# THE BREEDING BIOLOGY OF THE PARASITIC BLACK-HEADED DUCK[1]

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In his classic work on the ducks of the world, John C. Phillips (1925:93) wrote of the Black-headed Duck (*Heteronetta atricapilla*): "Less is known of this species than of any other South American Duck, excepting perhaps the Brazilian Merganser." The careful work of Partridge (1956) on the latter species left the Black-headed Duck as one of the great bird mysteries of South America. The species has been of special interest because of its uncertain taxonomic position and because of its apparent parasitic behavior; no nest of the species has been reported. The fact that it is a shy bird during the breeding season has complicated its study. Since 1925, South American naturalists gradually have accumulated information on the hosts and distribution of the species but much of its breeding biology has been unknown. This paper is the result of 11 months of study of the species in eastern Argentina. Additional work during the courtship and laying season probably may modify some of the conclusions.

## *History of the Species*

Salvadori (1895) and Phillips (1925) reviewed the synonymy of the species and Sclater and Salvin (1876) and Hellmayr and Conover (1948) summarized additional notes of interest. The Black-headed Duck is widely distributed in the marshes of the Pampas and Chaco regions of South America (Phillips, 1925). There are breeding records from most of its range in Argentina, Chile, and Paraguay, but only specimens of full-winged young and adults from Uruguay, extreme southern Brazil, and central Bolivia.

Phillips (1925) reviewed the information on the parasitic habits of the Black-headed Duck but the scarcity of his work and the additional interpretation of other notes merits summarizing. Rodriquez (1918) identified duck eggs, found in the nests of various water birds near Juancho, Province of Buenos Aires, Argentina, as those of the Rosybill, *Netta peposaca* (scientific names and classification follow Delacour, 1954-1964); and Daguerre (1920), basing his identification on a female collected with an egg in the oviduct, later attributed them to the Black-headed Duck. Holland (1892), Grant (1911), and Gibson (1920) also noted extensive parasitism but assumed it to be that of Rosybills. Friedmann (1932) presented a stimulating discussion of possible mechanisms of the operation of brood parasitism in ducks and of the

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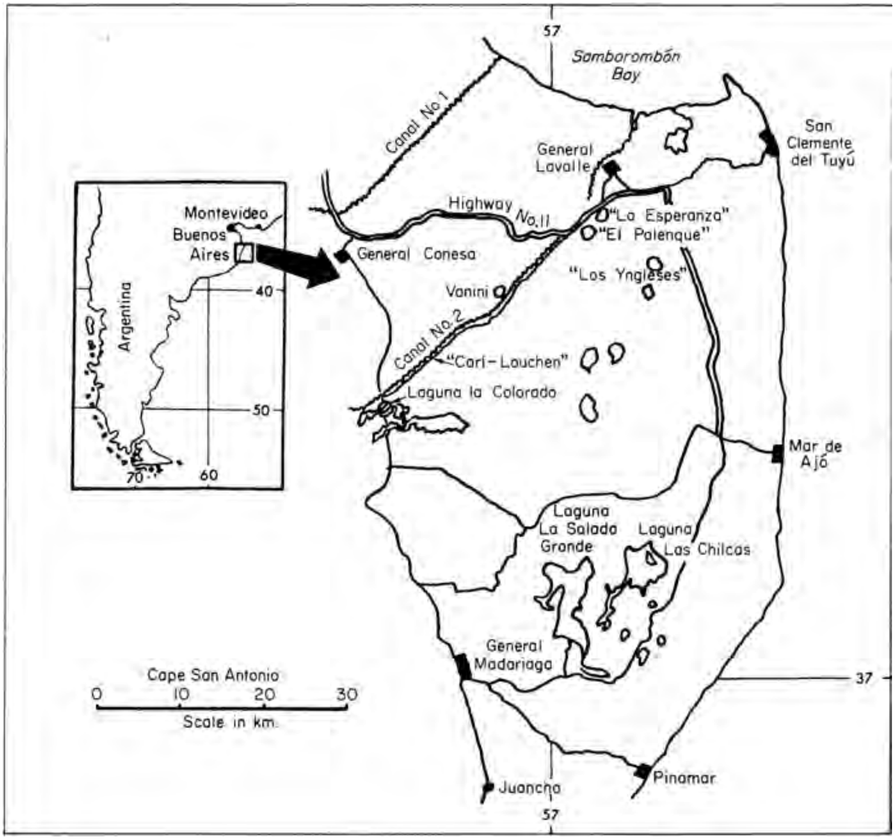


Figure 1. Location of the study area of the Black-headed Duck in eastern Buenos Aires Province, Argentina.

origin of the habit. Goodall, Johnson, and Philippi (1951) found eggs in nests of coots in Chile and attributed them to *Heteronetta.* These workers in Chile and others in Argentina placed eggs under hens and hatched the ducklings which proved impossible to rear. Peña (1962) has since reared the species by releasing them in a natural pond.

## *Study Areas and Methods*

Because of the numerous observations of the Black-headed Duck in the Cape San Antonio area of eastern Argentina (Rodriquez, 1918; Gibson, 1920; Wetmore, 1926) and because of recent reports by interested residents on the abundance of the species, I established my study area (see Figure 1) near General Lavalle, Province of Buenos Aires, a low grassland situation described elsewhere (Weller, 1967b). Specific research areas were Estancia "El Palenque," five miles southwest of General Lavalle on Highway 11 and the Vanini Estancia, 12 miles southwest of General Lavalle along drainage Canal Number 2. El Palenque contained a series of densely vegetated, fresh-water marshes (Figure 2) totaling nearly 1,000 acres, contiguous with the extensive marshes of the adjacent Estancia "Los Yngleses" where Ernesto Gibson and Alexander Wetmore observed this species. The Vanini Estancia was approximately 1,000 acres, but I worked in one unit of about 250 acres, a marsh ideal for birds because of the many isolated pools in the emergent vegetation.

To obtain data on the laying habits of the species and the incidence and success of its parasitism, we made an intensive search from late August through December 1964 for nests of all the larger birds nesting in the marsh. Although we rechecked these nests when we encountered them on later searches, the marshes were so extensive that it was impossible to mark all nests so that we could find them easily and yet not make them conspicuous to the chief predators, Chimangos, *Milvago chimango,* and Caracaras, *Polyborus plancus* (locally known as Caranchos). We observed as many nests as possible, but we obtained our data on hatching success only from nests we could recheck after the eggs had hatched.

To determine the approximate stage in the incubation of the parasitic eggs in relation to those of the host species, we floated or candled most eggs (Weller, 1956).

## *Results*

### General Habits

Black-headed Ducks (Figure 3) have the general size and body proportions of a teal (*Anas* spp.) but are far less terrestrial, only rarely coming to land to sleep. They walk poorly, but occasionally stand in shallow water to preen. During much of the year they frequent isolated pools in dense marshes or open lakes where they get out of water only by clambering on bent tules as a submerged roost-site. They have an extremely large oil gland and very shiny plumage.

Figure 2. Prime habitat of the Black-headed Duck includes the *Azolla*-covered pools in extensive marshes of tules (*Scirpus californicus*) near General Lavalle, Buenos Aires Province, Argentina.

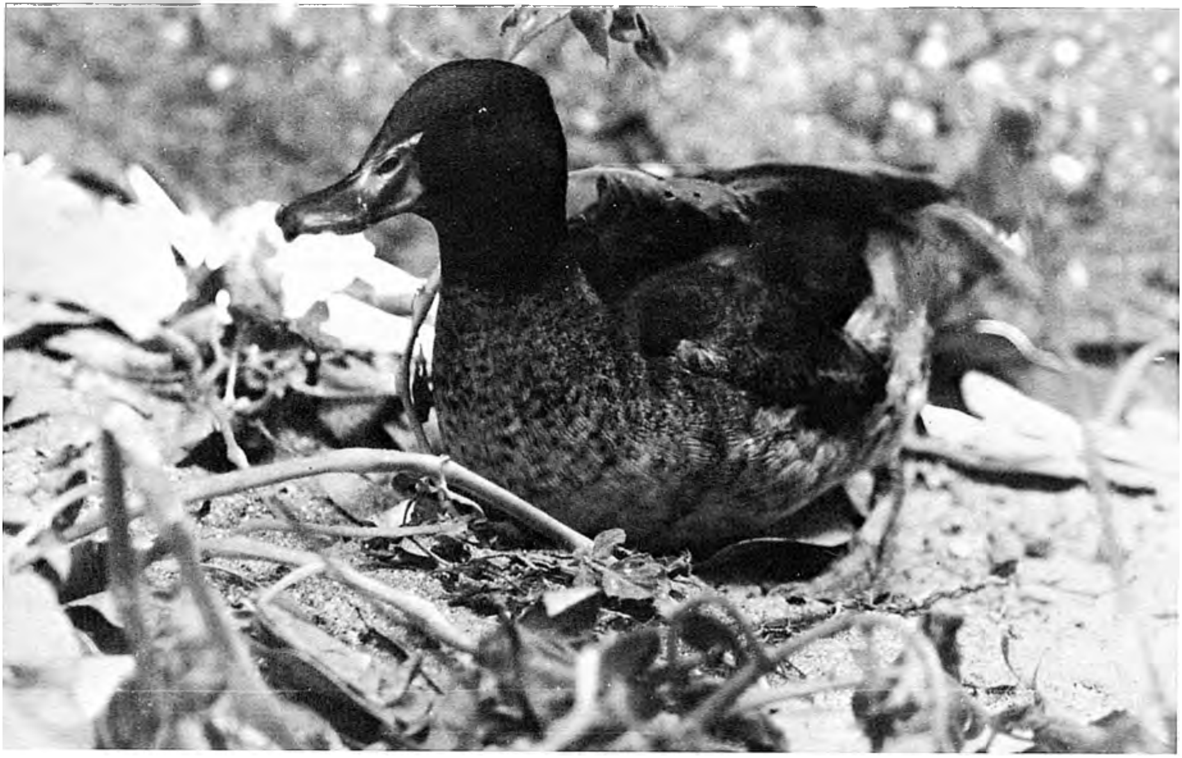


Figure 3. The Black-headed Duck (here a captive yearling male) has the general size and body proportions of teal (*Anas* spp.) but it is far less terrestrial.

Black-headed Ducks ride relatively low in the water and, like Ruddy Ducks (*Oxyura jamaicensis*), may have their tail on the water or uplifted at a 30-degree angle (Figures 4 and 5A). In general, they are more like divers than like dabblers in profile, being high above the water in the upper back area rather than the tail. Black-headed Ducks move through dense floating vegetation rapidly and easily in a sneak-like "scooting" position (Figure 5B).

Although not prone to flight, especially during the day, Black-headed Ducks are excellent flyers. They rise quickly, sometimes striking the water with their wings as do many dabbling ducks, at an angle of approximately 45 degrees in the absence of wind. They fly very fast and can be identified by their small, rapidly moving wings, elongate body, and low-head position (Figure 6). Birds often took flight without any preliminary actions, but most individuals, when alarmed by intruders, became alert, holding their heads and tail higher. Nervous birds sometimes head-pumped, gave head-flicks (terminology from McKinney, 1965), head-shakes, or the both-wings-stretch, but these movements did not seem sufficiently regular to be considered part of the preflight behavior.

An apparent escape reaction, possibly preflight behavior or perhaps prediving or even displacement-aggressive behavior, was an extreme wing-up, tail-up posture (Figure 5C). I saw this on three occasions, twice in response to potential predators, and once to the noise of the camera. Once, when a Caracara sailed over, several Black-headed Ducks gave the wing-up, tail-up posture as they moved into deeper water away from the potential predator. In another case, a juvenile, surprised by a landing Brown-hooded Gull (*Larus ridibundus*), gave this posture and moved away quickly until it recognized the gull as harmless. The adults nearby ignored the gull.

Black-headed Ducks proved to be excellent divers, this being a common method of feeding during the summer months. They dive easily and skillfully and do not use their wings as Wetmore (1926) thought they might. They jump fairly high before submerging and are much more skilled divers than are most dabbling ducks (Figure 5D). We saw them diving regularly with coots and Argentine Ruddy Ducks (*Oxyura vittata*). Several Black-headed Ducks dived continuously for 45 to 55 minutes. Dives averaged 11.4 seconds (range 3 to 14) for 76 dives of full-grown juveniles or adults in water of two-and-one-half to three feet deep. Adult Argentine Ruddy Ducks, in the same area, stayed under much longer, averaging 24 seconds (range 21 to 26) for eight dives. Between dives Black-headed Ducks tended to ride low in the water with the lower neck and upper back sometimes under water and the crown feathers depressed. When diving continuously Black-headed Ducks had a diving interval — surface rest — of 7 seconds (range 2 to 12) for 29 intervals.

