a short bout of shaking. They then rested and swam to and fro, till a solitary hen appeared near by, when my cock went up to her. They started to shake, but suddenly the cock changed his attitude and drove the stranger away. This change of front was probably due to, and certainly coincident with, the approach of its rightful mate. Then both swam off in one direction. The cock, who was leading by about 50 yards, went close up to a solitary hen who was calling, but at the last moment turned and swam back to his mate, with whom he had a short bout of shaking. After a long spell of swimming about and fishing, they called to each other, approached, and had a long bout of shaking, with less habit-preening than usual. Again they ended by doing the "back-to-back" trick, and again they dived simultaneously. This time, however, when they came up (some twenty yards apart), though the hen had nothing, the cock had a very large bunch of weed in his mouth. They swam together and went through the regular penguin-actions, he shaking the weed from side to side. Unfortunately, here again it could not be seen what eventually happened to the weed. When they settled down on to the water they did not shake, but separated and swam off together for fifty yards or so. Then he dived; she followed suit after two or three seconds. They came up about twenty-five yards apart, he once more with weed, she once more without it. They swam together, but he dropped the weed when only a couple of feet off, and all they did was to shake for a short time. They then went off fishing, and were lost sight of.

This pair is also interesting in various ways. The "back-to-back" position was never seen in any other birds. Here, too, the pair itself and both the individual birds of the pair had well-marked idiosyncrasies. The very frequent bouts of shaking, the several "flirtations" of the cock, and the fact that the cock brought weeds up three times (the hen not at all) are all worthy of note. The twice-repeated dropping of the weed just before the cock reached the hen is very curious; perhaps the hen's having no weed had something to do with it.

Once more, too, it is seen that all these emotional actions may take place far from the nest, and so without any direct relation to the act of pairing.

13. April 18. 2.50–3.35 p.m.

Two birds, one certainly a cock, the other doubtful, were swimming about and fishing, 10 to 30 yards apart. Each frequently went into the Dundreary attitude and barked, apparently at the other, the obvious cock less frequently. Once the doubtful bird dived and came up a dozen yards or so from the other; both advanced a couple of yards, stopped, regarded each other for some moments (rather fiercely, it seemed to me), and then retreated. I watched them for three-quarters of an hour, and their general behaviour was the same throughout, except that they "Dundrearied" less frequently as time went on.

I do not understand the relation between these two birds. I think it was a hostile one; possibly they were two cocks on the borders of their respective territories and jealous of their frontier rights.

14. April 19. 6.30–6.40 p.m. Close to the reeds.

Here was a curious little "domestic drama":—

A pair was swimming about together, and a solitary hen with a very small ruff was not far off. She was obviously very much wanting some emotional excitement, for she kept on swimming up towards the cock, especially when the other and "rightful" hen was some way off. The lone bird would swim up to within three or four yards, eagerly, yet nervously, then turn and go off as if frightened. The cock was rather indifferent; once or twice he began swimming after her, but never got far. Once he was left mid-way between the two hens, and behaved exactly like the legendary Ass between the two equidistant bundles of hay. He looked first one way, then the other, back and forth, back and forth. At length his mate came a bit nearer, and he at once turned and swam towards her.

At length the cock's mate dived: the "wrong" hen at once dived too, and when she came up found the other hen between herself and the cock. After a minute or so she approached again, and this time all three birds dived several times, and finally the single bird was driven right away.

Throughout, curiously enough, there was no sound, nor any erection of crests, nor any going into Dundreary-position; all three birds stayed always in the normal swimming attitude. Whether the late hour had anything to do with this I cannot say. The diving and driving away, however, showed that there was some very real jealousy aroused.

It is worth noting that the second time his mate dived to drive the strange hen away, the cock joined her, but not the first time.

