The Condor 86:242–250
© The Cooper Ornithological Society 1984

THE BREEDING BIOLOGY OF CAPTIVE BLACK-HEADED DUCKS AND THE BEHAVIOR OF THEIR YOUNG

EILEEN C. REES
AND
NIGELLA HILLGARTH

ABSTRACT.—The behavior patterns of captive Black-headed Ducks (*Heteronetta atricapilla*) at the Wildfowl Trust, Slimbridge, Gloucester, were studied for three consecutive breeding seasons to investigate the breeding biology of this parasitic species. The birds fed mostly in the early morning and swam most actively in the evening, while they mainly rested on land during midday. In the evening, both males and females patrolled or skulked near nest sites of other birds, apparently searching for a suitable host to parasitize. The existence of pair-bonds during the breeding season was fully established; copulation and egg-laying were observed.

Two Black-headed Duck eggs were returned to the nest of a Rosy-billed Pochard (*Netta peposaca*) to determine the post-hatching behavior of the young and the role of the host bird. One Black-headed duckling hatched before any of the host's own clutch and left the nest on its own one day after hatching. The second duckling, which hatched with the young pochards, accompanied the family to water and returned to the female for warmth and protection (at increasingly infrequent intervals) for two days.

These findings emphasize the uniqueness of the species and reinforce the case for placing *Heteronetta* in a tribe of its own.

The Black-headed Duck (*Heteronetta atricapilla*) frequents freshwater marshes in the temperate regions of South America, ranging from central Argentina to Bolivia and across the continent from central Chile to southern Brazil. Breeding has been recorded in Argentina, Chile, and central Paraguay (Delacour 1959, Weller 1967, Todd 1979).

Since Phillips (1925) first remarked about the lack of information on the Black-headed Duck, studies of its morphology and behavior have revealed its singularity; even its taxonomic position is still disputed. Similarities in anatomy and certain behavior patterns link *Heteronetta* to the Oxyurini, with whom they are most commonly classified. However, Black-headed Ducks also exhibit a number of behavioral characteristics of the Anatini, and may be descendants of a primitive group from which both tribes evolved (Weller 1968a).

The parasitic breeding behavior of the Black-headed Duck is considered unique among waterfowl. Several species of Anatidae, most notably Redheads (*Aythya americana*) and Ruddy Ducks (*Oxyura jamaicensis*) occasionally lay eggs in other birds' nests (Friedmann 1932), but they usually hatch and rear their own young. The Black-headed Duck, however, neither builds a nest nor incubates its eggs, but leaves these duties entirely to host birds. The female tends to lay during the host's laying period, thereby making full incubation more likely, and usually adds her egg to the host's nest with little or no damage to the main clutch. Black-headed Duck eggs have been found in nests of a wide range of birds, including birds of prey (e.g., Chimango Caracara, *Milvago chimango*) and gulls (e.g., Common Black-headed Gull, *Larus ridibundus*). However, the preferred hosts appear to be coots (*Fulica rufifrons* and *F. armillata*), probably because their nests are common in marshy areas (Weller 1968a).

Although the Black-headed Duck in its natural environment has been studied extensively by Weller (1967, 1968a, b), the species' unobtrusive nature and preferred habitat have made it difficult to observe its breeding behavior and a number of points still require clarification. We describe here the diurnal activities of captive Black-headed Ducks during the breeding season, including their pre-laying and pre-copulatory behavior, as well as the behavior of ducklings that hatched in the nest of a Rosy-billed Pochard (*Netta peposaca*).

MATERIALS AND METHODS

In 1974 the Wildfowl Trust collected eggs of Black-headed Ducks in Argentina in order to establish a captive breeding population of this species at Slimbridge, Gloucestershire, England. The five males and two females from

these eggs were pinioned and placed in a pen (36 × 19 m) in which the terrain was designed to resemble their natural habitat (M. R. Lubbock, pers. comm.). The pen contained a pond (380 m^2 surface area) and four small islands. Rushes and sedges were planted at the water's edge so that the area was like a miniature marsh. Other South American birds were put in the enclosure to provide suitable hosts for the Black-headed Ducks. These included Rosy-billed Pochards, Lake Ducks (*Oxyura vittata*), Southern Versicolor Teal (*Anas versicolor fretensis*), Red Shovelers (*A. platalea*), and Black-necked Swans (*Cygnus melanocoryphus*). Wild Mallards (*A. platyrhynchos*), Gadwalls (*A. strepera*), and Moorhens (*Gallinula chloropus*) also bred in the pen. The first nine captive-bred Black-headed Ducks were reared at Slimbridge in 1977.

During the 1977 breeding season, we observed as many as 11 adult Black-headed Ducks (five males and up to seven females), at intervals at least 1-h apart, throughout the day for 18 days. Observations were usually of only 5-min duration, unless the birds were particularly active. In the latter case, the percentage of time spent on each activity for the whole watch was determined, then converted into the corresponding time for a 5-min period, to avoid biasing the results.