Escape reactions observed in this study usually involved flying rather than diving. Wetmore (1926) reported that several pairs dived at the firing of a gun, an event noted only once in the collecting of numerous specimens during the present study. In this case the bird surfaced after its dive and took flight with only the slightest pause on the surface.

As noted by Gibson (1920), Wetmore (1926), and others, Black-headed Ducks are difficult to observe. They have been called "shy," but this shyness varies, depending on the season and their experiences with man. Although they were definitely wary at laying time, they were inconspicuous at other times mainly because of their habitat preference which has produced a false impression of rareness.

All comfort movements reported by McKinney (1965) were seen during this study and I noted no major differences between this species and other anatids.

In interspecific relationships all species of grebes, coots, and ducks, except the Versicolor Teal (*Anas versicolor*), clearly dominated the Black-headed Duck. We occasionally saw Cinnamon Teal (*Anas cyanoptera*) with Black-headed Ducks and noted no aggressiveness. However, Peter Scott (1954) re-

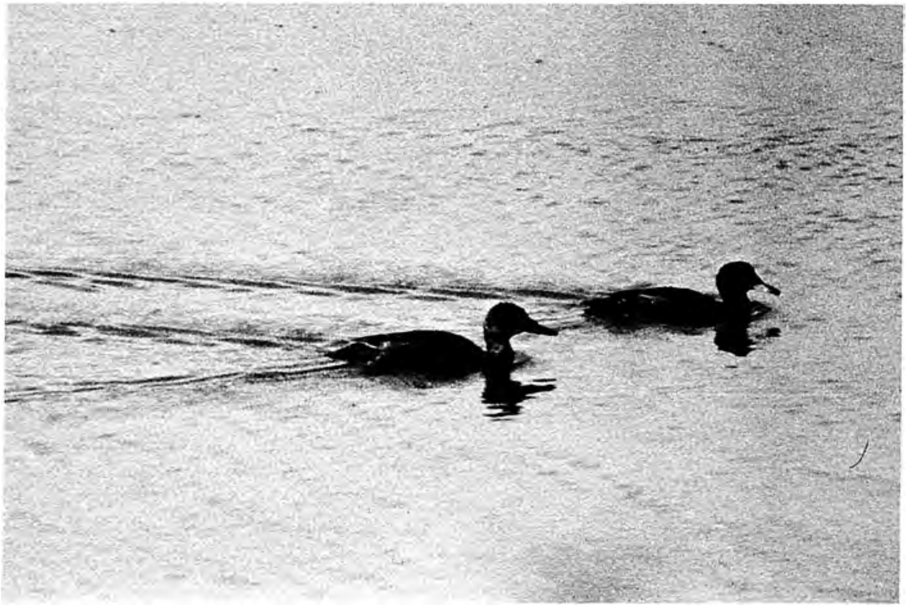
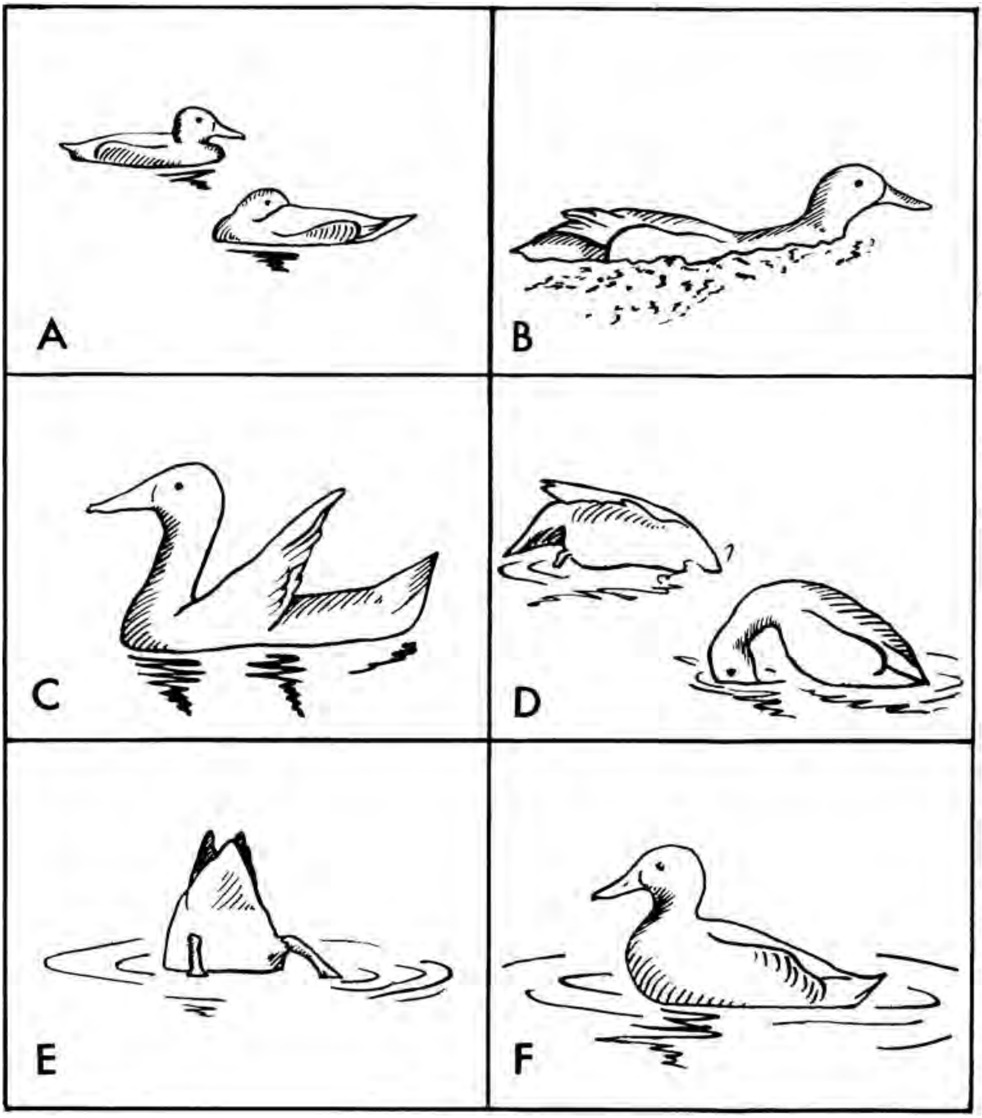


Figure 4. A pair of Black-headed Ducks swimming. The tail is frequently held in a horizontal position on the water, as shown here.

Figure 5. Behavior of the Black-headed Duck. (*A*) Note the tilted tail of the sleeping birds. These ducks swim easily through dense floating vegetation in a "scooting" position (*B*). I saw the extreme wing-up, tail-up posture (*C*) only several times as an alarm response. Black-headed Ducks are excellent divers, jumping fairly high *(D)* before submerging. They dive in water only two to three feet deep and remain submerged for 11.4 seconds (average of 76 dives). Typical feeding postures include up-ending (*E*) in water too deep for dabbling and treading (*F*) in shallow water.



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ported seeing a male Cinnamon Teal courting an immature *Heteronetta* (the sexes are erroneously reversed in Delacour's, 1959, reporting of this incident) and I saw a similar one.

## Foods and Feeding Habits

The food habits of both young and adults have been virtually unknown. In fact, I found only a single report of foods of an adult in the literature (Zotta, 1934) — of a bird which contained unidentified seeds, as well as some vegetable material and sand. Delacour (1959) noted that the species had a somewhat spatulate, strainer-type bill (Figure 7). In total, I examined 27 full-grown *Heteronetta* specimens (10 adult males, 12 adult females, 2 immature males, 3 immature females) for foods at various seasons.

**Figure 6. Black-headed Ducks fly swiftly and can be identified in flight by the rapid beats of their small wings and by their elongate body and low head posture.**

Throughout the year, seeds of the tules evidently are the main food, being found in 24 of the 27 birds and making up almost the total volume of food in 20 birds. In summer, the ducks also take snails (five of 27 birds); three individuals had fed almost entirely on snails. Black-headed Ducks swallowed snails whole, whereas a young Argentine Ruddy Duck, collected in the same area, had crushed the snails in its bill before swallowing them. Diving and water-treading (Figure 5F) suggested that other benthic organisms constitute part of the diet, but I identified no animal foods other than snails. The straining of duckweeds also may produce microscopic crustaceans. However, the presence of tule seeds in nearly every specimen suggests that seeds are the major food and that the well-developed lamellae of the bill function mostly in seed-getting. The ducks occasionally eat small unidentified seeds other than those of tules and one bird had eaten a few seeds of cut-grass. Some birds ate duckweeds, especially smaller varieties like *Wolfiella oblongata* and *Lemna valdiviana*. The unidentified green material found in the gizzard probably was duckweed.

The manner of feeding varies with the water depth. When surface-feeding in duckweed, the bill is held nearly horizontal as in most dabbling ducks.

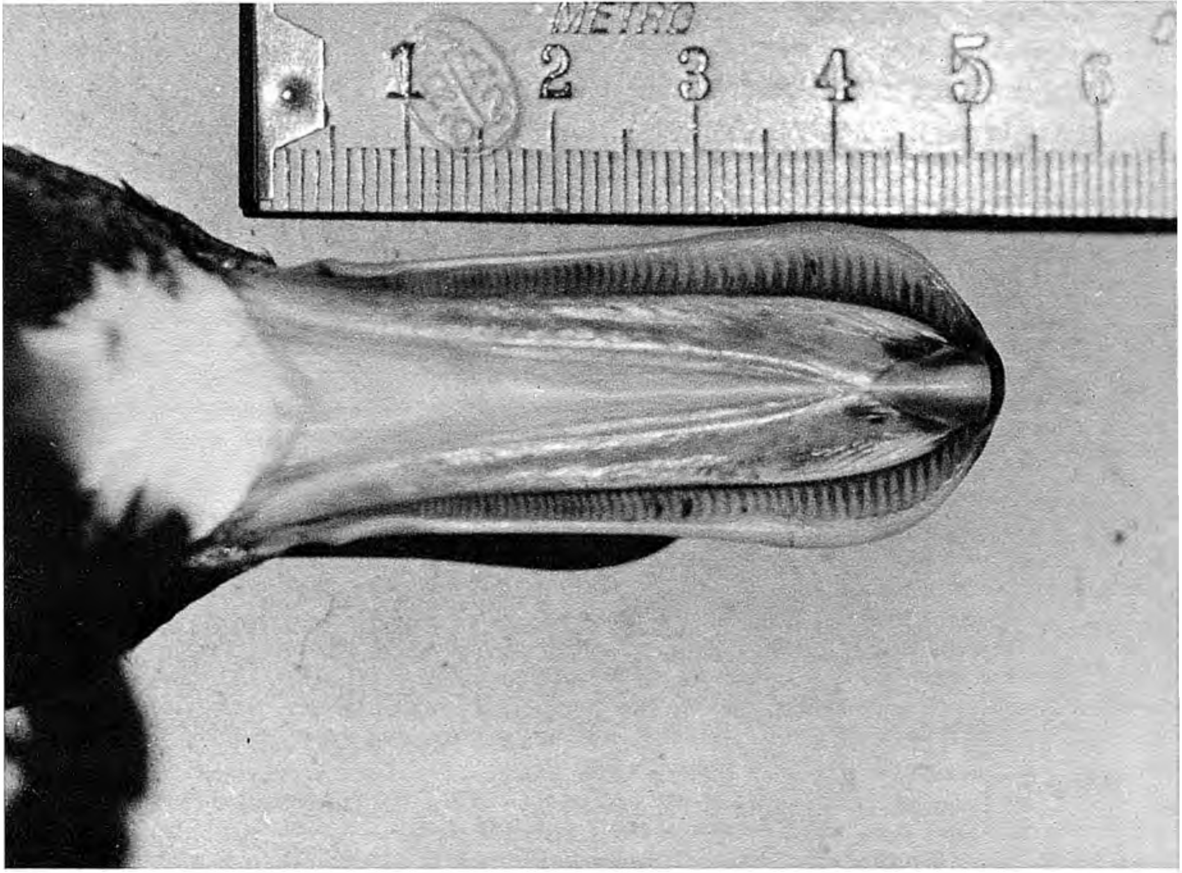


Figure 7. Ventral view of a Black-headed Duck showing the slightly spatulate, strainer-type bill.

When straining mud in shallow water, the bill is held at an angle of 45 degrees unless the water is extremely shallow. In slightly deeper water, feeding is swan-like with the head and neck under. When the water is too deep to reach the food by dabbling, the birds up-end (Figure 5E). During the summer months, full grown juveniles and adults dived in water two to three feet or more in depth.