15. April 20. a.m.

I noticed two birds shaking vigorously. At the close of the bout, a third bird—a hen—came slowly up to the shakers from where she had been resting some twenty yards away. As she came nearer, the cock seemed to look with some hostility at the bird with whom he had just been shaking. This bird, as the event conclusively proved, was only a stranger, and the hen that had been approaching was his rightful mate. The "right" hen then swam at the "wrong" one and drove her away (no flying or diving); then she turned and swam towards the cock. When still three or four feet apart they started shaking, in the excited forward shaking-attitude, with ruffs well up. There were about twenty shakes; as the bout went on the birds lapsed into the ordinary shaking-attitude. The strange hen stayed close by, but after the shaking was over, the cock's rightful mate swam at her, and there was "confused diving," eventually "involving" all three birds, and ending in the odd bird being driven off.

The stimulus given to emotional excitement by jealousy is here well brought out; but it is curious that the cock's true mate, although so close, did not interfere until his bout of shaking with the stranger was over and done with.

11. Miscellaneous Notes.

1. *Fishing.*

The birds may often be seen to pick small objects off the surface of the water, often going on for a considerable time. These objects seem certainly to be eaten, but what they are I do not know. This habit does not appear to have been previously noted.

One bird which I saw fishing by itself for over an hour (a very long time for a Grebe to do anything continuously) had a curious habit of putting its head right down into the water, with bill vertical, till the eyes were just covered. It once stayed like this for a good quarter of a minute, but usually it took its head out after a few seconds, then after a few more seconds put it in again, and so on, all the while swimming slowly forwards. It was apparently looking for prey. I saw it dive while its head was below the surface, but it once dived from the normal position—*i. e.* without any preliminary searching. In other Grebes I have never noticed this habit.

When fishing, they often go along the bank and look for shoals

of small fish, for when they dive for food close in shore one often sees swarms of little silvery fish spring into the air all round.

2. *Relations with birds of other species.*

When a Grebe is on the nest, it resents the too close proximity of other birds. One hen that I saw sitting was twice annoyed by Moorhens coming too close; she raised herself from the resting position, bent her neck forward, and definitely (though rather slightly—about to the "half pear-shaped position") erected her ruff (I am doubtful as to her "ears"). Once she was silent, but once she gave a low rasping note. On this the Moorhens retreated.

This same hen was also roused from her snoozing by the call of a Coot near by; their sleep on the nest must be very light.

Once, on the open water, I saw a hen Tufted Duck happen to come close by a Grebe. The Grebe, strange to say, seemed greatly alarmed, flapped off for some yards, and dived, regaining calm again when the surface was regained at a safe distance.

When neither bird is sitting, the Grebes' nests and platforms are often ascended by other birds. Several times I have seen Moorhens climb on to nests with covered eggs, peck about for food, and swim off. On what was probably a pairing-platform I once or twice saw a pair of Wild Duck, and several times a pair of Shovellers; they were enjoying a comfortable nap!

On one occasion a Mallard was seen on a nest: a Grebe came along with a mouthful of weed for the nest, and at its approach the intruder hastily got off; the Grebe, however, pursued him for three or four yards, before turning and laying the weed on the nest.

3. *The Grebe essentially diurnal.*

In the spring of 1911 I had been on the Welsh coast, where there was an abundance of shore-birds. Of these, certainly the Redshank, Sheldrake, and Curlew (and very likely others) seemed to be as wakeful by night as by day, and the special and unmistakable courtship-notes of the first two species were heard all night long, especially on moonlight nights.

My brother and I each slept out a night at the reservoirs to see whether the Grebes behaved in a similar way. During the dark hours, however, there was nothing to be seen or heard of the birds. In the early morning, at the first faint showing of the false dawn, a few Grebes began to call, and various other birds, too, showed signs of activity. Unfortunately, between this and actual sunrise I fell asleep again. My brother, however, watched the whole period without noting anything of interest. Pycraft ('11) finds the same hold good in September. Selous ('01) says that, like many other birds, the Grebe is most active in the first hour or two after it has become light.

The Crested Grebe is thus a purely diurnal species: such birds as Owls and Nightjars are purely nocturnal (or perhaps late-

crepuscular would be more accurate, especially for the Nightjar, who is silent for at least the three or four midnight hours); while in some species, like the Redshank (or the cock Nightingale in spring), periods of activity and rest alternate throughout the twenty-four hours.

