

THE PARASITIC HABIT IN THE DUCKS, A THEORETICAL CONSIDERATION

By HERBERT FRIEDMANN

Curator, Division of Birds, United States National Museum

It has been well known for many years that a number of kinds of waterfowl are rather careless in their egg-laying habits, not infrequently laying one or more eggs in a near-by nest of another bird of the same or other species, but still caring for their own nests and eggs. Thus, among North American birds, some of the grebes, the great auk, certain of the auklets and murrelets, a number of gulls and terns, pelicans, ducks, rails, herons, a few shore birds, and others have been known to drop an occasional egg in another bird's nest. Gallinaceous, picarian, and passerine birds have been known to act in a similar fashion at times, and I have such records for not fewer than 54 species of North American birds, not counting the regularly parasitical cowbirds. Years ago Paul Leverkühn compiled a great mass of data on this and allied topics in his book *Fremde Eier im Nest: Ein Beitrag zur Biologie der Vögel* (Strange Eggs in the Nest: A Contribution to the Biology of Birds), published in 1891. Since the publication of this work a still greater mass of data has been put on record, while other writers, such as Swynnerton,¹ have attacked the problem of rejections by birds of eggs unlike their own.

Among all the groups of birds involved, the habit is met with most frequently in the Anatidae. The literature is so full of records that a few quotations may here be sufficient. Shepardson² writes that waterfowl are addicted to this carelessness, “* * * many species leaving their eggs to the care of other birds. Thus the eggs of the Ruddy Duck, the Redhead, the Shoveller, and others are frequently found in the nests of other ducks and coots.” Job³ found “* * * nests of Gadwall, Baldpate, and Scaup that had each 1 or 2

¹ *Ibis*, 1918, pp. 127-154.

² *Condor*, vol. 17, p. 100, 1915.

³ Among the wild fowl, p. 201, 1902.

Scoter's eggs in them, and that these first three also intermingled with one another." He calls the ruddy duck, the most given to the habit, "semiparasitic." Bent⁴ notes that the redhead and the canvasback "* * *" have a peculiar habit of building what we called dumping nests in which large numbers of eggs are deposited but apparently not incubated; we found two such nests, one of which contained 19 eggs, 9 of the Redhead and 10 of the Canvas-back piled up indiscriminately and some of them had rolled out of the nest which was partially broken down and evidently deserted." In another place⁵ the same author writes that the redhead "* * *" seems to be particularly careless about laying its eggs in other ducks' nests. We found one of its eggs in a Ruddy Duck's nest "* * *" and in three cases found from three to four of its eggs in nests of the Canvasback. "* * *" All the Canvasbacks' nests that we found contained one or more eggs of the Ruddy Duck or Redhead "* * *." Job⁶ found "* * *" Red-head's eggs in a Canvas-back's nest, Ruddy's twice in a Red-head's, Lesser Scaup's in a Shoveller's, and "* * *" Shoveller's eggs in the nest of a Baldpate." The ruddy duck has also been known to deposit its eggs in nests of grebes and bitterns, while the Canada goose has been recorded laying an egg in an osprey's nest, and the osprey was seen to incubate the egg.⁷

In view of the widespread tendency among the ducks to drop an occasional egg in another bird's nest, it was no great surprise when it was discovered that the Argentine black-headed duck (*Heteronetta atricapilla*) was regularly and entirely parasitic in its reproductive activities. This remarkable duck, rather closely allied to the ruddy duck, has been found by Daguerre, Wilson, and others to be parasitic on coots, ducks, limpkins, and other birds, and its eggs have been found in a hawk's nest as well. Phillips⁸ has summarized these data as follows:

It is very extraordinary that no nest of this species has ever been found, or at any rate described. This gap in our knowledge of the bird's life-history may be due to the fact that the species is extraordinarily parasitic, depositing its eggs in the nests of such birds as the Coscoroba Swan (*Coscoroba*), the Crested Screamer (*Chauna*), the South American Limpkin (*Aramus*), Gulls (*Larus*), Coots (*Fulica*), White-faced Ibises (*Plegadis*), Black Rails (*Pardirallus*), and even the nests of the Chimango, or Southern Caracara Hawk (*Milvago chimango*). Ducks' eggs found in such situations were at first attributed to the Rosy-billed Duck "* * *" but a later writer (Daguerre "* * *") has discovered that these parasitic eggs are slightly different from those of the Rosy-bill, being more whitish and the surface very finely granulated; they are also thicker and more blunt. Most convincing is his statement that these sup-

⁴ Auk, vol. 24, p. 422, 1907.

⁵ Auk, vol. 19, p. 9, 1902.

⁶ Auk, vol. 16, p. 165, 1899.

⁷ Fannin, Auk, vol. 11, p. 322, 1894.

⁸ Natural history of the ducks, vol. 3, p. 96, 1925.

posed Rosy-bill eggs are identical with a mature egg which was taken from the oviduct of a female of the Black-headed Duck. It may be remarked in this connection that the Black-headed Ducks are not uncommonly seen in the company of Coots.

Since the time this was published, a few additional data have been forthcoming, all of which tend to show that *Heteronetta* is regularly parasitic in its breeding habits. It lays a relatively large egg for its size, usually larger than the eggs among which its own are deposited.

Of all the nonparasitic forms, the ruddy ducks (*Erismatura* or *Oxyura*) are certainly the most frequent offenders, and it is of great interest and suggestive value that, for their body size, they lay the largest eggs of any of the ducks except *Heteronetta*, which lays a similarly large egg. At first sight it might seem that the large size of the eggs, as compared with the smaller ones of the other ducks in whose nests they are laid, is a factor directly correlated with the relatively greater frequency of parasitism in the ruddy ducks, paralleling in a way the case of the cowbirds parasitizing birds smaller than themselves; but while the facts are perfectly sound, the correlation appears to be only an indirect one. Ruddy ducks are notoriously shy at their nests; this is true not only of the North American species *Erismatura jamaicensis*, but of the Old World forms as well. In fact, so marked is this trait in the Palearctic *Erismatura leucocephala* that there are many stories to the effect that the bird sits on the eggs for a few days only, and that after the embryos have gotten well started in their development the parent ceases incubation entirely and actually does not even revisit the nest.

Phillips⁹ writes that *leucocephala* occasionally uses old nests of coots, thus sometimes not building for itself. Of the North American ruddy duck he records some very significant facts. The birds do not mate early, or, at least, often not until after reaching their breeding grounds. Some of the nests are—

* * * very poorly constructed and in some cases the eggs have actually been found wet in a carelessly made nest * * *.

Another curious thing about the Ruddy is that not all the eggs found are in the same stage of incubation and it is certain that the females lay more or less in each others' nest, for their nests are often rather close together * * *.

As a general thing so shy is the female that she is never seen near the nest at all, even when the eggs are well along in incubation * * *.

* * * The male retains some little pride in his own or other families (we hardly know which) and is seen with the young broods until they are a third or half grown, behaving in a most gallant fashion, displaying on any or every occasion and rushing at real or imaginary intruders with a great show of jealousy. He is therefore wholly an exception to any other North American duck (excepting only the Tree Ducks) for he goes into molt much later than any other species and spends the summer parading about in the full glory of his rich, red plumage.

⁹ Natural history of the ducks, vol. 4, p. 156, 1926.

Another bird allied to the ruddy ducks, the African white-backed duck (*Thalassornis leuconotus*), is similarly shy about the nest, and the egg is similarly large in size.

When a species begins to show a loss of some of the instinctive behavior usually exhibited by the female, one is led to wonder if it may not be becoming what Riddle and others might call a "male species," that is, one in which the females are more malelike and the males "normally" masculine. It is of great interest to find, then, that Wetmore¹⁰ observed that the female ruddy ducks very commonly mimic the males in display postures and even make a rattling noise with their bills against their cheeks. He noted that this was given at times by females that were apparently unmated. This suggests a latent form of maleness in the females, and I suspect that in these individuals this type of homosexual urge was stronger than in most, and that they were not displaying because they were unmated but were unmated because they were displaying.