## Annual Cycle and Sex Relationships

I have found no nests of Black-headed Ducks and observed no females behaving as though they had nests or broods hidden from me. Despite the fact that I spent considerable time in areas where Black-headed Ducks parasitized nests of other birds, I saw no broods. On the basis of these observations and the absence of documented reports by other observers, I assume that the Black-headed Duck is completely parasitic.

In east-central Argentina, I watched birds in pairs regularly from mid-September to early December. I have no data on pair bonds of marked birds but the pairs behaved much as do other species of ducks. Some pairs were close-knit while others seemed to be less definite and even switched partners temporarily without great animosity. I saw several lone females during the laying period. Such birds became involved in courtship groups but the stage of their sexual cycle was unknown.

The sex ratio of 548 adults observed in the area near General Lavalle was 58 per cent males to 42 per cent females.

Daguerre (1922) stated that the species was found in pairs or groups of pairs throughout the year. I found no such relationship during the post-laying period of January to March when there were few birds in pairs — 5 per cent as compared with 60 per cent from early October through December.

After the laying period ended in late November and early December, lone females and small groups of *Heteronetta* became conspicuous. Because I saw few birds in December, I presume such groups underwent the flightless period together. The groups were common again in early January. The first birds with fully regrown primaries were collected on 31 December (a male) and 1 January (a female), but the majority of the birds probably molted somewhat later. The postmolting groups gradually increased in size so that in February and early March such gatherings numbered from 10 to 15 birds.

I saw no evidence of courtship during the fall — March to June in the southern hemisphere — and winter as occurred in the Argentine dabbling ducks. In fact, no pairs, or signs of courtship, were evident in late July; nor were they observed by Peter and Martha Miles who watched for such behavior in the nearly 150 birds that they observed on 28 August 1965 at Iturralde Marsh, Murphy, Santa Fe. Presumably, as in both the North American and Argentine Ruddy Ducks, Black-headed Ducks pair relatively late — in early September — despite the fact that laying may start in late September.

Table 1 shows data on the size of the gonads for specimens collected or observed from hunters' bags from October 1964 to July 1965. I collected few specimens during the breeding season to avoid the possibility of disturbing the birds at this time. As a result, there is little noticeable variation in the size of the gonads except between immatures and adults. Obviously, the specimens taken in July were not yet in breeding condition.

Although I have no proof that yearlings breed, I assume that they do because all the birds that I saw in spring were in breeding plumage and courting. However, I noted considerable variation in depth of the bursa of Fabricius. Most adults during the non-breeding period had either no bursa or one that measured up to 12 millimeters in depth (pocket only). This is a rather large variation. Moreover, two birds, a male and female collected at General Lavalle in July, had nearly adult plumage characteristics yet had bursas from 15–17.5 mm in depth. I assume that these birds were yearlings which still had a bursa even though the female had an open oviduct and the male had an adult-sized penis.

In the more northerly parts of its range the Black-headed Duck seems to breed in the fall, timing its cycle to coincide with the nesting of other water birds. Fall nesting of subtropical water birds seems to be regulated by the late summer flooding of marsh areas which are normally dry in spring and early summer. From one fall breeding area in central Paraguay, where the host species are unknown, two specimens were collected in March, 1937: a newly-hatched duckling (University of Michigan, Number 93120) and an adult male with enlarged gonads (Steinbacher, 1962). In addition, Dr. C. Olrog told me that he captured flightless young in May at the Banada de Figueroa, 40 miles northeast of La Banda in the province of Santiago del Estero. Dr. Olrog and I tried to find the host species there in late March but water conditions were not conducive to nesting. Several potential host species, seen in the area, were White-winged Coots *(Fulica leucoptera)*, Common Gallinules *(Gallinula chloropus)*, and Little Waterhens (*Porphyriops melanops*), birds which apparently nest in flooded cornfields as well as marshes.

TABLE 1

Gonad Sizes of Black-headed Ducks* Collected or Observed in Argentina from 31 December 1964 to 16 July 1965

| *Adult males* | | | *Adult females* | | |
|---|---|---|---|---|---|
| *Date* | *Testes size (mm)* | | *Date* | *Ovary (mm)* | |
| | *Left* | *Right* | | *Size* | *Largest* |
| 31 December 1964 | 4.3 x 14.2 | 4.1 x 16.0 | 29 October 1964 | – | 25.0 |
| 26 January 1965 | 4.0 x 12.5 | 2.8 x 14.0 | 18 December 1964 | – | 4.2 |
| 28 February 1965 | 4.2 x 13.8 | 4.3 x 15.2 | 1 January 1965 | 10 x 22 | 2.7 |
| 1 March 1965 | 4.2 x 12.1 | 4.0 x 11.7 | 11 January 1965 | 10 x 20 | 2.8 |
| 18 March 1965† | 2.4 x 9.0 | 1.9 x 9.6 | 5 February 1965 | 11 x 18 | 3.3 |
| 6 May 1965 | 4.7 x 11.9 | 3.2 x 11.1 | 1 March 1965 | 8 x 23 | 3.0 |
| 15 July 1965 | 2.6 x 9.6 | 2.6 x 10.5 | 18 March 1965† | 10 x 23 | 2.5 |
| 16 July 1965 | 4.3 x 9.1 | – | 28 March 1965‡ | 12 x 20 | 3.0 |
| 16 July 1965 | 3.6 x 10.7 | 2.8 x 11.9 | 17 April 1965 | 12 x 22 | 2.6 |
| 16 July 1965 | 3.3 x 11.2 | 3.5 x 13.0 | 16 July 1965 | 9 x 25 | 2.8 |
| 16 July 1965 | 3.6 x 9.6 | 3.9 x 11.0 | 16 July 1965 | 11 x 22 | 2.8 |
| | | | 16 July 1965 | 9 x 23 | 2.5 |
| *Immature males* | | | *Immature females* | | |
| 18 January 1965 | 1.9 x 9.0 | 2.0 x 7.5 | 6 January 1965 | 7 x 20 | –1 |
| 16 April 1965 | 2.2 x 7.3 | 2.3 x 8.9 | 11 January 1965 | 8 x 12 | –1 |
| | | | 28 February 1965 | 7 x 12 | 1.0 |

*All are non-breeding birds, except the female taken on 29 October 1964, and are from the Province of Buenos Aires except where noted.

†Province of Santiago del Estero.

‡Province of Tucumán.

## Courtship

I saw courtship displays in the parasitic Black-headed Duck from the time I observed the first birds in mid-September until the ducks stopped laying in early December. Possibly courtship starts somewhat earlier in some areas. We did not notice it in July 1965 at General Lavalle or during August 1965 at Venado Tuerto, Sante Fe Province.

*Displays.* — The males responded to the presence of females or, to a lesser degree, to human intruders by a display which involved several movements and a call. Because the male inflates his throat as part of this display, the common name of the species is "pato sapo" or toad duck. Thus I have termed the entire display *Toad-call.* Wetmore (1926) described this display as: "neck down in and throat puffed out, at intervals raising the point of the bill and giving a low note *quah quah,* barely audible at 45 meters." The Toad-call actually involved several movements given almost synchronously. Some of its components also are given separately and may function as separate displays.

Males in groups and, in some cases, paired males were seen in a posture I termed the *toad-posture* which possibly functions as a threat as well as a

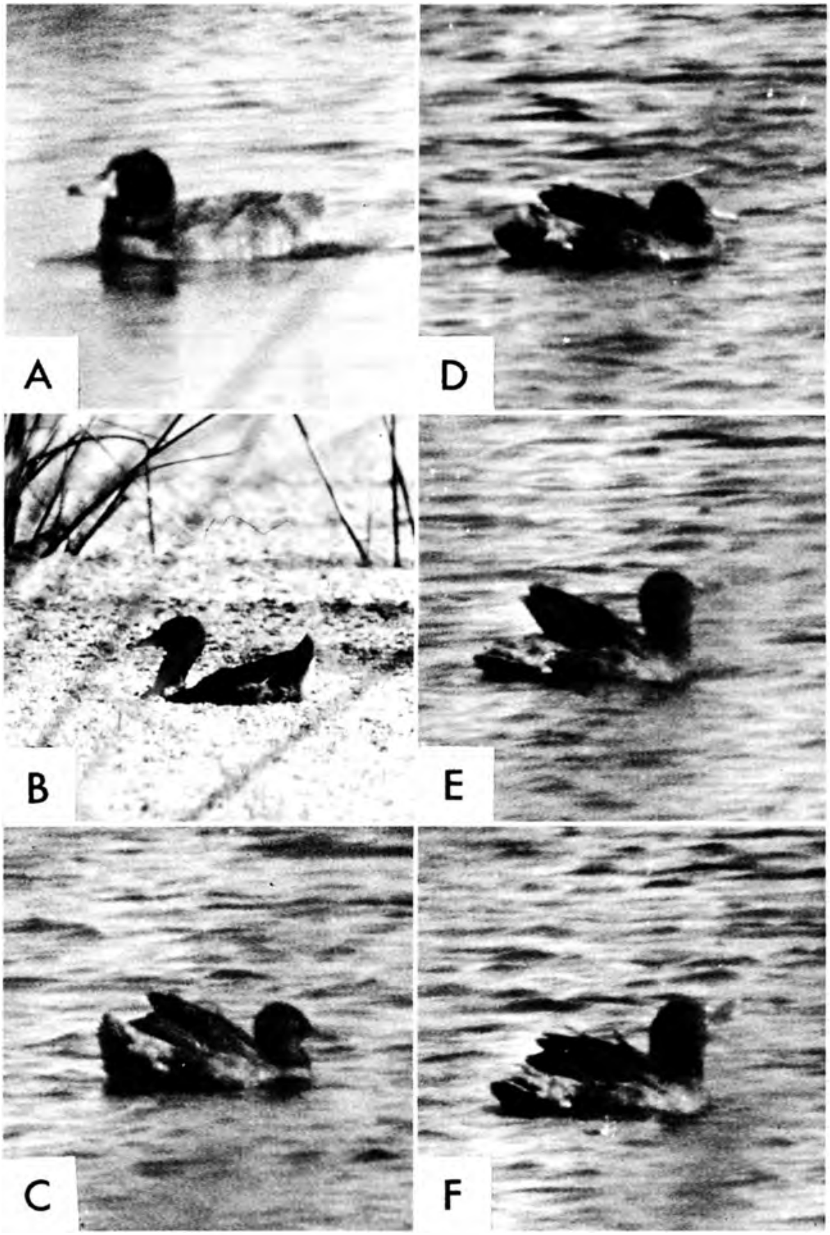
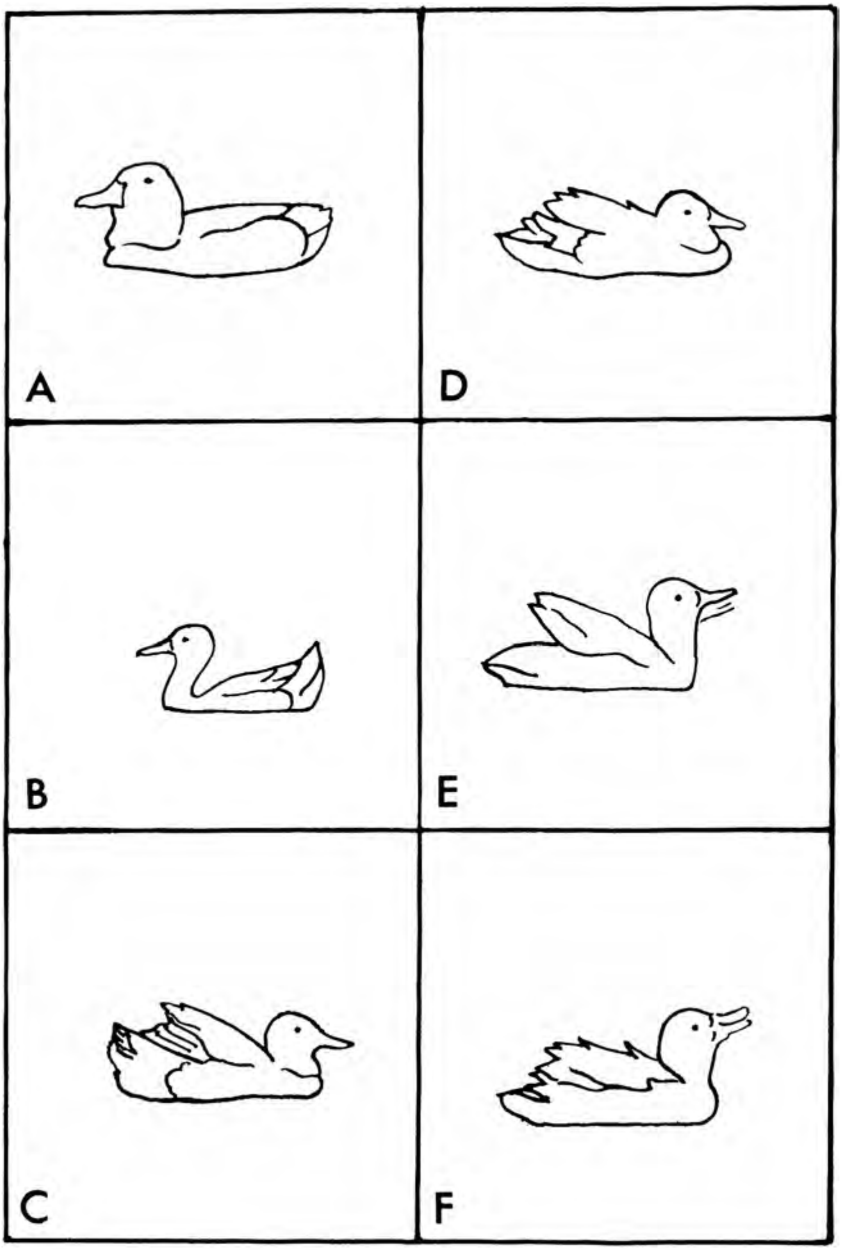