4. *Rest and reserve.*

In spite of its being active only during the daylight hours, the Grebe spends many of these resting, in the attitude so well described by Selous as resembling a pork-pie (see Pl. I. fig. 2). This is but one further instance of the principle of reserve that runs through all life. In watching birds two forms of this are especially brought under notice—the reserve of time and the reserve of nervous energy that are present in normally favourable conditions.

In the Grebe, the many hours of the day spent in sleeping, or at least in what Sidis calls the hypnoidal state, represent the time-reserve. These extra hours of sleep, of course, increase the energy-reserve. This latter is, in most birds, got rid of in actions which seem entirely without biological significance—they merely excite pleasure by releasing the energy in bodily movement or in sound: think of the pleasure-flights of gulls in early spring, or of swallow-broods in late summer (here accompanied by twitterings), or the antics of wagtails in fine autumns on the lawns. In the spring, however, the surplus energy of many birds has been seized upon by Sexual Selection, and used up in fighting or in display (*cf.* Wallace's general ideas on the rôle of energy in Sexual Selection, and Howard ('13)). In the Grebe, similarly, it has been diverted into fresh channels through Mutual Selection, and thus pressed more directly into the service of the species.

5. *Powers of learning by experience.*

As an interesting side-light on the psychology of these birds, I will record an incident seen by my brother.

A Grebe had caught a very large fish and was trying to swallow it in the usual way, first throwing its head violently back and then stopping it suddenly, thus jerking the fish (which, of course, is held so that its head was foremost) down the throat. This fish, however, was too big. After a long period of fruitless jerking, the bird was forced to put the fish out into the water. The fish, being still alive, swam off. This was too much for the Grebe, who at once dived, caught it again, and again attempted to swallow it. Naturally it had again to put it out and the whole process was repeated. It attempted to swallow the fish four times; the fifth time it let it swim off as best it could. The whole thing is thus a reflex chain: "See fish—catch fish—try to swallow—no use—put fish out:—See fish . . . ." and so on. It did, however, profit by experience, for each time it made rather fewer efforts to swallow it, and at last stopped its fruitless trying altogether.

6. *Calls.*

I give a brief list of the chief calls employed by the Grebe. As we should expect in a bird with such a complex emotional life, different calls are used in different circumstances—we have in them another method of expressing emotions.

(i.) *The groan.*—Typically, a deepish, fairly loud groaning sound, not guttural or rolling; occasionally it was given on a somewhat higher note, and then "rolled" slightly.

This is not a common call: I only heard it coming from birds in the reeds. I do not know with what emotions or actions it is associated.

(ii.) *The bark.*—This is given when one bird is searching for its mate (first stage of Discovery ceremony), or as an indication of hostility towards a bird of another pair; and, I think, on no other occasions: it seems, also, only to be uttered when the bird is in the Dundreary attitude. There are two chief variations:—

(*a*) A loud, rolling, rather shrill and "trumpeting" bark, several times repeated.

(*b*) A much less loud bark, not so long, not shrill at all, nor rolling; repeated quite quickly, but only a few times.

(iii.) *The shaking call.*—This is only given during a bout of shaking. I believe the two are always associated (except perhaps at the end of very long bouts). It is especially marked when shaking takes place in the "forward" position.

It consists in a rapid alternation of two sounds on two notes:—a consonantal sound—*k'p* or *t'c*—on the low note, and an indefinite vowel sound about a tone higher.

(iv.) *The "Double Trumpet."*—This is a very strange-sounding call, generally given from the reeds, often when near the nest. It is somewhat of the same timbre as the love-call of the Tufted Duck, but lower, louder, and more throaty—being, indeed, extremely guttural.

It is composed of two halves, with a slight pause between. The first half is something like *ah* or *aw*, three or four times repeated, and rises very slightly. The second half may be represented thus:—*kwaa-aa-ah*: it sinks rapidly, and is as it were pressed out, being loudest in the middle.

(v.) *The "Dentist-call."*—I have given it this name as it reminded me irresistibly of that rotating instrument of torture used by dentists for boring. Imagine the biggest burr grinding very stiffly for a few seconds, then suddenly running more freely and whirring for a little. This will give a very good idea of the sound: and this double sound is repeated several times. I have only heard it from the reeds: it often follows the "groan."

