Observations on the behaviour and relationships of the White-backed Duck and the Stiff-tailed Ducks

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Summary

1. A number of behavioural and anatomical sources of evidence indicate that the White-backed Duck (*Thalassornis*) should be placed in the tribe Dendrocygnini and be regarded as a whistling duck rather than an aberrant Stiff-tailed Duck.
2. Behavioural evidence supports earlier views that the Black-headed Duck (*Heteronetta*) is the most generalized of the true stiff-tails, and it is suggested that the numerous unusual aspects of sexual behaviour found in this tribe can be traced back to a reduction of pair-forming and pair-maintaining mechanisms which can already be detected in *Heteronetta*.
3. The distinctive aspects of morphology and behaviour found in the Musk Duck (*Biziura*) can be attributed to the predictable effects of intense sexual selection resulting from the breakdown of pair bonds and the establishment of a completely polygamous or promiscuous breeding system in *Biziura*.
4. There is still too little behavioural information concerning the Masked Duck to advocate its generic separation (*Nomonyx*), although it is suggested that this species is probably the most isolated of the typical stiff-tails and presumably represents a less specialised evolutionary line than do the other stiff-tails of the genus *Oxyura*.
5. Recent behavioural evidence tends to support earlier views that the remaining five species of *Oxyura* fall into two broad evolutionary groups; including *leucocephala* and *jamaicensis* on the one hand, and *maccoa, vittata* and *australis* on the other.

The Stiff-tailed Ducks have traditionally been a relatively undisputed and well-defined group of species in the family Anatidae, most members of which may be easily distinguished from all other waterfowl by their elongated and pointed rectrices with stiffened shafts and by their bills having recurved nails. When Eyton (1838) produced the first comprehensive classification of the Anatidae he separated the stiff-tails as a distinct subfamily (Erismaturinae) containing three genera, *Erismatura (Oxyura), Biziura,* and *Thalassornis,* the last genus being erected for the newly discovered White-backed Duck, which Eyton first formally described. He regarded this species as a "connecting link between the genera *Clangula* and *Biziura,* the structure of the tail being nearly like that of the former genus, while the bill is like that of the latter." Later systematists accepted this classification almost without modification, the only change being that the genus *Nomonyx* was erected by Ridgway (1880) to distinguish the Masked Duck from the other typical stiff-tails, primarily on the basis of its less recurved bill nail. This arrangement persisted until the classic revision of the family by Delacour and Mayr (1945), who reduced the stiff-tails to tribal rank (Oxyurini), merged *Nomonyx* with *Oxyura,* and transferred the Black-headed Duck *Heteronetta atricapilla* into the tribe from its former position in the dabbling duck group, largely on the basis of Wetmore's (1926) anatomical observations.

At the species level the classification of the stiff-tails has been hampered by the considerable plumage similarities of most species of *Oxyura,* as well as the meagre information available on their ranges and comparative anatomy. The problem has been especially vexing in southern South America, where the affinities of the forms *vittata* and *ferruginea* to one another have been in doubt, and their possible relationship to the North American Ruddy Duck *O. j. jamaicensis* has also been a problematic matter. Delacour and Mayr (1945) initially regarded these two South American forms and the African Maccoa Duck *O. maccoa* as races of a single southern hemisphere species that also included the Australian Blue-billed Duck *O. australis.* Boetticher (1952) later took the more extreme view that all of the southern hemisphere populations were subspecies of *O. jamaicensis.* However, Helmayr and Conover (1948) pointed out that both South American forms breed together in central Chile, thus two species must be recognised. Lehmann's description, in 1946, of a Colombian race of Ruddy Duck *O. jamaicensis andina* supported the view that the North American Ruddy Duck is thus geographically connected to the South American populations, and that *ferruginea* rather than *vittata* represents the southernmost representative of this geographic series.

In an earlier review of the behaviour patterns of the Anatidae (Johnsgard, 1960), I deplored the lack of behavioural

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information on the stiff-tails, and suggested that such knowledge might serve to evaluate the validity of including such aberrant genera as *Heteronetta* and *Thalassornis* in the tribe, as well as to help establish species limits and taxonomic groupings within the genus *Oxyura.* Since then it has been my good fortune to observe all of the nine species of Oxyurini (Delacour, 1959) in life, and to observe sexual displays among six of them. Although it is still premature to believe that an adequate knowlege of stiff-tail behaviour is at hand, it is nonetheless possible now to make some comparisons and conclusions that were impossible in 1960. Some such observations have since been published (Johnsgard, 1965a), but others were obtained too late to permit inclusion in my general survey of Anatidae behaviour. Thus, special attention will be paid here to the re-evaluation and probable relationships of the various genera included in the tribe, and to a review of the available behavioural information on the more typical stiff-tails *(Oxyura),* insofar as it may reflect and further clarify their evolutionary relationships.