Figure 8. Courtship postures of the Black-headed Duck. (*A*) Toad-posture of a male characteristic of males courting in a group. It precedes the Toad-call and may also function as a threat display. Note the inflated neck. (*B*) The tail-up, tail-wag posture usually follows the toad-posture and Toad-call, which, in turn, is followed by a wing-up, tail-up (*C*). Now the male draws the bill close to the breast and partially lowers the wings and tail (*D*). The male then raises his head quickly with up-tilted bill, inflates the throat, raises the wings above the back (*E*). Finally (*F*), the male pumps his head rapidly. These are all moves of the Toad-call display.



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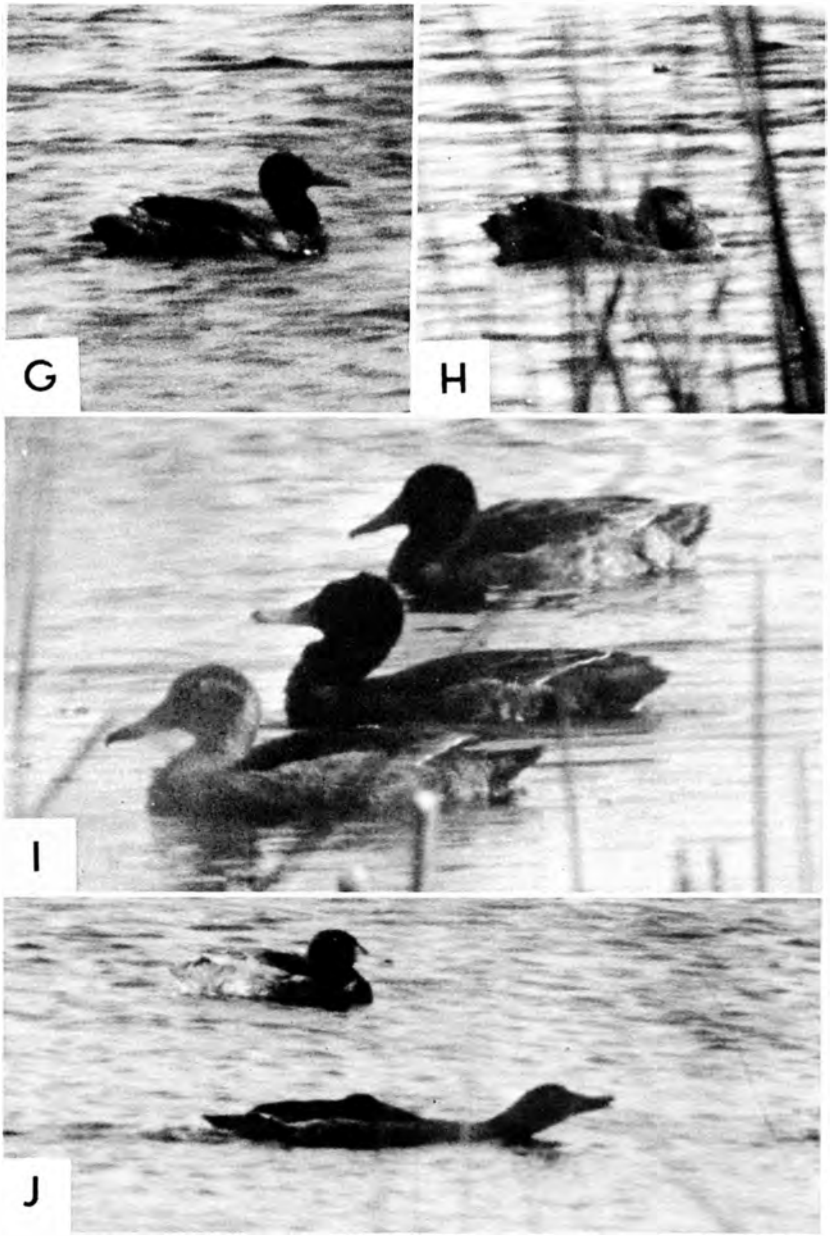
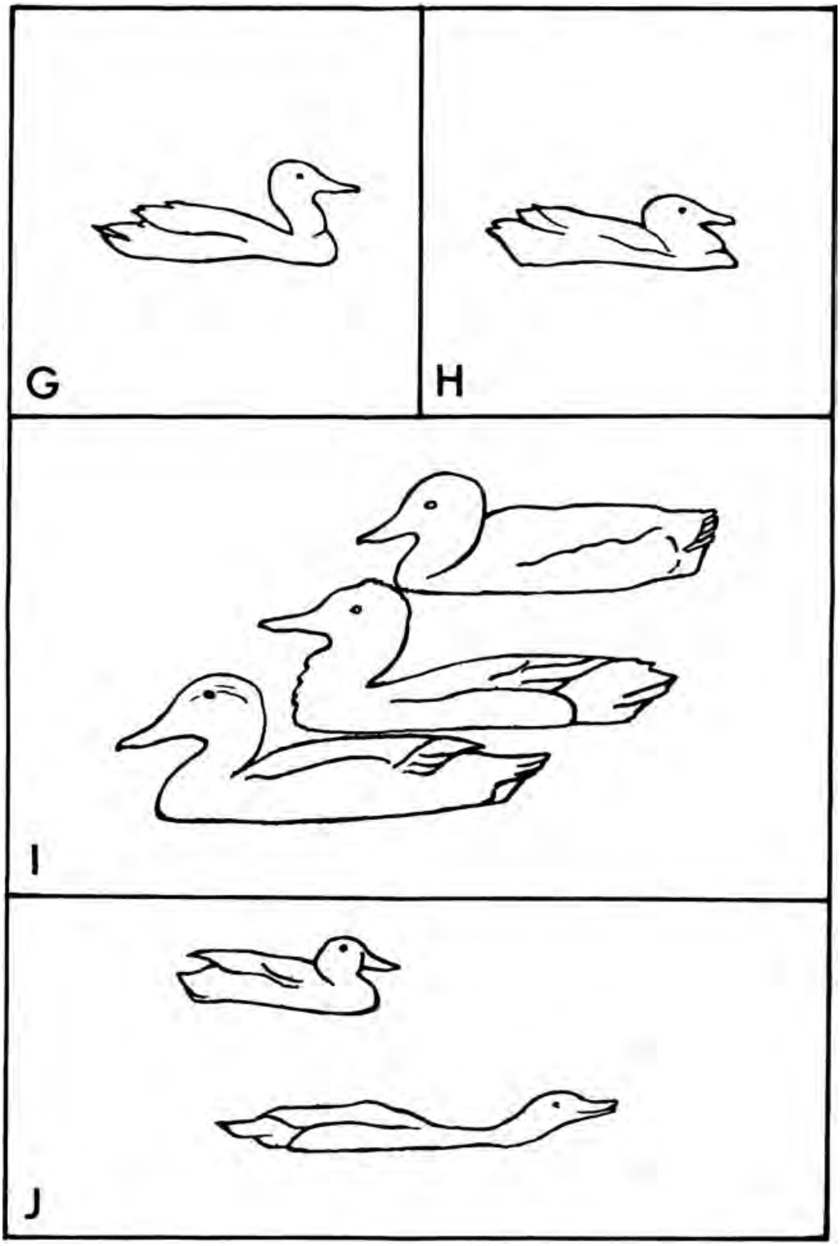


Figure 8. (*G*) The head-back high position sometimes follows the bill-up, head-pumping movement of the Toad-call display. (*H*) An extreme toad-posture. (*I*) The head-back high position is highly variable among individual males. Here, a male (middle) erects the feathers on the occiput and neck. (*J*) A female shows high-intensity aggression as she attacks a male with her neck outstretched and head lowered, mouth open, and a rushing movement.



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preliminary to the Toad-call. Such males holding the head lower than normal inflate the throat and probably the cheeks and erect the feathers of the head, cheeks, and neck so that the swelling of the neck emphasizes the black-feathered area (Figure 8A). This posture, held for several seconds, is often followed by the Toad-call. Lone males also gave this call when disturbed but the movements never seemed as extreme as when the call is part of the courtship display.

The Toad-call involves the following moves: The male may or may not fully inflate the neck and cheeks. Most birds assume a toad-posture. This is followed by a *tail-up, tail-wag* (Figure 8B), then a *wing-up, tail-up* (wing-lift one) with the head held at near-normal level (Figure 8C). The secondaries and scapulars show prominently as the male lowers his head and tail. The bill comes very close to the breast as the wings and tail are partially lowered (Figure 8D). Then, the head is raised quickly with the bill 20 to 30 degrees above the horizontal; the throat seems to be inflated further as the wings again are lifted to a more extreme posture than during the first wing-lift (wing-up, bill-up — shown in Figure 8E). The tail is not raised during wing-lift two. The male now pumps his head very rapidly (Figure 8F), too rapidly to be stopped by a movie camera with a shutter speed of 1/160th of a second. Presumably, the pumping of the head produces the sound. The wings are lowered more slowly and completely and there is at least one tail-wag synchronized with these wing movements.

In some instances, the bill-up, head-pumping is followed by a head back-high position (Figure 8G) which varies considerably in degree among individuals. At times, the head feathers seem depressed on the crown but erected on the occiput, forming a crest (Figure 8I). The neck feathers also seem to be erected in most individuals. The head is pulled back in an angular posture strikingly different from the rounded appearance of the head during most displays.

One of the four males that I filmed performed an extreme toad-posture with the head very low and back (Figure 8H).

It seems probable that the male's plumage with its distinctive patterns and colors, the black head and neck so conspicuous when the head feathers are erected, the inflated cheeks, and the moving head may reinforce the Toad-call. The wing-bars are conspicuous when the wings are raised; the rufous under-tail coverts are obvious when the tail is elevated. The bill-up position may show the rose-colored spots and also a white area on the chin and throat that is present in almost all males.

A bill-dip and side to side head-shake may precede the Toad-call. Wing-flapping and swimming-shakes also occur regularly during courtship.

The duration of this display in four filmed sequences was about 1.3 seconds in one sequence and only 0.7 second in another.

The call is an unduck-like two-note grunt followed by a whistle which may be syllabized as *gr-rump-freet.* Wetmore (1926) apparently did not detect the whistle but Johnsgard (1961) noted it. Wetmore reported that the call was extremely soft and that 45 meters is the maximal distance one can hear it even on a quiet day. The sources and causes of the sounds are uncertain but Wetmore noted cheek air sacs and an esophageal swelling but no tracheal air sacs or osseus bullae. The male emits the grunt with the head in a lowered position and with the wings either up or starting down; and the whistle as the wings are lowered and the tail-wag starts. The regular rhythm of the calls — at 10- to 12-second intervals — suggests that the air sacs must be refilled after each call. I suspect that males can inflate the air sacs and call only during the breeding season. I had no specimen of post-breeding males with air sacs in the cheeks, and it was impossible to prepare the specimen by passing the skin over the head as Wetmore (1926) did with a male collected during the breeding season.

Johnsgard (1961) also noted a *Turn-the-back-of-the-head* display during courtship. I did not observe this behavior.