Throughout May 1978, six male and six female Black-headed Ducks were watched closely between 05:15 and 07:20 since Weller (1968a) thought it likely that egg-laying occurred in the early morning. One male was removed from the pen during the month because we thought that his aggressive behavior, and particularly his frequent pursuits of the females, would interfere with their laying activities.

In May and June 1979, intensive observations of five males and five females were made near dusk (usually 20:00–22:00) since the females had neither exhibited definite pre-laying behavior nor laid eggs during the early morning sessions the previous year.

During each observation period we determined the total number of minutes that males and females engaged in each of five activities: active swimming, passive swimming, resting, feeding, and patrolling or skulking close to the nest site. "Active swimming" includes rapid movements in the water, pursuing other ducks (or being pursued by them), making threats, performing the male "toad call" display (as described by Johnsgard 1965, Weller 1968a), and copulating. "Passive swimming" means loafing on water, as opposed to "resting" which indicates sitting, preening, and sleeping on land. "Feeding" includes foraging at the water's surface, dabbling, and up-ending. "Patrolling" is an activity in which a duck swims repeatedly to-and-fro along the bank beside a suitable nest site and pauses frequently, neck stretched, to look in the direction of the nest. "Skulking" is an activity in which a duck sits quietly or moves stealthily among the vegetation close to a nest, usually facing it. We combined the categories of patrolling and skulking because both kinds of behavior denote an interest in nest sites.

In 1978, we were also able to study the post-hatching behavior of Black-headed ducklings, with particular reference to the role of the host bird, because Black-headed Duck eggs were found in a Rosy-billed Pochard's nest that could easily, but unobtrusively, be observed at close range. During the first week of incubation for the seven pochard eggs, three Black-headed Duck eggs were laid in this nest. The latter were removed and incubated by Bantam hens (*Gallus gallus* var. *domesticus*) and, later, in a Schumacher incubator. Two eggs were subsequently returned to the pochard's nest (the third was hand-raised at the Propagation Centre). The first experimental egg hatched ahead of the main clutch, but the second hatched with the pochard ducklings. The activities of the ducklings and parent bird were continuously monitored from 04:30 to 22:00 for 1.2 days in the case of the first duckling, and 2.8 days in the case of the second.

The reaction of the female to the ducklings was determined by measuring the frequency with which she made positive and negative responses toward them. Contact movements, in which the female gently pushed a duckling with her bill or adjusted her position to allow it to pass under her wing, were categorized as "positive." Movements of the female that produced "distressed" cheeping from a duckling (e.g., rotating on the nest and vigorous preening), particularly when the duckling was squashed or thrust to one side, were considered "negative."

Chi-squared tests and the Wilcoxon test were used to evaluate the data.

RESULTS AND DISCUSSION

GENERAL ACTIVITIES OF THE ADULTS

The proportion of time that the Black-headed Ducks devoted to each activity during the 5-min spot checks illustrates changes in their behavior patterns throughout the day (Table 1). The birds were most active during the early morning and evening, and spent the middle of the day mainly resting. Similar diurnal activity patterns have been noted in a wide range of Anatinae, both during and outside the breeding season, including White-headed Ducks

TABLE 1. Time budgets of adult Black-headed Ducks throughout the day during the 1977 breeding season.

Period of observation	Duration of observations (min)	Time spent (% of total observation time)				
		Active swimming	Passive swimming	Resting	Feeding	Patrolling and skulking
Before 09:00	250	36	32	14	15	3
09:00–13:00	165	14	31	47	8	0
13:00–17:00	70	6	36	48	10	0
After 17:00	275	22	40	26	12	0
Overall	760	19	35	34	11	1

(*Oxyura leucocephala*; Matthews and Evans 1974), teal (*Anas crecca crecca* and *A. c. carolinensis*; Tamisier 1974, 1976), South African Black Ducks (*A. sparsa sparsa*; Siegfried 1968), Northern Shovelers (*A. clypeata*; McKinney 1967), and Mandarin Ducks (*Aix galericulata*; Bruggers and Jackson 1977).

Chi-square tests on the activities of each male Black-headed Duck during the intensive early morning observations showed that individual behavior patterns differed significantly ($\chi^2 = 132$, $P < 0.001$, 20 df). One male, for example, was significantly more aggressive than the others, pursuing females 24% of the time he was in view ($\chi^2 = 25.5$, $P < 0.001$, 1 df). After he was removed from the pen, the proportion of active swimming of all males combined declined markedly (from 41% of the observation period before his removal to 15% thereafter). The chasing of females by male Black-headed Ducks has also been noted in the wild by Weller (1968a), who suggested that the most persistent and aggressive males were lone birds. Our observations reinforce this view since the two most aggressive males were unpaired, although paired males also pursued females other than their mates. Vocalizations have not been reported previously in female Black-headed Ducks (Johnsgard 1967, Weller 1968a), but we noted that the female emitted low, hooting distress calls when chased by aggressive males. They also frequently tried to escape by diving or attempting to fly.