Without question the White-backed Duck *Thalassornis leuconotus* is one of the most inadequately studied species of waterfowl. The downy young were first correctly described by Delacour and illustrated by Peter Scott in 1959, the tracheal anatomy remained undescribed until 1961, and it also was not until then that the reticulated tarsal surface condition of the species was first noted (Johnsgard, 1961a). The unusual tracheal structure, the associated whistling voices of both sexes, and the reticulated tarsal pattern suggested to me that perhaps the White-backed Duck had been incorrectly placed in the Oxyurini, and that it might actually be an aberrant whistling duck. However, during my two years of study at the Wildfowl Trust between 1959 and 1961, the species, although represented by nine individuals, failed to breed, and very few behavioural observations of taxonomic significance could be obtained (Johnsgard, 1965a). Then, during a return visit to the Trust in July of 1966, I learned that, following a relatively unsuccessful breeding attempt in 1965 (Johnstone, 1966), a second nesting had begun shortly before my arrival.

Accounts in the literature (e.g., Mackworth-Praed and Grant, 1952) indicate that under natural conditions the nests of White-backed Ducks are usually built in rushes or reeds over water and contain no down. However, they are sometimes located at the edges of ponds as well (D'Eath, 1965). The clutch size has been variously reported as ranging between two and 14 eggs, although the latter figure doubtless represents "dump-nests" produced by more than one female. The eggs are surprisingly large (Dr. Janet Kear informed me that the average weight of 21 eggs was 82.5 grams), and are of a distinctive pale rusty brown colouration. This colour and their very smooth surface distinguish them from typical stiff-tailed duck eggs. Each egg represents more than ten per cent of the adult bird's weight, which ranges from 680 to 790 grams (Phillips, 1926). This surprisingly large size is roughly equivalent to the situation in stiff-tails, since unincubated eggs of North American Ruddy Ducks average 74.7 grams (Janet Kear, pers. com.), and adults of this species range from 560 to to 680 grams (Phillips, 1926). It may be hypothesized that in both species this large egg size is a functional adaptation that permits the development of unusually precocial young that are able to forage independently by diving shortly after hatching. Thus, Clark (1964) reports that downy Maccoa Ducks may spend ten to fifteen seconds under water when foraging. Interestingly, Johnson (1965) reports that unusually large eggs are also typical of Torrent Ducks *(Merganetta armata)* which likewise have extremely precocial young that are able to dive and navigate swift currents with ease (Johnsgard, 1966a).

In 1965, the first nesting attempt by the White-backed Ducks at Slimbridge was in a clump of willow herb *Epilobium* and reeds within a foot or two of the water's edge, perhaps because no emergent vegetation is present in their pond. Likewise, in 1966, a nest was built in a similar clump of willow herb and reeds approximately 18 inches from the water, but in this case it was also immediately adjacent to the gravelled public pathway that is used by visitors to the Trust. Indeed, several large pebbles an inch or more in diameter were incorporated into the nest scrape, which was lined with grass but lacked any contour feathers or down. The nest was approximately one foot above the level of the water, but no ramp led to it. Rather, the birds climbed up on shore a foot or two to the side of the nest and entered it indirectly. At the time I arrived on 4th July, six eggs had already been laid at approximately daily

intervals. These eggs had been initially replaced with white wooden dummy eggs until it was found that the adults were ejecting these substitutes, and it was not until domestic fowl eggs that had been dyed brown were tried that they were accepted. This unusual egg discrimination suggests that possibly the unique brown colour of their own eggs enables White-backed Ducks to recognize and eject the white eggs of Maccoa Ducks, which are otherwise identical to their own. It is known that Maccoa Ducks probably perform parasitic egg-laying under wild conditions (Siegfried, 1964).

During my first visit to the nest I noticed that both birds were present in the clump of vegetation that contained the nest. The female, which I learned to recognize on the basis of her smaller head, slightly more mottled cheeks and a more uniformly blackish bill, had been sitting beside the nest but immediately entered the water as I approached. The male initially remained on the nest, hissing and raising his scapulars, then jumped into the water and made several vigorous but abortive attacks. This fierce nest defence by the male was most surprising, since male stiff-tails normally take no interest in the nest. I was further astonished by the male's remarkable threat posture, with ruffled scapulars, wings raised and spread somewhat in the manner of a threatening owl, the head low with neck outstretched and bill gaping (Fig. 1), and with intermittent loud hissing as he paddled his feet so rapidly as to make the water fairly boil. During this display the white back feathers, normally hidden below the wings, were readily visible and greatly ruffled. I have observed somewhat similar but less intense displays in various whistling ducks defending their nests or broods, although none of these has involved wing-spreading. At lower intensities of threat display the male assumed a posture similar to the "Head-back" threat of whistling ducks. These displays contrast with those of *Oxyura* females when protecting their broods, which latter involve stretching the neck forward, gaping, sometimes uttering repeated squeaking notes, and repeatedly raising and lowering the folded wings. Frequently an attack or threat by the White-backed