*Threat Behavior.* — Males exhibit threat and possibly sexual interest by a bill-down position which resembles the bird in a toad-posture. However, the head is held at the normal level, is less inflated, and the crown is directed forward by the low bill position. This posture needs further study as I saw it only five times; it may represent individual or motivational variation in the toad-posture such as in Figure 8H. I saw this posture in lone birds approaching groups of Black-headed Ducks in which there were females. Paired males also gave it in groups. One paired male approached me in this position, then turned and gave the Toad-call.

Black-headed Ducks expressed more clear-cut aggressive behavior when they moved toward the intruder with one of the following postures, each manifesting a higher intensity of aggression: (a) swimming-forward with head only slightly lower than the normal swimming posture, (b) a head-low threat with the neck outstretched, (c) mouth-open threat, and (d) attack, normally with the mouth open and a rushing movement (Figure 8J).

*Display Sequences.* — Lone males in search of females were conspicuous by their alert appearance, active swimming, occasional Toad-calls, and their tendency to fly, apparently seeking females. Such males often gave Toad-calls as they approached pairs, inducing similar behavior in the paired male. Usually the mated male attacked and successfully chased the intruder, but highly aggressive (presumably unpaired) males sometimes returned again and again. Such males wing-flapped and gave head-shakes, swimming-shakes, and head-flicks between encounters. Males avoiding attacks, but persistently maintaining a position by the females, took flight briefly to rise above the attacker. In a few cases, where several lone males as well as a paired male were fighting, the attacker also took flight so that a brief aerial attack occurred. Courtship battles always were brief, involving intense rushing, splashing, and flapping. I noted one possible shallow diving attack but, generally, diving played no part in courtship; nor did I see aerial chases or displays.

When several lone males pressed the same pair, the female often attacked calling males (Figure 8J). In a few cases, females and even males attacked their mates but seconds later allowed them to retain a position by their side, between them and the intruders. I did not observe inciting movements by females but, because courtship observations were mostly at long range, I could have missed such displays. Females nibble-preened the sides of their necks.

The largest courtship group observed contained five males and four females. In one case, a male drifted toward cover leading a female. When the female did not follow, the male returned to her side and drifted off again, whereupon the female followed him to an isolated pool. I witnessed no copulation during this study.

Apparently, females have almost no vocalizations. In several cases of alarm or threat, I suspected that the male responded to a low call by a female but I never actually heard a sound.

## Hosts and Laying

During the laying season, pairs of *Heteronetta* frequented pools in areas used by many other nesting marsh birds. The lone males, seen occasionally

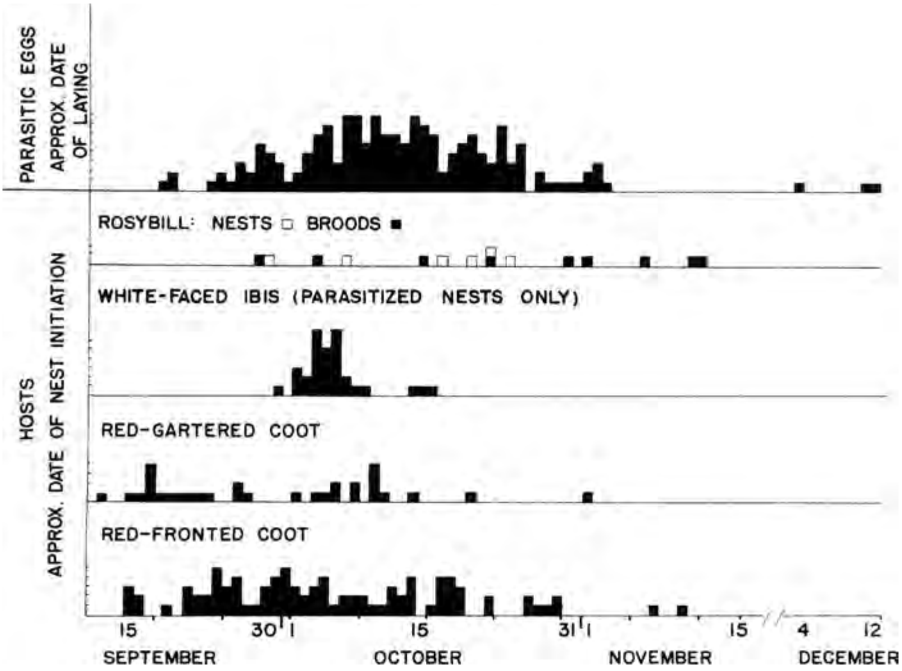

Figure 9. Chronology of nesting of hosts and of parasitic egg-laying by the Black-headed Duck, based on observations at two study areas near General Lavalle, Buenos Aires Province, Argentina. Height of bars indicates the number of eggs (parasite) and nests (host).

in the pools, may have been awaiting laying females. Although I also observed lone females at this time of year, the birds more commonly moved about in pairs through the semi-open tules as if in search of nests. When alarmed at this season, the female sometimes seemed to have difficulty rising from the water, possibly because of the extra weight of the reproductive tract during the laying period.

The prevalence of pairs in the late morning and afternoon and of lone males in the early morning suggests that laying normally occurs in early morning as it does in most ducks.

I never observed the parasitizing act. Host species were shy and deserted nests; female Black-headed Ducks avoided areas where we put up blinds. Nest parasitism in this species probably will be observed only as a result of several years of patient efforts, or of a chance observation such as that of McKinney (1954) on a Redhead (*Aythya americana*) parasitizing a Canvasback (*A. valisineria*). Indirect evidence — the fact that we found no eggs cracked or knocked into the water — indicates that *Heteronetta* lay their eggs in the nest when the host is absent. The two parasitic eggs, found outside a nest, had been incubated and probably were accidentally pushed out by the host. There was no duck down in the nests of the hosts.

The laying chronology of the Black-headed Duck was well synchronized to the nesting chronology of the Red-fronted and Red-gartered Coots (*Fulica rufifrons* and *F. armillata*), encompassing most of the nesting period of the former and all of the latter (Figure 9). It was also well synchronized to the early nests of Rosybills. Most laying occurred from 15 September to 13 November, but undoubtedly some females laid throughout November and early December, because three fresh *Heteronetta* eggs were found in a gull nest on 12 December. Also, the presence of a few very young juveniles in late February suggests that hatching occurred in late December or early January.

Information on dates of nest initiation and laying for *Heteronetta* eggs is derived from nests both at El Palenque and the Vanini Estancia (Figure 9). Laying dates for parasitic eggs probably are less accurate because the back-dating depended on estimated incubation period of the *Heteronetta* egg. In cases where eggs contained dead embryos, this estimate is minimal. Possibly the minimal incubation estimates exaggerate the peaks of parasitism which are, in general, six to ten days later than the peaks of nest initiation by the hosts.

The list of host species seems to include any marsh bird that nests in fairly dense marsh emergents regardless of the color or size of the hosts' eggs or the type of nest. Table 2 lists the host species recorded in the literature. Most unusual is the nest parasitism of predaceous birds like the Chimango and huge marsh-nesting birds like the Crested Screamer *(Chauna torquata)*. We tried to locate nests of various marsh birds and determine the relative incidence of parasitism of various species and the success of eggs in nests of different hosts. In this way, we hoped to determine the most significant host species. Unfortunately, we found relatively few nests of Rosybills and Fulvous Whistling Ducks *(Dendrocygna bicolor)*.

Figure 10. The parasitized nest of the White-faced Ibis. The bowl of the nest is nearly 20 inches above the water. The parasitizing Black-headed Duck probably used its wings as well as its feet in reaching the nest.

Parasitism proved highest on the species nesting in the dense marsh areas (see Table 3): the Red-fronted Coot (55 per cent of 133 nests) and the Rosybill (83 per cent of six nests). Red-gartered Coots, which use the open marsh and semi-open emergent, were parasitized less often (16 per cent of 51 nests). In the huge colony (15,000 to 18,000 nests) of White-faced Ibis (Figure 10), the percentage of parasitism was low (1.5 per cent of 2,071 nests). However, since this is the only colony of the species in that part of Cape San Antonio, its birds were probably very important hosts for Black-headed Ducks.

Although data are not available to appraise the abundance of marsh-dwelling species in the Cape San Antonio area, there can be little doubt that the coots greatly outnumber the marsh-nesting ducks and probably most other

TABLE 2

Host Species of the Black-headed Duck Reported in the Literature

| *Host Species* | *Location* | *Observer or reference* |
|---|---|---|
| White-faced Ibis<br>(*Plegadis falcinellus*) | Rosas, Buenos Aires, Argentina | Daguerre, 1920 |
| Black-crowned Night Heron<br>(*Nycticorax nycticorax*) | Rosas, B.A., Argentina | Daguerre, 1934 |
| Black-crowned Night Heron | Chile | Goodall, Johnson and Philippi, 1951 |
| Roseate Spoonbill | General Lavalle, B.A., Argentina | Pereyra, 1937 |
| Crested Screamer | Rosas, B.A., Argentina | Daguerre, 1920 |
| Coscoroba Swan<br>(*Coscoroba coscoroba*) | Rosas, B.A., Argentina | Daguerre, 1920 |
| Coscoroba Swan | General Lavalle, B.A., Argentina | Gibson, 1920* |
| Rosybill | Rosas, B.A., Argentina | Daguerre, 1923 |
| Limpkin<br>(*Aramus guarauna*) | Rosas, B.A., Argentina | Dabbene, 1921 |
| Spotted Rail<br>(*Pardirallus maculatus*) | Rosas, B.A., Argentina | Daguerre, 1920 |
| Maguari Stork<br>(*Euxenura maguari*) | General Lavalle, B.A., Argentina | Gibson, 1920* |
| Red-gartered Coot | Venado Tuerto, Santa Fe, Argentina | Wilson, 1924 |
| Red-gartered Coot | Chile | Goodall, Johnson, and Philippi, 1951 |
| "Coots" (probably Red-fronted) | Rosas, B.A., Argentina | Daguerre, 1920 |
| Chimango | Venado Tuerto, S.F., Argentina | Wilson, 1923b |
| Brown-hooded Gull | Rosas, B.A., Argentina | Daguerre, 1920 |
| Brown-hooded Gull | Venado Tuerto, S.F., Argentina | Wilson, 1923a |

*Identified as Rosybill eggs

TABLE 3

Incidence of Parasitism, Nest Success, and Success of Black-headed Duck Eggs in Two Marsh Areas near General Lavalle, Argentina, September–December 1964

| *Potential host species* | *Total number nests observed* | *Incidence of parasitism in total nests observed* | *Total nests observed to termination* | *Incidence of parasitism in terminated nests* | *Nest success of all nests terminated* | *Nest success of parasitized nests* | *Nest success of parasites in terminated nests* | *Nest success of unparasitized host nests* | *Egg success of parasites (total number hatched of total laid)* |
|---|---|---|---|---|---|---|---|---|---|
| *Estancia El Palenque* | | | | | | | | | |
| Red-fronted Coot | 114 | 62 (54%) | 46 | 31 (67%) | 38 (83%) | 25 (81%) | 10 (22%) | 13 (87%) | 10 (18%) |
| Red-gartered Coot | 51 | 8 (16%) | 49 | 8 (16%) | 28 (57%) | | 0 (0%) | | 0 (0%) |
| Crested Screamer | 15 | 0 | 6 | 0 | 6 (100%) | | — | | — |
| Rosybill | 6 | 5 (83%) | 6 | 5 (83%) | 1 (13%) | | 1 (17%) | | 1 (9%) |
| Fulvous Whistling Duck | 2 | 0 | 2 | 0 | 0 (0%) | | — | | — |
| *Vanini Estancia* | | | | | | | | | |
| Red-fronted Coot | 19 | 11 (58%) | 12 | 9 (75%) | 10 (83%) | | 5 (41%) | | 6 (64%) |
| Brown-hooded Gull | 7 | 1 (14%) | | | | | | | |
| White-faced Ibis | 2071 | 32 (1.5%) | — | — | — | | | | — |
| Roseate Spoonbill | 22 | 0 | | | | | | | |
| Common Egret (*Casmerodius albus*) | 15 | 0 | | | | | | | |
| Snowy Egret (*Leucophoyx thula*) | 4 | 0 | | | | | | | |
| Black-crowned Night Heron | 8 | 0 | | | | | | | |

birds. Coot nests are common, easily found, well cared for, and have a high nest success (83 per cent for 46 Red-fronted Coot nests and 57 per cent for 49 Red-gartered Coots as compared with 13 per cent for six Rosybill nests; see Table 3). I found coots to be the most important host for *Heteronetta.* The abundance of different hosts probably assures the success of *Heteronetta* eggs. Most of the host species are solitary nesters but breed in dense populations because the habitat suitable for nesting is restricted. At least two major hosts are colonial — the White-faced Ibis and Brown-headed Gull. In addition to employing a wide spectrum of hosts, Black-headed Duck females probably vary in time of laying. Most females seem to deposit eggs in October when most of the hosts are nesting. Whether imprinting of young influences subsequent host selection is a challenging, but presently unanswerable, question.