Throughout the early morning observations, two males appeared to have well-established pair-bonds with females, since they associated closely with a female during each observation period. Both birds fed much of the time but differed in other behavior patterns ($\chi^2 = 33.8$, $P < 0.001$, 1 df). The only instance of possible pre-laying activity seen during the early morning sessions was performed by one of these pairs: the female moved onto a vacated Rosy-billed Pochard's nest for 1 min while the male stood nearby, but no egg was laid on that occasion. After the removal of the aggressive male (described earlier), the degree of pair-bonding of the other males in the pen apparently increased, since each remained consistently with one female. After mid-May, only one male remained unattached, which runs counter to Johnsgard's (1967:103) observation that "the apparent absence of a recognizable inciting display in this species and in the more typical stiff-tails suggests that distinct pair bonds may be weak or lacking in this tribe." He mentioned, however, that Weller told him of noting *seasonal* pair-bonds between Black-headed Ducks. We found that males not only remained close to their mates, but also protected them by moving between them and approaching males and then occasionally performing the "toad call" display. They defended their females with threats that ranged in intensity from head-low-with neck-stretched displays to open-billed threats, pecks at the intruder, and finally chases. Females also used these aggressive displays, but mainly in self-defense. Mutual preening of the neck feathers by paired Black-headed Ducks was noted twice. We concur with Johnsgard (1967) that female Black-headed Ducks lack an inciting display. Only one observation could possibly be construed as incitement: a female followed her mate (who was giving intermittent "toad calls") and every 2–3 min gave a head pump, accompanied by a slight rotation of the head and neck. However, this does not seem to be a common feature of courtship behavior among Black-headed Ducks.

COPULATION

We observed one copulation between the female and one of the males in an established "trio" of Black-headed Ducks in June 1977, and two others between paired birds, during the early morning in May 1978. No obvious display was performed by either sex beforehand. In the first instance, the pair was not disturbed by other birds in the pen and after copulating they bathed and then moved onto land to preen. During the two subsequent copulations, however, another male attempted to mount the mating pair. On one of these occasions, the female finally dived and then threatened her mate, who was performing the "toad call" display as he approached.

A fourth copulation occurred during the evening in June 1979, again with no apparent preliminary display. The male mounted his mate, who was sitting in the water beside him, for about 20 s, pulling hard at her neck feathers. She, meanwhile, floundered, half submerged, with her wings outspread, and con-

TABLE 2. Behavior of male and female Black-headed Ducks during early morning and evening.

Period of observation	Sex	Total observation time (min)	Time spent (% of total observation time)						
			Active swimming					Patrolling or skulking	
			Total	In pursuit of female	Passive swimming	Resting	Feeding	Total	Time on bank
Early morning (05:15–07:20)	♂	348	15	5	49	8	27	1	1
	♀	263	5	—	45	12	36	2	1
	Both	611	11	—	47	10	31	1	1
Evening (17:45–22:02)	♂	767	20	1	35	9	8	28	14
	♀	793	9	—	39	12	11	29	11
	Both	1,560	14	—	37	11	9	29	12

tinuously emitted low hooting calls. These resembled the distress calls of pursued females, which suggests that this may have been a "forced copulation." A male from a nearby pair approached and pecked at the first male's neck, but did not dislodge him. When he dismounted, the female washed and preened while he performed "toad call" displays at 5-s intervals. The pair then moved to the bank to sit and preen.

PRE-LAYING AND EGG LAYING BEHAVIOR

Patrolling and skulking as prelaying activities. During our intensive evening observations, we noted that adult Black-headed Ducks spent much more time patrolling and skulking than they had during the early morning sessions the previous year (see Table 2). While doing so, they frequently inspected nests, their necks stretched, presumably searching for a suitable one to parasitize. Several nest sites might be inspected in this way in one evening and the ducks frequently returned to sites that they had already investigated. They also drove other intruding Black-headed Ducks from the nest area. We recorded 16 threats uttered in defense of a nest site, nine by males and seven by females.

Black-headed Ducks usually patrolled or skulked in pairs and on two occasions when the female moved into a nest-box, the male remained nearby, occasionally looking in. No eggs were laid, however. The ducks spent nearly half the time recorded as patrolling and skulking sitting quietly among the vegetation at distances up to 3 m from the nest, usually facing it. We could not always see the sitting host, but those that were visible generally ignored the Black-headed Ducks. On only three occasions did a nesting Rosy-billed Pochard hiss at a lurking pair of Black-headed Ducks, but without effect. On another occasion, a male Black-headed Duck pecked at the base of the pochard's nest and then vocalized, but the sitting female did not respond. Todd (1979) reported an instance in which a pair of Black-headed Ducks *forced* an incubating Red Shoveler (*Anas platalea*) from her nest after which the female *Heteronetta* laid an egg in it. During our observations, however, the Black-headed Ducks did not threaten or attack potential hosts, but simply watched and waited until the nest was vacated before adding eggs to the clutch.