(vi.) *The Owl call.*—This very much resembles the common "*ker-wick*" of the Brown Owl, except that the initial *k* and *w* are not given by the Grebe. It may be repeated, and is often heard. Perhaps it is the simplest, least definitely emotional call-note (recognition-note).

7. *Territories.*

For a general review of the subject, see H. Eliot Howard ('13).

Like most (or all) monogamous birds, each pair of Grebes appears to stake out for itself a definite region or territory, from which intruders of the same species are jealously driven off.

The Grebe, however, differs from birds like the Warblers, and from the Kingfisher. Such birds live almost exclusively in their own territory during the whole of the breeding-season, feeding, sleeping, courting, and nesting in it. With the Grebe, on the other hand, the territory (to judge from my own experience and from certain of Selous's observations) is a comparatively small piece of water in the vicinity of the nest, and therefore near the reeds. The open water and the shore, when bare of reeds, is "Common Land," so that almost all the fishing is free to all. And thus, as a matter of observation, nearly all the feeding and nearly all the courtship of the birds takes place on this common ground. This fits in very well with the fact that all the hostilities I have ever seen on open water were apparently always due to sex-jealousy. It is only in respect of nesting, of pairing and the pairing-ceremonies (and probably of sleeping) that the birds restrict themselves to their territories.

So far as the relation of food and territories go, one might draw parallels between birds and man; the affairs of the Warblers would correspond to (present-day) agricultural conditions, the Kingfisher gives us riparian ownership of fisheries, while the free deep-sea fisheries are represented by the common open-water of the Grebe.

8. *Swimming Abilities.*

Two feats of skill call for notice. In the first place, I have twice seen birds swimming forwards, in a comparatively straight line, and apparently with intention, while their heads were tucked away under their wings.

In the second place, I have seen a Grebe, when frightened off her nest, dive and swim a good forty yards under water before rising, although the water was so shallow that she made a ripple on the surface all the time, and so overgrown with reeds that the bird's course had to swerve continually round the obstacles.

9. *Stretching of Wings.*

Every bird-watcher must be familiar with the habit of Cormorants and Shags, of holding their wings out from the body, apparently for the purpose of sunning them. I have observed this in the Grebe, but curiously enough only in one bird, which acted thus twice in ten minutes. It had been preening itself, and suddenly, raising its anterior end slightly, it stretched its wings horizontally. They were much arched, and showed the

white bars very distinctly. After 15 or 20 seconds, during which I think a little further preening was done, the wings were brought back to the normal position.

12. Postscript.

Owing to accidental circumstances, it was unfortunately only after the completion of the MS. of this paper that I was able to read Mr. W. P. Pycraft's interesting book on the Courtship of Animals (Pycraft, '13).

As I intend to attack the problem of the relations of Mutual and Sexual Selection in a more general article, it will be unnecessary to discuss his general conclusions here in detail. Let me only say that had I, before writing this paper, read his general discussion of female choice and of the modifications required in Darwin's original Sexual Selection theory, much of my own theoretical conclusions would have been differently expressed, although perhaps not essentially altered.

Let it be particularly noted, however, that Mr. Pycraft himself is careful to point out that Darwin's main conclusions stand firm. As I understand it, the chief modification necessary relates to female choice. Display and ornament do not act on the æsthetic sense of the female, but on her emotional state; they are—using the words in no narrow or unpleasant sense—excitants, aphrodisiacs, serving to raise the female into that state of exaltation and emotion when alone she will be ready to pair. This is brought out most vividly in the nuptial behaviour of the Newts (Pycraft, '13, p. 170). No one, after reading this, can fail to understand not only that the pure Darwinian theory needs modifying, but also the direction in which it must be modified.

But the element of choice does, in another form, remain. In animals such as Birds, where there is a regular pairing-up season, and where, too, the mental processes are already of considerable complexity, it is impossible to doubt but that mating may be, and in some species is, guided by impulse, unanalysable fancies, individual predilection. There, in a rudimentary state, we find that form of "choice"—intuitive, unreasoned, but none the less imperious, and none the less in its results a true choice—which reaches its highest stage of development in the intensely-felt affinities of man and woman—in that condition known as "falling in love," where the whole of the subconscious mental activities become grafted on to the inherited sexual passions, the whole past of the mental organism is summed up in the present, in the intensely real act of choice which chooses one from among thousands and says, whether in words or no, "that one being, and no other, is the being that I desire for my mate."