In the tree ducks (*Dendrocygna*) the males take some part, if not the major part, in the incubation of the eggs. Shields¹¹ found the fulvous tree duck (*Dendrocygna bicolor*) to be occasionally parasitic. Another species, *Dendrocygna javanica*, is known to make use of old nests of cormorants, kites, and crows very frequently. Another instance of increasing "maleness" in the female is shown by the New Zealand sheldrake, *Casarca variegata*. Of this duck Phillips¹² writes as follows:

It is a very interesting fact that the female is very forward, very active and very amatory, while the male assumes a rather passive rôle. Taken in connection with the fact that the young resemble the male, and that the female plumage is so different and perhaps the result of more recent specialization, the relation of the sexes would well repay further investigation * * *.

All Sheldrakes are prodigious fighters, at least during the breeding season, but this species leads them all in strength and combativeness * * *. Here again the female takes the initiative, egging her mate on with loud calls and excited movements.

For our immediate purpose, however, it is sufficient to know that the females of the ruddy duck are not so "feminine" in their breeding behavior as what we are accustomed to consider "normal," or, to use a better term, usual, in ducks. This diminution of the care of the eggs, coupled with the high frequency of carelessness with regard to the nest in which they lay them, opens the path to parasitism as a regular, well-established habit.

Even if we grant the above conditions, the parasitic habit could not become successfully established unless the eggs laid in strange nests materialized into young birds. If they did not, then all this care-

¹⁰ Auk, vol. 37, p. 247, 1920.

¹¹ Bull. Cooper Orn. Club, vol. 1, pp. 9-11, 1899.

¹² Natural history of the ducks, vol. 1, p. 253, 1922.

lessness would only result in a form of check upon the increase of the species population. The fact that the female ruddy ducks seem to incubate but little after the first few days suggests that their eggs may have a higher viability than most, or may be able to keep on developing under rather adverse conditions. If this were so, then the eggs laid at random in other birds' nests might well survive even if only incubated a little now and then. It is therefore of pertinent interest to find that such is definitely the case in the European ruddy duck (*Erismatura leucocephala*). Henke¹³ took some eggs of this duck, and, after putting them in a bowl at room temperature, found that they kept as warm as if they had been incubated. Not only was slight cooling, such as room temperature, ineffective in harming them, but extreme heat was likewise survived by the embryos. By accident Henke left the eggs on a warm stove for some hours, and then removed them, and after a week he was agreeably surprised to see the eggs hatch. Apparently they were not injured by the stove heat, but still the heat was probably considerably more than that of ordinary incubation. This experiment, while crude and still unchecked, serves to indicate the high degree of probability of ruddy ducks' eggs surviving rather untoward conditions.

Recently Meyer and Stresemann¹⁴ have suggested that megapodes' eggs and ruddy ducks' eggs hatch by virtue of the heat they retain or generate themselves after the first few days of embryonic development. The notion that the heat is supplied the megapodes' eggs by the fermentation and decay of the vegetable matter in the mound is thought to be questionable; the mound may serve merely to prevent the loss of heat from the eggs after the first few days, when the eggs do actually receive heat from the mound or sun. As far as I know, there is no positive evidence in favor of these eggs possessing any mechanical or structural peculiarity in their thermal adjustments not found in eggs of other birds, but the facts of their incubation seem quite well founded.

It seems, from the above, that in the ducks there is a tendency to drop an occasional egg in another nest; this tendency becomes more pronounced in some species, and reaches its climax in the ruddy ducks and their near allies, and its very pinnacle in the parasitic *Heteronetta*. With the growth of this tendency is correlated an independent factor, namely, the heat-retaining, or perhaps heat-generating, properties of the eggs. Thus it may be that the so-called "dumping nests" of the redhead and canvasback, mentioned by Bent, are extra nests of birds that have lost some of the single-nest limitations and contain eggs that have been partially incubated and that are left to their own heat resources. Whether the eggs

¹³ Zool. Garten, vol. 21, pp. 142-147, 1880.