Although *Heteronetta* eggs have been reported in heron nests, we found none in heron, egret, or Roseate Spoonbill (*Ajaia ajaja*) nests. Parasitized nests were mostly low. However, we found several 15 to 20 inches above water, and, unless there had been a drastic decline in the water level, the parasitizing females must have used their wings as well as their feet to enter them (Figure 10).

As noted for Redhead parasitism (Weller, 1959), the Black-headed Ducks parasitized nests in certain areas more intensively than others. These areas usually were associated with large *Azolla-* or *Lemna*-covered pools where, presumably, numerous parasitic females loafed and fed.

## Eggs and Egg Success

*Egg Shape, Size, and Texture.* — The eggs of the Black-headed Duck closely resemble those of the Rosybills. Daguerre (1922, 1923) reported that *Heteronetta* eggs differed in shape, had a finely pitted surface (which can be felt when rubbed, as well as seen), and were whiter in color. He also stated that *Heteronetta* eggs usually were wider for their length than were those of Rosybills. We measured too few Rosybill eggs to allow a sound analysis but the differences, shown in Table 4, were not significant at the 0.05 level. Moreover, the measurements are too similar and variable to provide a practical field technique for distinguishing individual eggs of the two species. However, shape differed considerably in most cases. Eggs of the Rosybill were "longelliptical" or "subelliptical" (terms from Palmer, 1962) while those of Black-headed Ducks were "short oval." In addition, the shell of the *Heteronetta* egg, when candled, has a more granular density than those of Rosybills and the Fulvous Whistling Ducks. In this character the *Heteronetta* eggs resemble the eggs of Ruddy Ducks yet are not as rough, while the eggs of dabblers and inland divers have more translucent and less granular shells. A few *Heteronetta* eggs were found which resembled those of Rosybills in shape but not in shell texture. The shells of four eggs from which Black-headed ducklings hatched varied considerably in shape and color. For this reason, I suspect that many eggs, still attributed to Rosybills, are, in fact, those of *Heteronetta.* The only case I noted of interspecific parasitism by a Rosybill was an active ibis nest containing one Rosybill egg and one *Heteronetta* egg.

*Number of Eggs per Nest and Time of Laying.*—We found one parasitic egg per nest in 55 per cent of the successful nests of Red-fronted Coots at El Palenque, and in 82 per cent of 11 nests at Vanini Estancia. Thirty-two per cent of the nests at El Palenque had two eggs (Table 5). Up to five eggs were found in one Red-fronted Coot nest. The maximum—eight eggs—was found

## TABLE 4

Measurements in Millimeters of the Length and Width of Six Rosybill and 23 Black-headed Duck Eggs

| *Species* | *Measure-ments* | *Sample size* | *Mean* | *Standard deviation* | *Range* |
|---|---|---|---|---|---|
| Black-headed Duck | Length | 23 | 58.05 | 1.85 | 55.1–62.6 |
| Rosybill | Length | 6 | 58.35 | 2.27 | 55.8–62.0 |
| Black-headed Duck | Width | 23 | 43.23 | 1.66 | 39.5–45.9 |
| Rosybill | Width | 6 | 42.37 | 1.15 | 40.5–43.3 |

at various levels in another Red-fronted Coot nest where later one *Heteronetta* egg and five coot eggs hatched. In some cases, coots buried the *Heteronetta* eggs and incubated their own eggs on the layer of "foreign" eggs. Rodriquez (1918) reported seven *Heteronetta* eggs in one nest.

I do not know whether some mechanism limits the number of eggs deposited in a nest or whether laying is random, as appears to be the case in cowbirds (Mayfield, 1965), as data are insufficient for a statistical analysis of randomness of distribution. Apparently no visual stimulus limits laying if one egg already is present. Probably no elaborate mechanism is involved. Hens frequent certain areas and tend to lay one egg per nest. Actually, since the laying period of the host is about the only time the Black-headed Duck can visit a nest inconspicuously, it seldom has an opportunity to lay in a nest more than once — unless, of course, its laying period coincides exactly with that of the host.

## TABLE 5

Frequency Distribution of Black-headed Duck Eggs in Nests of Marsh Birds at Estancias El Palenque

*Number of Black-headed Duck eggs in nest*

|  | *1* | *2* | *3* | *4* | *5* | *6* | *7* | *8* |
|---|---|---|---|---|---|---|---|---|
| Red-fronted Coot (El Palenque) | 17* (55%) | 10 (32%) | 2 |  | 1 |  |  | 1 |
| Red-fronted Coot (Vanini) | 9 (82%) | 1 | 1 |  |  |  |  |  |
| White-winged Coot (El Palenque) | 6 | 2 |  |  |  |  |  |  |
| White-faced Ibis (Vanini) | 28 | 4 |  |  |  |  |  |  |
| *Totals* | 60 (73%) | 17 (21%) | 3 (4%) | 0 | 1 | 0 | 0 | 1 |

*Number of nests observed followed by per cent of total number of parasite eggs for the host species.

Figure 11 (*above*). Coot nests are heavily parasitized. This Red-fronted Coot nest has a single Black-headed Duck egg in the bowl. One of three buried eggs of the Black-headed Duck is visible.

Figure 12 (*below*). A "dump" nest containing 22 Rosybill eggs and four Black-headed Duck eggs (white).

There was no evidence that parasitizing birds destroyed or removed eggs of the host or battled with host females for a laying position on the nest. I found no cracked eggs or eggs in the water as I did in nests parasitized by Redheads (Weller, 1959). Obviously, the parasite has evolved a more efficient and successful mechanism for timing its egg-laying during the period when the host is least likely to be present — the laying period. This also assures a full incubation period. The fact that the females lay in nests of large and predatory birds supports this hypothesis. Nocturnal laying is a possibility.

*Egg Success.* — Because of the problems of maintaining a small nest with a large number of eggs during times of fluctuating water levels, the chances of egg and nest success probably are lower in nests containing several parasitic eggs. The relative density of hosts and parasites may affect the success. With numerous hosts in relation to parasitic females, success may be high because the eggs are well dispersed and well synchronized. When hosts are less numerous the number of eggs per nest may increase and lower the success of the parasite. Population size also must be directly related to habitat quality in marshes which regulates the abundance of host species. Obviously, the parasite can never exceed its host in abundance without creating a problem of availability of laying sites.

In the El Palenque marshes, 23 of the 62 parasitized Red-fronted Coot nests had at least one *Heteronetta* egg that was half buried; some were completely out of view. At the Vanini Marsh only one of 11 parasitized nests had a partly buried *Heteronetta* egg. The tendency of coots to bury parasitic eggs suggests that, although they recognize such eggs, they do not attempt to eliminate them from the nest (Figure 11). The burial of eggs may be unintentional as Pereya (1938) suggested, or it may be the result of fluctuating water levels — of the host species attempting to raise its own eggs above the rising water and neglecting the foreign ones.

It is doubtful whether Rosybills or other ducks distinguish the similar *Heteronetta* eggs from their own, and thus losses of eggs due to burial are unlikely. However, too few nests of these species were observed to determine this.

The system of Black-headed Ducks laying in active rather than deserted nests, possibly by chance alone, results in high hatching success. Whether they can or do determine the status of such nests is uncertain. It seems unlikely that warmth of the eggs could be the stimulus since the first three or four eggs of a coot and the entire clutch of a duck are deposited before intensive incubation starts. Moreover, Black-headed Ducks do lay in Rosybill "dump" nests as shown by a Rosybill nest of 26 eggs, of which four were *Heteronetta* eggs (Figure 12). Possibly, the Black-headed Ducks follow the host females when they are nest building or laying, as parasitizing Redheads seem to (Weller, 1959), and thereby visit only active nests. Black-headed Ducks deposited no eggs in eight artificial nests containing chicken eggs.

Black-headed Ducks usually parasitized nests in which the host had already laid three to five eggs; one parasitized nest of a coot had only two cold eggs. Many eggs were laid after the host began incubation and some even after intensive incubation was well under way. In a few cases fresh Black-headed Duck eggs were found in coot and ibis nests containing eggs which were near hatching. At Estancia El Palenque, the synchrony of 76 *Heteronetta* eggs in 43 Red-fronted Coot nests could be judged from information gathered from candling eggs in nests. Of these, 40 (53 per cent) obviously were deposited during the hosts' laying period (a considerably better percentage than in the parasitic Redheads according to Weller, 1959); 25 (35 per cent) appeared to be about two to five days late and may have hatched when the young coots were being brooded on the nest; and 14 per cent were laid so late there was no chance of survival. In spite of this fair synchrony, hatching success at Estancia El Palenque was low, being only 18 per cent for the most important host species, the Red-fronted Coot. I believe that this low hatching success was due to the high rate of burial of eggs.

At Vanini Estancia the hatching success was higher. But possibly the figures are biased because we observed only late nests of coots there. At El Palenque we found that coot nests started late in the season were more successful than the early nests. Of 14 eggs in 19 Red-fronted Coot nests at Vanini Estancia nine (64 per cent) were well synchronized and hatched; five (36 per cent) were not well synchronized and did not hatch. In ibis nests, 12 of 36 eggs (33 per cent) were within a few days of perfect synchrony and probably would have hatched. Thus, the species may have a high egg success under ideal conditions.

## Hatching and Incubation Period

The incubation period of *Heteronetta* eggs was determined by reference to incubation periods of the host. In three cases, *Heteronetta* ducklings hatched in nests prior to the hatching of young coots. In one case, a duckling hatched a full day before the first coot. Because coots begin intensive incubation in the middle of the clutch (found in this study to be the fourth egg in Red-fronted and Red-gartered Coots), the incubation period differs for early and late-laid eggs. The first egg of both Red-gartered (one nest) and Red-fronted Coots (two nests) required 28 to 29 days from laying to hatching, while the last egg required only 24.5 to 25 days. Thus, an egg of a Black-headed Duck may be deposited after the first two coot eggs (the earliest record in this study) and be incubated in the nest for 27 days. Or, it may be laid with the host's last egg and have only 25 days incubation. Apparently, *Heteronetta* eggs may hatch in as little as 24 or 25 days. Observations of a Rosybill nest in which incubation of all eggs starts simultaneously and appears to last about 28 days supports this suggestion; the single *Heteronetta* egg in the Rosybill nest hatched two and one-half to three days before the Rosybill eggs. Thus, it appears that the eggs of Black-headed Ducks have a relatively short incubation period.

In one case, a *Heteronetta* hatched in a coot nest nearly four days after the last of the coot's brood. I found this duckling dead in the water. The egg probably hatched because of the warmth created by the coot's brooding of the young on the nest. Both Red-fronted and Red-gartered Coots often reline their nest for use as a brood ramp. Thus, the total warming period for unhatched eggs may be 30 to 33 days. It also is possible that *Heteronetta* eggs may hatch after the hatching of the host's eggs in ibis nests where the young are brooded for several weeks (Figure 13).

## Responses of Hosts to Parasitism

Judging from observations at five Red-fronted Coot nests, one Rosybill nest and one ibis nest, all of which contained a *Heteronetta* duckling, foster parents brood *Heteronetta* ducklings as if they were their own. In two cases I saw Red-fronted Coots eating *Heteronetta* eggshells. On the other hand, I found shell fragments commonly in nests where Black-headed ducklings had hatched. Presumably, Rosybills eat or carry away shells as do other members of the family (Weller, 1959), and ibises carry off *Heteronetta* shells as they do shells of their own eggs. At least I found no shells in ibis nests where ducklings had hatched. Eighty-seven per cent of the unparasitized nests and 81 per cent of the parasitized nests of the Red-fronted Coot were successful. We had too few nests of the other host species for comparative figures. There was no egg breakage and only twice were eggs of the Black-headed Duck found outside nests — one of a Red-fronted Coot and one of a Red-gartered Coot. Because I saw egg ejection so rarely and because we found at least one coot egg outside a nest, I do not believe that the *Heteronetta* eggs were pushed from the nests.

Based on egg and nest success, there was no apparent increase in predation due to the conspicuous, white *Heteronetta* eggs. Presumably, hosts incubated steadily, never leaving the eggs exposed to predators.

To observe the response of a host to a parasitic egg, I added a *Heteronetta* egg to an unparasitized nest containing four Red-fronted Coot eggs. As I watched from a blind both adults visited the nest; one looked into the nest and got on without hesitating; the second bird looked but did not get on. The *Heteronetta* egg as well as the coot eggs eventually hatched.