That a choice of this type can exist in birds is shown by the subject of this memoir. The individual variations in the courtship-actions provide the raw material for preferential mating, and the fact that the birds of a pair often both show some

special variation in the form of action, in itself proves that such preferential mating may and does occur.

The first modification of Darwin's ideas leads to a second—to a modification of the way in which Sexual Selection works. If display is normally an excitant, then there is no "need" for a preponderance of males, nor for actual rivalry between several males. Selection is primarily a matter of level. The female does not choose the "best" out of a bunch of suitors; but those males in which the ornaments and display-habits do not reach a certain standard, will not be able to raise the female's emotional state to the requisite pitch, and so will die without offspring. (This statement as it stands goes too far; it will serve, however, for the time, to show the general idea.)

This primitive condition has been modified in two ways (and on the existence of these two quite distinct lines of development I feel Mr. Pycraft has not laid sufficient stress). In the first place, in polygamous and polyandrous (and perhaps "promiscuous"?) species there may be a rivalry between several males in the presence of the females, as in the Ruff and Prairie Hen.

In the second place, the line of *mutual selection* was started. Whether in origin mutual displays too acted as excitants, it is not yet possible to say until more observations are at hand. That such may be the case, is possible from some observations of my own on the Herring-Gull. At any rate, in specialized forms of this form of courtship, such as that of our Grebe, this excitatory function is completely in abeyance.

With Mr. Pycraft's insistence, first, on the principle of Orthogenesis and its importance for the origin of sexual (and other) forms of ornamentation, and secondly, on the necessity for a psychological point of view in our interpretation of the courtship-phenomena of animals, I am in entire agreement.

List of Literature.

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'01. Selous, E.—An Observational Diary of the Habits—mostly domestic—of the Great Crested Grebe (*Podicipes cristatus*). Zoologist, May 1901, pp. 161–183, Sept. 1901, pp. 339–350, Dec. 1901, pp. 454–462, Apr. 1902, pp. 133–144.

'02. „ (Reversed pairing in Moorhens.) Zoologist, May 1902, pp. 196, 197.

'13. „ (Display of Swans.) Zoologist, Aug. 1913, pp. 294–313.

Scientific Names of Birds mentioned in the Text.

To save constant reference to birds by both English and scientific names, and to help foreign readers, I append this list.

Blue Tit.	*Parus cæruleus* L.
Bustard.	*Otis tarda* L.
Coot.	*Fulica atra* L.
Dabchick.	*Podiceps fluviatilis* (Tunst.).
Egret.	*Ardea*, *Egretta*, *Herodias*, *Garzetta*.
Fulmar Petrel.	*Fulmarus glacialis* (L.).
Guillemot.	*Uria troile* (L.).
Heron.	*Ardea*.
Herring-Gull.	*Larus argentatus* Gmel.
Kagu.	*Rhinochetus jubatus*.
Mallard.	*Anas boschas* L., ♂.
Moorhen.	*Gallinula chloropus* (L.).
Peacock.	*Pavo cristatus* L.
Prairie Hen.	*Tympanuchus americanus*.
Razorbill.	*Alca torda* L.
Redshank.	*Totanus calidris* (L.).
Shoveller.	*Anas clypeata* (L.).
Snipe.	*Gallinago cælestis* (Frenz.).
Swan (Whooper).	*Cygnus musicus* Bechst.
Tufted Duck.	*Fuligula cristata* (Leach).
Warblers.	Sylviidæ.
Wild Duck.	*Anas boschas* L.

EXPLANATION OF THE PLATES.

[The figures were drawn from my notes and rough sketches by Miss Woodward, to whom I am much indebted for the interest and care she has shown. Taken as a whole, they give a far more graphic and accurate idea of the birds' general appearance and behaviour than any other illustrations of which I know.]

All figures refer to *Podiceps cristatus*.

Plate I.

Fig. 1. Head and neck, showing ruff and ears relaxed.