¹⁴ Orn. Monatsb., vol. 36, pp. 65-71, 1928.

of the redhead and canvasback are able to meet such a situation is immaterial; the fact that such a habit is practiced indicates that it may well be expected in the ruddy ducks as well, and probably was a stage in the development of the present parasitic habit of the black-headed duck of Argentina. In the ruddy ducks the eggs seem to be able to meet such a thermal situation. The large size of these eggs is possibly correlated with their heat-adapting abilities, and may therefore be an indirect correlative of the parasitic habit. It has not yet been demonstrated whether the eggs of *Heteronetta* also possess these thermal abilities; there are two alternatives to be here considered. If the eggs of this duck are heat adaptive, their survival in strange nests is easily accounted for, as the victims undoubtedly do take care of them to some extent. If they are not heat adaptive, then the parasitic habit is the sole cause for the survival of the species, for if eggs unable to cope with thermal difficulties are laid in nests where they are uncared for, as in the "dumping" nests, the chances are all against their survival. If, however, they are laid in nests where they are given incubation by some other bird, they will have a good chance to hatch out. Therefore, if the eggs of *Heteronetta* are not thermally adaptive, the fact that they are laid in cared-for nests is the secret of their survival. If they are able to cope successfully with the thermal difficulties attendant on the lack of regular incubation, then the parasitic habit is due merely to the loss of the nest-building instinct, as the eggs would get along in uncared-for nests just as well as in others where they receive incubation. If the eggs were laid in uncared-for nests, that is, old or abandoned nests, the birds could hardly be called parasitic. Whichever of these two possibilities is correct, however, the fact remains that *Heteronetta* appears to have lost the nest-building habit. The problem of the parasitic habit then must be considered unsettled until this angle is delved into more fully.

We have seen that the ruddy duck sometimes uses old nests of coots; at other times it builds very poor nests; we have seen, incidentally, that the concept of territory is not well maintained, as the nests are often close together; the mere fact that females with nests of their own lay in one another's nests shows how poorly established are the territorial limitations of the actions of the individual birds. The diminution of the territorial and nest-building instincts are seemingly correlated with the diminution of incubating activity on the part of the female parent; if the bird comes to the nest relatively little, it follows that it will not be apt to respect its territorial boundaries as much as a bird with a strong instinctive attachment (through incubation) to the nest. In the case of ducks the territory as such vanishes after the eggs hatch, as the parents take their offspring into

the water, and from then on any place is home to them. Hence the territory lasts only as long as the incubation activities of the parents. Thus it seems that the cause of the diminution of the potency of territorialism is dependent on the lessening of the incubation activities. Inasmuch as the lessening of incubation is merely a step in the path toward a complete lack of incubation, such as in the case of those eggs laid in strange nests (that is, lack of incubation on the part of the bird that laid the eggs), it follows that as this diminishes, approaching zero as a limit, so too the territory as such becomes less and less real and finally vanishes. In an analysis of the cyclical instincts of birds during the reproductive period, the nest is merely something constructed within a territory for the purpose of being a receptacle for the eggs that are to come. Therefore, with the disappearance of the territory as such, there must inevitably come about a loss of the nest-building instinct. It is impossible to construct something in a nonexistent space. Hence it follows that the loss of the nest-building instinct is also dependent on the decrease in the amount of incubation given the eggs by the female parents. Furthermore, to carry this idea a little further, it appears that the origin of the parasitic habit in the Anatidae is bound up with the heat adaptability of the eggs of the ruddy and black-headed ducks. If their eggs did not have this peculiarity, any lessening of incubation would have resulted in the extermination of the species; the fact (?) that they have, has allowed for the development of parasitism in this group of birds.