Observations of egg-laying. We observed nest parasitism on just one occasion (May 1979). A Rosy-billed Pochard's nest, situated in a clump of rushes along one bank of the pond, contained four eggs at 17:30. At 20:48, the female left the nest to preen and feed with her mate. Two minutes later, a pair of Black-headed Ducks swam along the bank close to the nest, the male displaying. After 3 min, the male climbed onto the bank and moved to the base of the nest while his mate remained at the water's edge. The female pochard returned immediately, drove the male off, and then moved back onto the nest. The Black-headed pair, meanwhile, retreated to a nearby island.

Five minutes later, the female pochard again left the nest to feed. A female Black-headed Duck swam by the pair of pochards, which ignored her, and positioned herself about 10 m from the nest. At 21:05, a displaying male pochard approached the nesting pair and was chased away by them, all three birds moving out of sight of the nest. The female Black-headed Duck sat quietly for four more minutes and then swam slowly and directly toward the nest. She paused briefly at its base, then climbed on, just as the pair of pochards returned rapidly (at 21:11) to their perch on the bank and began to preen. At 21:19, a male Black-headed Duck swam toward the nest, stopping 1 m short of the bank. The female Black-headed Duck joined him immediately, having sat on the nest for 8 min. The female pochard approached the pair and the male Black-headed Duck started displaying, after which both Black-headed Ducks moved away, followed by the two pochards. The nest, which was checked imme-

TABLE 3. Reactions of a female Rosy-billed Pochard to her own and two Black-headed ducklings while on the nest.

Part of observation period	Duckling*	Total observation time (min)	Number of positive responses to the duckling		Number of negative responses to the duckling	
			Pushes with bill	Moves to cover	Movements causing cheeping	Duckling squashed or thrust aside
First half	1st B-HD	600	13	3	14	2
	2nd B-HD	510	3	0	13	0
	R-BP	600	20	1		0
Second half	1st B-HD	600	7	1	24	6
	2nd B-HD	510	5	0	2	2
	R-BP	600	4	1		9

* B-HD = Black-headed Duck; R-BP = Rosy-billed Pochards.

diately, contained the four pochard eggs plus one Black-headed Duck egg (A. J. Powell, pers. comm.).

Comparison of early morning and evening behavior patterns. The time budgets of the adult Black-headed Ducks (after the removal of the aggressive male in 1978) differed significantly between the sexes (Table 2). Males did significantly more active swimming than females during both morning and evening ($\chi^2 = 14.5$, 37.3, respectively, $P < 0.001$, 1 df), whereas females spent more time feeding than males during the early morning ($\chi^2 = 5.4$, $P < 0.02$, 1 df). An increase in the foraging activity of females during the egg-laying period has also been noted in other species of wildfowl (e.g., Bengston 1972, Bruggers and Jackson 1977) and would be expected in view of their need for sufficient food reserves for egg formation. However, the feeding activity of the two sexes during the evening did not differ significantly ($\chi^2 = 2.9$, $P > 0.05$, 1 df), perhaps because they search for nests at this time of day and lack an energy-demanding incubation phase in their reproductive cycle.

Both sexes spent significantly more time patrolling and skulking during the evening than in the morning ($\chi^2 = 112$ for males and 88.9 for females, $P < 0.001$, 1 df). They also did significantly more active swimming at this time ($\chi^2 = 4.1$ for males and 4.0 for females, $P < 0.05$, 1 df). Feeding was most common in the morning ($\chi^2 = 71.9$ for males and 90.1 for females, $P < 0.001$, 1 df). Male Black-headed Ducks did less passive swimming during the evening ($\chi^2 = 19.1$, $P < 0.001$, 1 df), but females showed no such diurnal difference ($\chi^2 = 3.1$, $P > 0.05$, 1 df).

BEHAVIOR OF BLACK-HEADED DUCKLINGS

The first duckling. The first Black-headed Duck egg that was returned to the pochard's nest hatched early on June 29 and the duckling was already dry when one of us (ECR) first saw it at 05:00. Throughout that day the pochard continued to show normal incubation behavior, turning on the nest at regular intervals (usually every 10–25 min), repositioning the eggs with her bill, shuffling them under her, and occasionally preening (especially the belly and breast). She brooded the duckling for 81.5% of the post-hatching observation period (20 h). The duckling was highly active when exposed and frequently scrambled over and around the female, vigorously attempting to burrow into her neck or breast feathers. When uncovered, it spent significantly more time climbing and burrowing (64%), than just sitting or loitering in the nest basin ($P = 0.01$, Wilcoxon test).