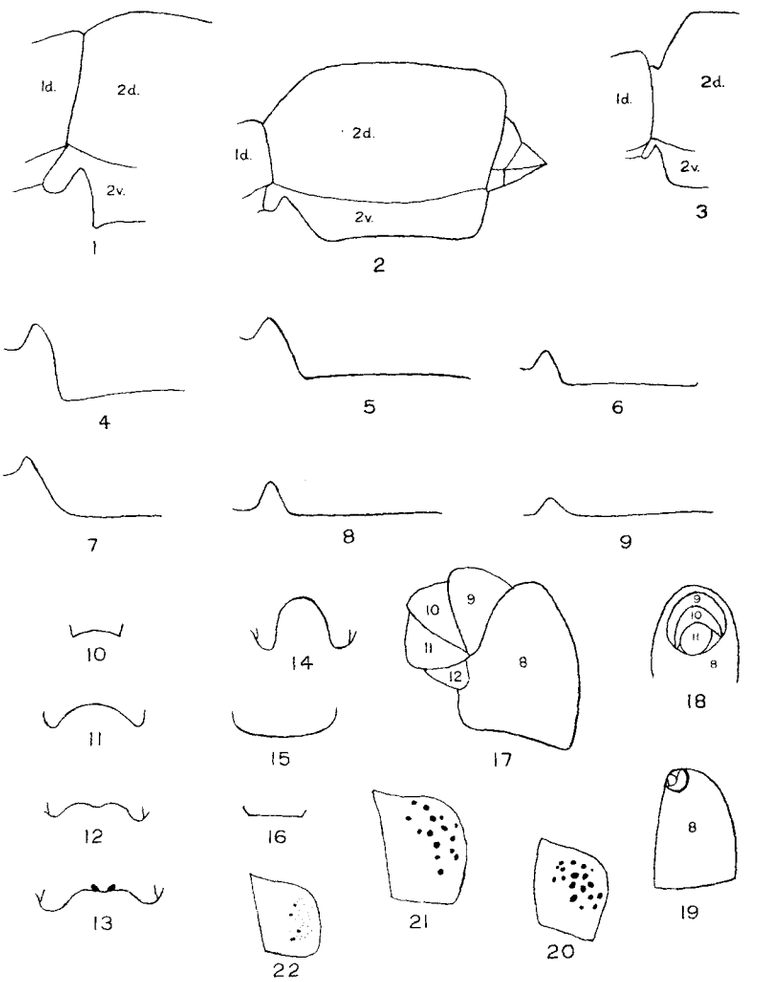
2. Resting attitude. Note the position of the head, and the curve of breast and rump. In most figures these are erroneously represented.

3. Search (Dundreary) attitude. Note the ears relaxed, the crest spread longitudinally (sometimes it may touch the water).

Fig. 4. Head and neck in Shaking-attitude (ears erected vertically, ruff pear-shaped).
5. Shaking-attitude from behind. Note the curious shape of the lower part of the neck.
6. A pair in the Forward (excited) Shaking-attitude. Note the head bent down, the neck strained forward; the slope of the body and cock of the tail are also very characteristic.
7. The Cat-attitude (Display). The general attitude is very well represented. More white should show on the breast; and the dark portion of the wings should be grey. To represent them black lessens the effect of the real black on the crest, which in actual life is the central and most conspicuous part of the picture.
8. The Passive Pairing-attitude. Note the strange stiff appearance, the humped back, and the total closure of the crest.

PLATE II.

Fig. 9. The "Ghostly Penguin" (attitude on emergence of the diving bird in the Display Ceremony). Note the head bent down, and the forward curve of the top of the neck.
10. The same as fig. 9, side-view. Owing to the short time occupied in the action, I cannot myself be sure that all the details in figs. 9 and 10 are accurate. The general appearance, however, is well given.
11. A pair shaking. Note the erect necks, and the tails slightly cocked up.
12. Display Ceremony: the diving bird just fully emerged. (This is the only figure which is not satisfactory. It gives the positions etc. well, but does not recall reality in the vivid way done by the others.)
13. The Penguin Dance. Here again the whole ceremony takes such a short time that I cannot vouch for details; but the general appearance is very well suggested.



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