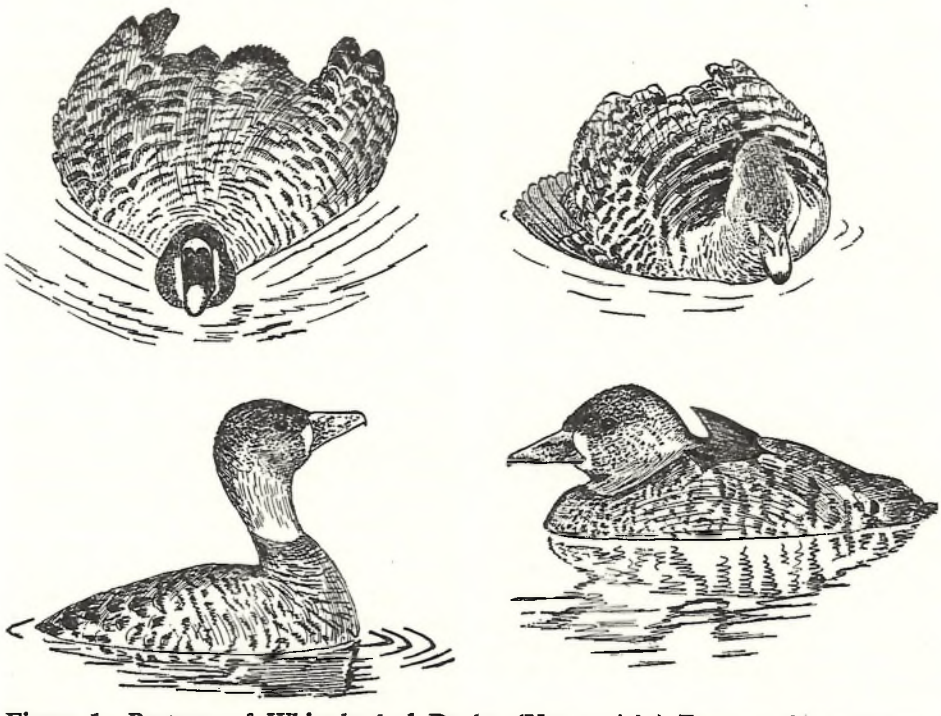

Figure 1. Postures of White-backed Ducks. (Upper right) Extreme threat posture assumed during nest defence. (Upper left) Less intense threat posture of male. (Lower left) Chin-lifting threat of female. (Lower right) Resting posture sometimes assumed by male. *Drawings by P. A. Johnsgard.* See also Photograph Section p. VIII upper.

Ducks was followed by a general body shake, which I have also observed in various whistling ducks but not in stiff-tails.

Following a threat or attack the male would quickly return to the vicinity of the nest and female, and occasionally both birds would then utter their whistling notes. I was unable to separate the sexes by their vocalizations, since both seemed to use the same calls. The loudest of these, an apparent alarm note, is a clear double whistle, rather similar to that of a Killdeer *Charadrius vociferus* but not repeated. Another common vocalization is a "conversational" or contact call consisting of from three to five notes uttered as a rising series of soft whistles.

After either member of the pair had been forced to leave the nest, the male was invariably the first to return to it. In instances when the male was foraging during a disturbance that forced the female from the nest he quickly returned to the nest site to defend it. Other than its mate, the male paid little heed to female ducks when they approached the nest, but actively chased other males as well as any individuals of other species that came too near, even including such large birds as male Comb Ducks *Sarkidiornis melanotos*. The female rarely chased any birds, but would vigorously threaten those other than her mate with strong chin-lifting movements associated with a trilled whistle (Fig. 1).