The female responded positively toward the duckling significantly less often during the second half of the observation period than during the first half ($\chi^2 = 6.49$, $P < 0.02$, 1 df; Table 3). Eleven pushes with her bill and four movements to cover the duckling were associated with the latter's scrambling behavior, but its climbing and burrowing activity were usually ignored.

The pochard left the nest twice during our observations of the first Black-headed duckling (at 15:17 on June 29 and at 08:30 on June 30). On both occasions, she covered her eggs with down and twigs before departing, but ignored the duckling and did not encourage it to follow her to water. On the first occasion, the duckling followed her for a short distance, cheeping, but soon returned to the nest where it remained quietly until she returned (after a 25-min absence). On the second occasion, the duckling did not follow the female, but sat by the nest, cheeping occasionally. After 8 min it moved into the vegetation near the nest and disappeared. It was found at the edge of a different pond (15 m away) 15 min later. When the pochard later returned to her nest, she uncovered her eggs and resumed incubation. (The Black-headed duckling was taken to the Propagation Centre for artificial rearing, since it seemed likely to perish if left in the pen.)

The second duckling. The second Black-headed Duck egg hatched with the pochard's own clutch. During hatching, the female did not discriminate between species, but pecked and pulled at the shells surrounding both Black-headed and Rosy-billed ducklings as they emerged. She ate the eggshells of all but the final pochard duckling.

The behavior of the second Black-headed duckling was totally unlike that of the first. During 17 h of observations at the nest, it was almost always under the female, making just six brief appearances of less than 1 min and displaying none of the vigorous clamberings of the first duckling. The regular movements of the female revealed it in the bottom of the nest, with the four pochard ducklings, occasionally preening and pecking at the female's plumage. The young pochards were more active than the Black-headed duckling and, when not being brooded, spent most of their time moving around the nest's rim, pecking at it and at nearby vegetation (Table 4). Only twice did we see them scramble over the female in a manner similar to that of the first Black-headed duckling. The first and second Black-headed ducklings and the downy pochards differed significantly in the amount of time they spent (a) climbing and burrowing ($\chi^2 = 254$, $P < 0.001$, 2 df), (b) sitting and loitering ($\chi^2 = 68.9$, $P < 0.001$, 2 df), and (c) exposed in the nest ($\chi^2 = 273$, $P < 0.001$, 2 df).

We could not quantify changes in the responsiveness of the female toward the second Black-headed duckling because we could not determine the species of duckling emitting distress calls in response to the female's movements. However, her responsiveness toward the whole brood did not decline significantly, unlike her behavior toward the first Black-headed duckling ($\chi^2 = 2.69$, $P > 0.05$, 1 df; Table 3).

During the early afternoon of 5 June, the female showed signs that she would soon leave the nest, stepping away from it on five occasions. Two Rosy-billed ducklings followed on her third exit from the nest and all the ducklings followed on the fourth. After each brief (about 3-min) departure, the female returned and resumed brooding. Each time she left the nest, she called softly, but persistently, apparently encouraging the ducklings to follow her down the bank. On the last two occasions, she returned to the nest, still calling, until the lagging Black-headed duckling also started to follow her.

The final departure occurred at 18:00. The female stepped off the nest and started to move toward the pond, giving low-pitched calls and stopping periodically to look around. The Rosy-billed ducklings preened and then followed her in file, leaving the Black-headed duckling cheeping in the nest. After 1 min, it too followed, calling continuously. At the edge of the pond, the group was joined by a male Rosy-billed Pochard, which brought up the rear of the procession. Both adults remained alert until they reached the rushes at the water's edge; then, partially hidden by the vegetation, they preened and fed. The female moved onto the water briefly at 20:17, but did not take the ducklings with her. On returning to the rushes, she made a "bivouac nest" by pulling the reeds around her sides, where all the ducklings were brooded overnight. The male pochard remained nearby.

The ducklings were first taken to water at 07:00 the next morning and the family spent longer periods on the pond thereafter. Much of the first day was spent in brooding (59%), but 23% was passed on the water and 18% in grazing, preening, and resting ashore. The Black-headed duckling associated with its host family throughout the day (Fig. 1), although it had difficulty keeping up when moving overland. It also tended to lag behind the others when feeding on the pond (where its sifting style of foraging was notably different from the pecking action of the pochards). It frequently remained among the rushes lining the water's edge as the family moved on, but then emitted distress calls and scurried to rejoin the others after a few minutes apart (Table 5). During 21 h of observation, from the ducklings' first excursion onto water until their removal from the pen, the behavior of the Black-headed duckling differed significantly from that of the Rosy-billed ducklings, which regularly forged ahead of the female ($\chi^2 = 43.0$, $P < 0.001$, 1 df). Only the youngest pochard duckling lagged