## Behavior of Ducklings

I collected data on the behavior of ducklings by observing young in nests from blinds, by recording behavior of ducklings found in or near nests, and by attempting to rear five captive ducklings.

*Wild Ducklings.* — I saw ducklings only in or near the nests of hosts and never in the broods of host species or alone in the marsh. We never observed female Black-headed Ducks with young or even behaving as though they had broods. After leaving the nest, the young apparently lead solitary and secretive lives in the emergent vegetation until able to fly. I saw only two flightless juveniles during the summer. They fed very close to the vegetation and were extremely wary.

Ducklings, hatched in coot nests and, presumably, in nests of other hosts, are brooded and cared for by the host as if they were their own and evidently remain in the nest one to two days (Figure 14). In one Red-fronted Coot nest, the duckling hatched during the night and left when between one-and-one-half to two days old. In a second case, the duckling hatched in early morning and was gone the next morning. There is no evidence that young return to be brooded at night but we need more observations. How long the host parent broods the young parasite may depend upon the hour of hatching and upon the synchronization of the parasite's hatching with that of the host. Because the incubation period of the Black-headed Duck is shorter than that of the ducks they parasitize, and since hatching is more closely synchronized in clutches of ducks' eggs than in coots', *Heteronetta* ducklings will hatch in advance of the hosts' young if laying occurs prior to the start of incubation. If it hatches in advance of the host's young, the *Heteronetta* duckling presumably leaves the nest. In nests of ibises and other marsh birds, its only hope of survival would be to leave the nest and feed independently.

Young *Heteronetta,* like most ducklings, show no fear of humans during their first three to five hours of life but they seem to dislike being gripped in the hand. In three cases, I observed that wild ducklings, disturbed in the nest, "froze" with neck outstretched and head low. In one case, the duckling left the nest after I moved away. When I returned it to the nest, it again froze — at least temporarily. Ducklings moved rapidly through the floating duckweed using the same "scooting" actions as the adults and swam toward emergent vegetation where they froze. Ducklings were handled in all cases and two, apparently older birds, squirmed and pecked and swam off when I freed them. However, in no case did the ducklings dive.

Figure 13 (*above*). A Black-headed duckling in a nest with a young White-faced Ibis. Note the distinctive, dark, vertical bar above the eye running through the superciliary line.

Figure 14 (*below*). A Black-headed duckling shares a nest with its host, the Red-fronted Coot. Two young coots have recently hatched. The duckling will remain in the nest for one or two days.

*Captive Ducklings.* — Because of the secretiveness of the young ducklings out of the nest and because it was impossible to observe them being brooded, we made observations on five captive ducklings, four hatched by a domestic chicken and one taken from an ibis nest. Three, including the wild bird, were kept in captivity to allow closer observation and to compare their behavior with that of other species. In general these birds were intolerant of confinement after the age of one day and were difficult to keep in cages. All died by the time they were four to seven days old, despite the fact that they ate well.

*Imprinting.* — The psychological attachment of a duckling to a parent normally assures a long-lasting bond which provides warmth and protection for the young during the preflight stage. But does imprinting occur in the parasitic species? Very quickly it was apparent that the Black-headed ducklings show no clear-cut following reaction and that they are not innately equipped to follow a parent or host.

Of the three Black-headed ducklings "imprinted" to humans, one taken from the hen at the age of two hours showed the best recognition of man and the least fear. Only this duckling tended to move toward both the human voice and figure after an intensive effort to teach it to follow. It gave contentment calls when several feet from human shoes and voice and moved toward them, but it would not follow any more distant or rapidly moving object. Neither of the other two, trained less intensively, showed even this slight inclination to follow.

Two ducklings reared by a domestic hen led generally independent lives. They left the nest, fed alone, and returned to it regardless of the whereabouts of the hen. In most cases they did not attempt to follow the hen when she left to feed or sunbathe. However, one duckling, failing in its repeated efforts to leave the enclosure, gave up normal feeding and nibbled on the hen's feathers instead. Becoming very weak at about three days of age it did follow the domestic hen several feet and once even left the box to seek her — presumably for warmth. It died a short time later.

Despite some attachment to the domestic hen, or to the human parent, at least four of the five ducklings (the fifth bird escaped before this point could be clearly observed) made efforts to leave the parent. Two ducklings, which gave contentment calls on seeing a human, ran away when placed outside their boxes. A one-and-one-half day-old duckling that did not run unfortunately escaped from its cage before further tests could be made. The captive ducklings liked the natural foods they were given so this desire for independence was not a result of foods.

My observations agree generally with those of several members of the Runnacles family of General Lavalle who have attempted to rear *Heteronetta* ducklings with other species and found that they do not remain with the broods in which they are hatched.

Data from the five ducklings demonstrate some variability but all showed the same tendency to leave the foster parent rather than to remain with it as has been reported for semi-parasitic ducks (Weller, 1959). Thus, the Black-headed Duck is unique in being the only truly parasitic species which is precocial.

The same domestic hen reared two Rosybill ducklings. Their behavior with this hen was typical of the young of most northern hemisphere anatids. There was no need to keep them in a cage. Although they also made some short excursions away from the hen, they kept close contact with her at all times, never displayed a tendency to escape if she was near, and did not fear humans nearly so much as did Black-headed ducklings.

It appears from these observations that the inclination to leave the host is strong soon after the parasitic duckling is dry and mobile. If for some reason it is not able to leave or is confined in the same general area as the host, the duckling apparently uses the host for warmth as did one captive duckling. Peña (1962) had a similar experience. He reared ducklings of this species by use of a foster parent, a domestic Muscovy Duck (*Cairina moschata*). The ducklings apparently returned to the female to be brooded at night. Generally, however, they reared themselves independently in a small pond where natural foods were available. In this situation there were several young and the behavior of a group may have influenced their response to the female since, normally, young are hatched singly.

*Alarm Reactions of Ducklings.* — *Heteronetta* ducklings soon developed reactions to foreign objects. When cornered, young Black-headed Ducks threatened with the neck-stretch and mouth-open hissing display, seen in both juvenile and adult Ruddy Ducks. Ducklings, imprinted to the chicken, feared humans and hesitated to show themselves when people were present. This was not true of young Rosybill ducklings imprinted to humans; these ducklings showed escape reactions toward humans only when the humans surprised them or moved quickly. All the hand-reared *Heteronetta* ducklings gave alarm calls when held in the hand. In general, however, the ducklings seemed to render fewer alarm calls as they grew older. Several ducklings of one-and-one-half days of age, when left in new cages, gave a few distress notes that lasted not more than a few seconds. The two ducklings reared by humans showed no distress reactions to low temperature and, when only three days old, slept, preened, and fed alone in outdoor temperatures varying from 50°F at night to 80°F in the daytime.

*Feeding.* — When ducklings were two-and-a-half hours old, I observed a nibbling action of the bill which eventually seemed to serve two purposes: preening and feeding. Nice (1962) observed this type of action in other duck species while the ducklings were still in the shell. Ducklings occasionally nibbled at irregular surfaces as ducklings of other species do, but they did not peck at spots. The tip of the bill seemed especially sensitive and nibbling often started as the head of a sleeping bird moved downward and the bill touched some surface. When water was placed under such a duckling, even the youngest, only seven hours old, responded to the contact immediately by dabbling. The head was held with the bill at approximately a 45-degree angle or less to the surface of very shallow water. The efficiency of this feeding action increased rapidly. The first captive bird fed when 13 hours of age and its nibbling created clear-cut swirls of water on each side of the bill (Figure 15). Water apparently enters the tip of the bill and is forced out each side, forming two circular currents which bring food organisms to the tip. The effectiveness of the straining undoubtedly increases greatly as the lamellae develop. Veselovsky (*in* Nice, 1962) reported that the lamellae do not develop in either divers or dabblers until ducklings are six to seven days old. Rosybills of six days had only the slightest trace of lamellae, but Black-headed Ducks, less than three days old, showed prominent and apparently functional lamellae.

Because the major food source of wild ducklings probably is in the duckweed mat found almost universally in these marshes, we presented the first captive bird with water containing some small duckweed. At its first contact with water it nibbled, then drank, and soon swirled and strained the water. During the first hour of feeding, the ducklings made the dabbling movement

Figure 15. A captive Black-headed duckling two days of age strains crustaceans from duckweed. Prominent and apparently functional lamellae appear in ducklings of this species when they are less than three days old.

with their bills whether water was present or not, suggesting that they learn where to feed by the intake of food. When it soon became apparent that they were eating very little duckweed, we added some chopped hard-boiled egg to the water. They consumed this eagerly, favoring the small bits of albumen especially, perhaps because of their more solid consistency. Then we separated macroscopic crustaceans from the duckweed mat and added them to the water-duckweed-egg solution. The ducklings took in the crustaceans easily with the effective swirling-straining action of the bills, and, by "searching" with the bill, covered the water area effectively and extracted all the amphipods of less than five or six millimeters in size.

We fed other ducklings by placing duckweed in water and they, too, soon learned to obtain food by trial nibbling and ate eagerly, effectively eliminating nearly all of the crustaceans from a shallow dish.

At first ducklings fed at the edge of the water but within a few minutes they entered the water and fed with a sweeping action of the bill from side to side. Several perfected this feeding action within 10 to 15 minutes after their first feeding. Within several hours they fed again and then quickly turned around to feed in the area immediately behind them. This was effective because the crustaceans tended to collect behind them away from the water currents. When two or more days old, several ducklings kicked in the water after feeding and then usually turned to feed behind them. This kicking action resembled the water-treading of adults in shallow water.

The first feeding periods lasted from five to ten minutes and were interspersed with preening and rest periods lasting 45 to 60 minutes. Later, when two or more days old, they fed almost continuously for 15 to 20 minutes with shorter rest periods in between. The ducklings often uttered delicate contentment notes as they fed, at least during their first two days of life, and, after each feeding, they preened and oiled thoroughly, especially in the ventral region.

*Comfort Movements.* — When less than three hours old (two hours and 45 minutes in one case) the ducklings began to nibble-preen the sides, breast, and lower back in the region of the oil gland. Such preening undoubtedly occurred earlier as noted in other species by Nice (1962), but I made no observations on these birds until they were virtually dry at two-and-one-third to four hours of age. Within the period of two-and-one-half to three hours of age I saw all the comfort movements. The ducklings were adept at keeping their plumage dry and spent time in the water only when feeding. None survived over seven days and I recorded no bathing activities during this period.

*Summary of Behavior in Relation to Breeding Biology of Species.* — Ducklings of this species seem highly precocial. They are innately and anatomically equipped to feed and care for their plumage at an early age. They give a minimum of alarm calls and even tolerate low temperatures without apparent distress. They display a high degree of independence and, in the wild, leave the parent host when one or two days old. In captivity, they do not, in most cases, remain with the foster parent. Since they are not seen in broods of other ducklings, all evidence suggests that they rear themselves. We do not know whether the ducklings leave the nest during their first day to feed (as other ducklings do) and then return. Such behavior would be possible in nests of coots and Rosybills but impossible in nests of ibises or herons because of their height above the water. This unique system of self-rearing is dramatically different from that of semi-parasitic Redheads and Ruddy Ducks where the ducklings are reared with the brood of the foster parent.

## *Discussion*

### Taxonomic Position of the Black-headed Duck

The systematic position of the Black-headed Duck has posed problems since its discovery. It has been classified in several different tribes. Delacour and Mayr (1945) recognized its uncertain position but placed it with the tribe Oxyurini (stifftails) on the basis of Wetmore's (1926) observations on both behavior and anatomy. Specifically, Wetmore pointed to the presence of: air sacs, loose skin of the neck of males, lack of an osseus bulla, diving ability, shiny plumage, small wings, and similarity of the sexes in the pattern of the adult plumage. Salvadori (1895) earlier had noted the similarity of its plumage with that of *Oxyura ferruginea* (Peruvian Ruddy Duck).

At the time of Wetmore's study, the literature contained no description of the plumage of the duckling although there were five specimens in museums. Observations of two of these specimens by Delacour and Mayr (1946) provided no simple solution, but they cited several similarities between *Heteronetta* and typical stifftail ducklings. My observations confirm these similarities. *Heteronetta* ducklings have the large head, heavy body, and wide-legged stance of Ruddy Ducks. Although they share the basic coloration with the dabblers, they are darker in color and have long down which gives them a "woolly" appearance. They have, in addition, a unique vertical line above the eye. Furthermore, the contour feathers of the juvenal plumage and the large rhachis and blunt ends of the juvenal tail feathers are similar to those of young Ruddy Ducks (Weller, 1967a).