TABLE 4. Activities of two Black-headed ducklings and pochard ducklings in the nest of a Rosy-billed Pochard.[a]

Duckling[b]	Duckling's activity (% of observation period)[c]			Number of brief (<1 min) appearances[c]	Number of comfort movements during observation period[c]	
	Time exposed	Climbing and burrowing	Sitting and loitering		Preening and scratching	Pecking, eating, and drinking
1st B-HD	19	12	7	28	22	22
2nd B-HD	0	0	0	6	2	4
R-BP	6	1	5	11	14	22

[a] The Rosy-billed Pochard figures are calibrated to reflect the activities of just one duckling by dividing the number of minutes of each activity by the number of pochard ducklings in the nest.
[b] B-HD = Black-headed Duck; R-BP = Rosy-billed Pochard.
[c] Total observation period: 1st B-HD = 1,200 min; 2nd B-HD = 1,020 min; R-BP = 1,200 min.

FIGURE 1. Female Rosy-billed Pochard followed by a Black-headed duckling (closest to her) and two of her own offspring. Photograph by Philippa Scott.

behind, so it was not surprising that it died overnight.

The female pochard appeared to accept the Black-headed duckling as one of her own brood. She frequently waited for it, calling to encourage it to follow, and on one occasion returned when it was tardy in joining her on the pond. She made contact movements with her bill towards both Black-headed and Rosy-billed ducklings, usually after they became separated from the group. We saw no significant difference in her reactions to the Black-headed duckling and her own offspring ($\chi^2 = 0.39$, $P > 0.05$, 1 df; Table 5).

In contrast, the Black-headed duckling became increasingly independent of its host family during the second morning after leaving the nest (Fig. 2), although it still returned to the family for protection. It remained close to the female's flanks when the family was attacked by Black-necked Swans at 09:06 and quickly found the group when pursued by a male Ruddy Duck at 12:00. (We noted, as did Weller (1968a), that, unlike other young stifftails, the Black-headed duckling did not dive, either to escape from attack or to feed.) After 09:00, the duckling remained behind for longer and longer periods and, between 12:00 and 13:00, it disappeared for 35 min. We considered it unwise to leave the duckling unattended in the large and heavily populated pen and therefore transferred the whole family to an aviary, which also contained a pond and bushes for shelter. Even there, however, the Black-headed duckling proved independent. It was last seen with the family at 13:30 on July 8 (four days after hatching) and was found in the adjacent aviary at 07:30 the following day (M. R. Lubbock, pers. comm.). Like its predecessor, it was taken to the Propagation Centre for hand-rearing.

TABLE 5. The behavior of the ducklings and reactions of the female Rosy-billed Pochard toward them after leaving the nest.

Behavior	Number of such behaviors during 21 h of observation	
	Black-headed ducklings	Rosy-billed ducklings
Duckling(s) moved ahead of female	2	27
Duckling(s) lagged behind female	63	8 (11)[a]
Black-headed duckling scurried to rejoin family	26	—
Female waited, called, or returned for duckling(s)	8	7
Female poked at duckling(s) with her bill	5	3

[a] ( ) = number of times the youngest Rosy-billed duckling lagged behind the family in 13 h of observation.

POST-HATCHING BEHAVIOR OF BLACK-HEADED DUCKLINGS

Our observations of the two Black-headed ducklings, one hatching before and the other with the host's clutch, clearly demonstrated the early independence of this species. The marked activity of the first duckling may perhaps have been intended to encourage the female to abandon her clutch and take it to water. Since the female became progressively less interested in this duckling and continued to incubate her own eggs, its voluntary departure after one day on the nest proved important for its survival, because the pochard's eggs were not due to hatch for another week. The first duckling displayed no innate urge to follow the female when she visited the pond, possibly because she was not in the late calling stage, so the duckling received only visual stimulation. Our observations suggest that auditory as well as visual stimuli (experienced by the second, but not the first Black-headed duckling) may be needed to elicit a following response in these independent birds. This is consistent with Weller's (1968a) observation that captive Black-headed ducklings are not readily imprinted.

The quiescent behavior of the second Black-headed duckling while in the nest was more typical of the species. Hand-raised *Heteronetta* ducklings at the Wildfowl Trust are less frantic than many young stifftails, tending instead to skulk around their enclosures (R. H. J. Graham, pers. comm.). The continued association of the second duckling with its foster family on leaving the nest indicates that these downies are not totally independent on hatching. Indeed, the variation in post-hatching behavior of the two Black-headed ducklings may be regarded as opportunistic, with the second duckling taking advantage of the favorable conditions. It returned to the female pochard for warmth and protection (albeit after increasingly long absences) for at least two days.

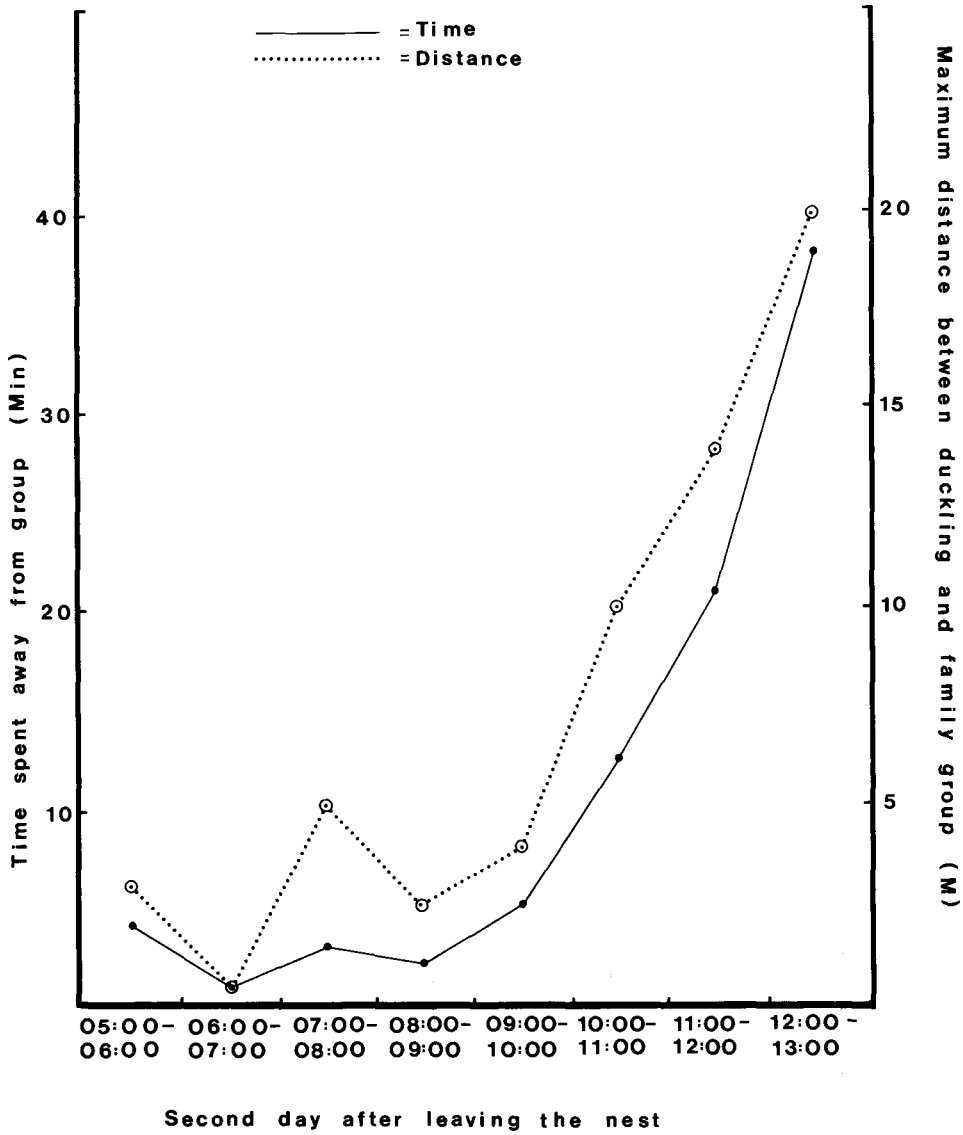

FIGURE 2. Time and distance separating a Black-headed duckling and its host family on the second day away from the nest.

TAXONOMIC CONSIDERATIONS

Our study suggests that the Black-headed Duck is a unique species, although it has several behavioral features both of the Oxyurini, with which it is most commonly classified (Johnsgard 1965, Weller 1968a), and the Anatini. The strongest behavioral evidence linking the Black-headed Duck with the Oxyurini is perhaps the female's apparent lack of an overt incitement and pre-copulatory display, which is typical of other stifftails. We saw a female use "head-pumping" in a manner reminiscent of the pre-copulatory display of dabbling ducks only once, so further observations are necessary before this can be considered an Anatini-like activity. Furthermore, Anatini pairs generally perform *mutual* head-pumping movements before copulating, but male Black-headed Ducks did not. The male post-copulatory "bridling" display, characteristic of the Anatini, is also absent in *Heteronetta.*

Weller's (1968a) report that female Black-headed Ducks, like female Ruddy Ducks, are silent needs modification since we frequently heard the former emit low hooting distress calls, usually while being pursued by males. Such vocalizations are also given by other female stifftails under similar circumstances (Johnsgard 1965), and their monotonous nature bears no resemblance to the distinctive "decrescendo call" display of female Anatini.