The penes of Black-headed Ducks and Ruddy Ducks also are similar, having isolated "papillae" rather than "rings" as I noted in several species of Argentine dabblers of the genus *Anas*. *Heteronetta* and the stifftails (Oxyurini) show strong similarities in their skeletal features (Woolfenden, 1961); but the Black-headed Duck with an elongate body is highly modified for a coot-like existence while the Ruddy has a broad body and is a highly adapted diver.

Both *Heteronetta* and *Oxyura* lay large eggs in relation to the size of the female. However, the *Heteronetta* egg is smooth whereas the eggs of both the Argentine and North American Ruddy Ducks are rough in texture.

Some behavioral similarities between the two groups exist, but are less clear cut than are morphological likenesses. Black-headed Duck females, like Ruddy Duck females, are silent. Males call only during the breeding season, using the air sacs. In the parent-young relationships Black-headed Ducks have achieved the ultimate in precocial behavior among the Anseriformes. It is worth noting that female Argentine and North American Ruddy Ducks regularly abandon their young, or the young leave the brood. These seem to be able to survive well.

The distinctive courtship behavior of Black-headed Ducks does not provide a simple guide to the taxonomy of the species; but elements of its breeding behavior resemble displays of both Oxyurini and Anatini. Like Ruddy Ducks, Black-headed Ducks have air sacs in the head region and perform a vertical pumping head movement that resembles the sound-producing pump of the North American Ruddy Duck. Similar pumping movements are common to many dabblers. Other dabbler-like components of display include the grunt and whistle (no homology with the Grunt-whistle of *Anas* is implied; nor can it be denied) and wing-up, tail-up followed by a tail-wag. Unfortunately the copulatory behavior is still unknown.

In a number of characters, both anatomical and behavioral, Black-headed Ducks resemble the dabbling ducks, tribe Anatini. In general, both are marsh dabblers and strain their food through mud and water by surface feeding and up-ending. Black-headed Ducks dive expertly as well. Although Ruddy Ducks differ markedly among themselves, similar diversity occurs in other tribes. Argentine and North American Ruddy Ducks surface-feed (at least the young do) and dive, but rarely up-end or dabble. Black-headed Ducks lack the large flap on the hind toe characteristic of typical stifftails and other divers, and they apparently lack the ability to submerge gradually as do the stifftails. They fly easily and rapidly and rise directly from the water without preliminary "water-walking." Presumably, this is an adaptation to life in small pools where a steep take-off is necessary. Another morphological similarity to dabblers is in the presence of double white wing-bars, although no colored speculum is present.

The similar behavior and precocity of the young, the laying habits of females, the plumages of young and adults, and the anatomical similarities of skeletons and the male copulatory organs seem to link the Black-headed Duck more closely with the stifftails than with any other group. Systematically there are two possible alternatives: (1) leave the species with the Oxyurini, recognizing that it may be an ancient species which links the dabblers and stifftails, or (2) place it in a separate tribe (Heteronettini) between the Anatini and Oxyurini because of its unique combination of physical and behavioral characteristics. The former system seems more in keeping with the efforts made by Delacour and Mayr (1945) to link the genera into meaningful tribes despite the fact that it places together birds of diverse form and habits.

## Evolution of Parasitism in *Heteronetta*

At the present time, there is no indication that Black-headed Ducks nest. Phillips (1925) suggested and local residents supported the idea that the species may nest in an inconspicuous site such as trees. However, one does not encounter the species in wooded areas but rather in marshes where trees are not common. There have also been suggestions that females may collect the ducklings after they hatch, but there are no well-documented reports of females with broods. Moreover, no one has found females with brood patches or observed brooding behavior as in females of non-parasitic species.

As with all parasitic birds the present breeding pattern presumably represents a modification of the normal nesting pattern. The pattern of pair formation, temporary pair-bond, and pair-defense seem to remain unmodified by the parasitic way of life.

Any theory of the origin of parasitism in the Black-headed Duck is difficult to postulate and preferably should be based on additional years of nesting data. However, in comparison with the semi-parasitic Redhead (Weller, 1959), there are some clear-cut differences which have resulted in successful parasitism in *Heteronetta* while a state of partial parasitism remains in Redheads and possibly North American Ruddy Ducks. The major difference is that the Black-headed Duck parasitizes nests of birds regardless of the egg color or shape while Redheads and Ruddy Ducks rarely do so. In addition, the evolution of self-rearing in the young is unique among parasites.

A key to success of a brood parasite entails the location of a suitable host species which: (1) is within the preferred habitat of the parasite, (2) is sufficiently abundant so that a clutch or several clutches of eggs may be distributed without placing a detrimental excess of eggs in one nest, (3) has a high rate of nest success, (4) will accept and normally incubate foreign eggs, and (5) will care for the young until they are able to care for themselves. For the Black-headed Ducks, coots (especially the Red-fronted Coot) seem to meet these requirements in Argentina. As a broody and abundant species with high nesting success, coots seem to be much better hosts than any species of duck could be. The ranges of the Black-headed Duck and the Red-fronted Coot coincide closely and their habitat preferences and adaptations are strikingly similar. Ecologically, numerically, chronologically, and from the standpoint of egg and nest success, coots seem the best host and the species most likely to have played a key roll in the evolution of this behavior in the Black-headed Duck.

There is little doubt that part of the success of the parasitic behavior is due to the fact that the species parasitizes a variety of hosts, five of which probably hatch and brood their young regularly: the Red-fronted and Red-gartered Coots, White-faced Ibis, Brown-hooded Gulls, and Rosybills. Local residents also reported *Heteronetta* eggs in nests of the Fulvous Whistling Ducks. Certainly Black-headed Duck eggs are highly successful in ibis and gull colonies, yet such colonies are very few in number. The Black-headed Ducks apparently parasitize Rosybills and probably other ducks regularly, but these species are not universally abundant and do not seem to be nearly as successful as are coots.

## Parasitism of *Heteronetta* in Comparison with Other Parasitic Birds

Although obligate parasitism is found in only one anatid, it is distinctive among the five families with parasitic members because it is the only precocial

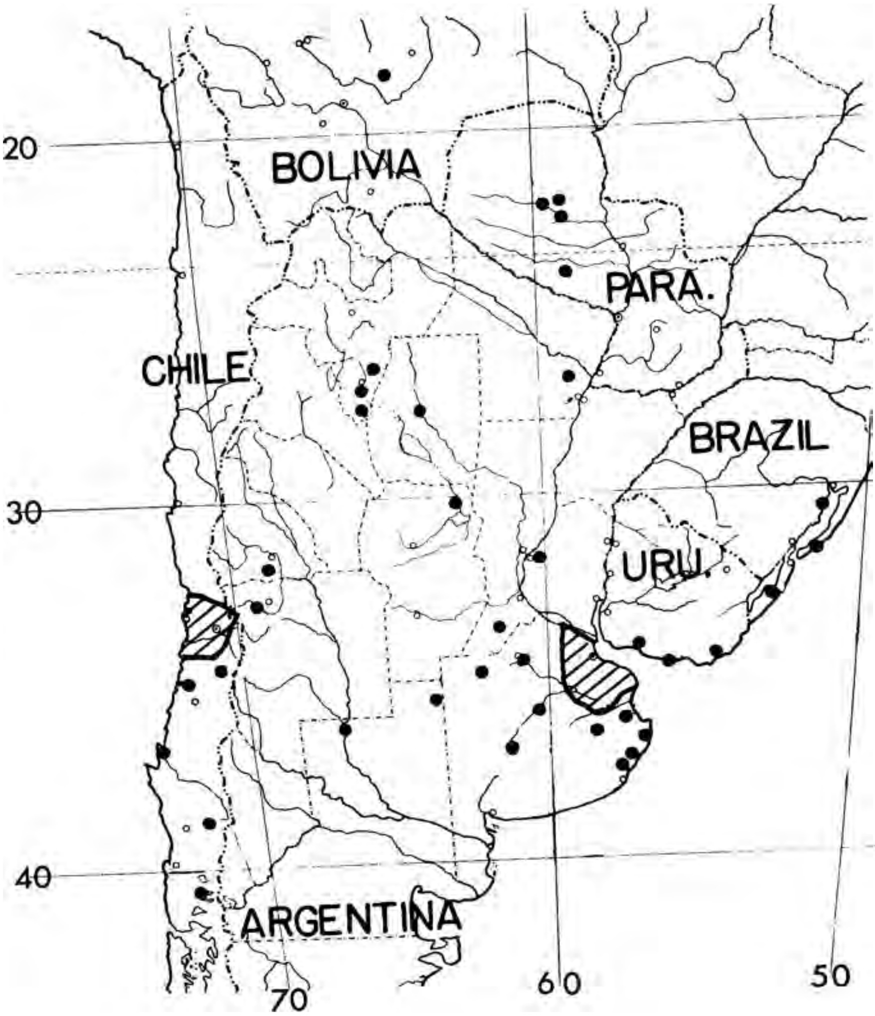

Figure 16. Distribution of the Black-headed Duck. Dots represent specimen records or sight records by professional ornithologists. Diagonal lines represent areas with numerous records.

species and appears to be the least damaging to its host. In this sense it is the most perfected of the brood parasites. The parasitic female does no damage to the eggs or nest of the host and, based on limited data, barely influences clutch size or nest success. Its young do not take food intended for the hosts' young. In fact, its behavior borders on commensalism rather than parasitism. Although highly specialized anatomical developments are non-existent, they do not seem necessary since the system functions simply and effectively. It appears that this is the only anatid in which the female is larger than the male (Weller, 1967a), but we clearly cannot attribute this fact to parasitism. For the above reasons, it is difficult to relate the chronology of evolution of this behavior in this group to that of other parasitic birds, based on the characters Friedmann (1955) has used — i.e., percentage of the species of the family which are parasitic with anatomical and behavioral specializations. The Black-headed Duck is neither abundant nor widespread (Figure 16), partly because it is habitat- and host-limited and partly because the system of self-rearing may produce a high rate of juvenile mortality.

## *Summary*

A study was made of the breeding biology of the Black-headed Duck (*Heteronetta atricapilla*) with special reference to its parasitic laying. Observations on laying were made mostly at two marshes near General Lavalle in the Cape San Antonio region of the Province of Buenos Aires, Argentina.

The Black-headed Duck was found to be adapted to dense marsh vegetation where it fed mainly on seeds of marsh plants and occasionally on snails and duckweeds. It is rarely seen on land but flies easily and rapidly and dives as well as dabbles for food. It forms pairs during the breeding season but becomes social during the fall and is migratory. Sex ratio seems to be about 58 per cent males to 42 per cent females.

Courtship behavior is distinctive. Some components resemble displays of stifftails while others resemble those of dabblers. The main courtship display involves a Toad-call with a head-pumping movement which produces a grunt-and-whistle followed by a wing-up, tail-up display. Pair bonds are formed and tested in courtship groups in a manner similar to that of other species.

Parasitism appears to be the sole means of reproduction as no nests or brood care is known in the species. Hosts are birds which nest in dense marsh vegetation with the highest incidence being Red-fronted Coot (*Fulica rufifrons*), Rosybills (*Netta peposaca*), Red-gartered Coot (*Fulica armillata*), and White-faced Ibis (*Plegadis falcinellus*). There was a tendency for the parasitic female to lay during the hosts' laying period without disturbing the nest or eggs. Egg success was 18 per cent and 64 per cent of eggs observed on two study areas. Losses were due mostly to egg burial by coots. Eggs hatched in 24 to 25 days.

Ducklings were cared for by the host during the first 24 to 36 hours of life. Both wild and captive ducklings left the parent host at less than two days of age. They proved impossible to keep and rear under artificial conditions because of their tendency to leave the brooding site. They showed little of the following reaction common to other species of ducks. They were remarkably precocial in the development of feeding and maintenance behavior and were not alarmed by isolation or cold.

The plumage, anatomy, and behavior of Black-headed Ducks suggest that they are most closely related to the stifftails and probably should be maintained in that tribe. However, since they share several behavior traits of the dabblers, they may be ancient birds of dual affinities.

The success of parasitism in *Heteronetta* seems to be due to the selection of coots and a variety of marsh birds as hosts. Such birds are more numerous and successful in nesting than most ducks. The Black-headed Duck has achieved success not by specializations in laying behavior or egg color but by the random placement of eggs in nests containing eggs of any color. Survival of the young in the nests of these divers is possible because the young rear themselves after only a brief period of parental care. Because it is the least damaging to the host, it may be considered the most perfect of avian parasites; indeed, it is nearly commensal.

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