The Black-headed Duck has been described as the least specialized member of the Oxyurini, both anatomically and behaviorally

(Johnsgard 1961, 1965; Woolfenden 1961). Our results indicate, however, that, if it does represent an early evolutionary link between the Anatini and Oxyurini, then it has not remained primitive in form, but has undergone considerable independent evolutionary change. For instance, its unique patrolling and skulking (pre-laying) activity is apparently well organized, involving coordination of behavior and a substantial investment of time (and probably energy) by both members of the pair. Furthermore, the parasitic nature of its reproductive behavior is perfected to a point where it could be considered commensalism. The remarkable precocity of its young may be viewed as an extension of the semi-parasitic habits of other species. The flexibility of the duckling's post-hatching behavior (depending on whether it hatches before or with the host's own clutch) is clearly an adaptation to enhance survival. On the other hand, the diving ability found in all other stifftail downies (and in adult Black-headed Ducks) is completely lacking in the Black-headed duckling, and is reason for placing *Heteronetta* with the dabbling ducks. The absence of this behavior, however, may also be interpreted as a particular adaptation to the marshy habitat of the species, where surface feeding in the undergrowth and freezing there if a predator approaches would be good defense mechanisms for the ducklings.

These specialized characteristics of the Black-headed Duck support the position that *Heteronetta* belongs in a tribe of its own. Nevertheless, current opinion favors grouping rather than separating species (since Delacour and Mayr [1945]) and we therefore conclude that the weight of the evidence still favors including *Heteronetta* with the Oxyurini.

ACKNOWLEDGMENTS

This study was made possible by the avicultural skill of M. R. Lubbock, who established the breeding population of Black-headed Ducks at the Wildfowl Trust, Slimbridge. A. J. Powell and C. R. Hodgson gave us invaluable assistance and encouragement during our project. M. Owen advised us on the statistical analysis. We also thank M. Ounsted and A. Richardson for their support; G. V. T. Matthews, M. E. Evans, C. W. Farr, and H. Owen for occasional observation of the ducklings; and R. H. J. Graham and M. Carbonell for useful discussions and comments on the text. G. V. T. Matthews also made constructive criticisms on drafts of the text.

LITERATURE CITED

BENGSTON, S. A. 1972. Breeding ecology of the Harlequin Duck, *Histrionicus histrionicus* (L.) in Iceland. Ornis Scand. 3:1–19.

BRUGGERS, R. L., AND W. B. JACKSON. 1977. Time budgets of Mandarin Ducks under semi-natural conditions. Wildfowl 28:87–93.

DELACOUR, J. 1959. The waterfowl of the world. Vol. 3. Country Life, London.

DELACOUR, J., AND E. MAYR. 1945. The family Anatidae. Wilson Bull. 47:104–110.

FRIEDMANN, H. 1932. The parasitic habit in ducks, a theoretical consideration. Proc. U.S. Natl. Mus. 80.

JOHNSGARD, P. A. 1961. The taxonomy of the Anatidae—a behavioral analysis. Ibis 103a:71–85.

JOHNSGARD, P. A. 1965. Handbook of waterfowl behavior. Cornell Univ. Press, Ithaca.

JOHNSGARD, P. A. 1967. Observations on the behavior and relationships of the White-backed Duck and the stifftail ducks. Wildfowl Trust Annu. Rep. 18:98–107.

MATTHEWS, G. V. T., AND M. E. EVANS. 1974. On the behavior of the White-headed Duck with especial reference to breeding. Wildfowl 25:149–159.

MCKINNEY, F. 1967. Breeding behavior of captive Shovelers. Wildfowl Trust Annu. Rep. 18:108–121.

PHILLIPS, J. C. 1925. A natural history of the ducks. Houghton Mifflin Co., Boston.

SIEGFRIED, W. R. 1968. The Black Duck in the southwestern Cape. Ostrich 39:61–75.

TAMISIER, A. 1974. Etho-ecological studies of teal wintering in the Camargue (Rhone Delta, France). Wildfowl 25:107–117.

TAMISIER, A. 1976. Diurnal activities of Green-winged Teal and Pintail wintering in Louisiana. Wildfowl 27: 19–32.

TODD, F. S. 1979. Waterfowl. Ducks, geese and swans of the world. Seaworld Press, San Diego, CA.

WELLER, M. W. 1967. Notes on the plumage and weights of the Black-headed Duck, *Heteronetta atricapilla*. Condor 69:133–145.

WELLER, M. W. 1968a. The breeding biology of the parasitic Black-headed Duck. Living Bird 7:169–207.

WELLER, M. W. 1968b. Notes on some Argentine anatids. Wilson Bull. 80:189–212.

WOOLFENDEN, G. E. 1961. Postcranial osteology of the waterfowl. Bull. Fla. State Mus. Biol. Ser. 6:1–129.

The Wildfowl Trust, Slimbridge, Gloucester, Great Britain, GL2 7BT. Address of second author: Somerville College, Oxford, Great Britain, OX2 6HD. Received 27 January 1983. Final acceptance 7 January 1984.