Although incubation had certainly not yet begun by my first visit on 4th July, the nest was never thereafter left unguarded so far as I could determine. On the morning of 5th July I noted that the male was on the nest when I arrived at 9.30 a.m., and later that morning he was replaced by the female. However, the male stayed near, and at 12.20 p.m. a second female approached the nest. The male did not threaten her, but instead the two birds swam about in a tight circle immediately in front of the nest. Suddenly the female went prone, and the male mounted her. The mating attempt was probably unsuccessful since no post-copulatory display by either bird occurred. That afternoon I observed another copulation which involved birds other than the nesting pair. In this case the preliminaries were not seen, but the treading was evidently successfully completed for, on its termination, the male whistled loudly once and both birds performed a "step-dance" parallel to one another in the exact manner of whistling ducks! The male also raised his wing on the side away from the female in the usual manner of whistling ducks, but the female raised hers little if at all. I regard this observation as providing the strongest possible behavioural evidence favouring whistling duck affinities of *Thalassornis*. Only one other copulation attempt was observed. In this case a male swam toward two females foraging near shore, approached one of them closely, and dipped its bill in the water two or three times. The female did not reciprocate, but almost immediately flattened out on the water. The male then mounted but this mating attempt was also apparently unsuccessful. In these three observations, and in another made by S. T. Johnstone (pers. com.), the copulations all occurred within a foot or two of the shore, whereas typical stiff-tails do so in deeper water. Furthermore, the precopulatory bill-dipping observed in the third instance was identically the same as that of various whistling ducks.

On 9th July, I observed a female examining clumps of willow herb on the shore opposite the nest under study and near the place where I had observed a copulation on 7th July. It was therefore no surprise when a second nest with one egg was located on 11th July in that area. Like the others, it was built in willow herbs and rushes only a foot or two from water. This second breeding pair, whose nest was built about 40 yards from the first, may have been responsible for the last two copulations I observed. Strangely, at about this same time five additional eggs were deposited in and near the first nest, so that ultimately eleven eggs were associated with that nest. In the second nest eggs were deposited daily after 11th July, but on several days two eggs rather than one were collected. This indicated that one or more additional females were depositing eggs in both the nests, and thus it is impossible to judge how many were produced by a single female. Altogether, 22 eggs were deposited in the two nests by three or more females. This sudden "explosion" of breeding activity by the White-backed Ducks is difficult to explain since these birds have been in the collection since 1960 and had previously made only a single attempt to breed. Possibly the presence of the initial nesting pair stimulated the remaining birds in some manner; at least the other White-backed Ducks seemed to take unusual interest in the nest and frequently gathered around it.

When not guarding the nest or incubating, the White-backed Ducks sometimes rested near the middle of the pond. Although on a few occasions I observed the birds thus sleeping with their bills buried in the scapular feathers (a posture I had not observed before), they usually adopted a curious resting position in which one or both feet would be lifted out of the water and placed anteriorly on the back so that the webs of the feet looked like miniature sails (Fig. 1). All of the foraging was apparently done by diving, and it is evident that in their abilities to remain submerged the birds are at least the equals of stiff-tails. In Table I some observed periods of submersion and intervening surfacing periods of White-backs can be compared with North American Ruddy Ducks and two representative whistling ducks that regularly forage in this manner. These observations were all made on the relatively shallow ponds of the Wildfowl Trust at Slimbridge.

Table I. Duration of dives and intervening pauses of White-backed, Ruddy and Whistling Ducks.

	Diving Periods (in seconds)			*Intervening Periods (in seconds)*		
	Observations	*Average*	*Range*	*Observations*	*Average*	*Range*
White-backed Duck	14	20.5	13-30	13	14.5	9-28
N. American Ruddy Duck	19	14.2	8-29	17	10.1	8-15
Fulvous Whistling Duck	7	13.6	9-15	6	11.0	10-18
Javan Whistling Duck	7	11.4	8-15	6	9.0	5-13

Another aspect of general behaviour that has not yet been previously reported is the occurrence of pre-flight movements in White-backed Ducks. Presumably this species flies very little, and an absence of such signals might not be surprising. However, I did once observe a pair that was oriented side by side, facing open water, and appearing very alert. Both performed rapid lateral head-shaking movements with their necks v e r t i c a l l y stretched, and they also occasionally rubbed their cheeks on the scapulars. The male then uttered a few short whistles and the pair attempted to take off. This sequence corresponds closely to the pre-flight behaviour of whistling ducks.

Because of the continuous guarding of the nest by one or both adults, it was difficult to determine when incubation actually began. However, incubation was probably begun at the first nest sometime during the period 13th to 17th July, during which interval no more eggs appeared, and I observed only the male attending the nest. I was not able to visit the Wildfowl Trust again until 27th July, when I noticed that the male was still sitting on the nest. It is well known that in several and possibly all of the species of *Dendrocygna* (Phillips, 1926, lists *viduata, bicolor* and *autumnalis*) the male performs much or all of the incubation. In *Dendrocygna* the incubation period ranges between 27 and 30 days (Delacour, 1954), whereas in the North American Ruddy Duck it is only 20—21 days (Delacour, 1959). Clark (1964) reports an incubation period of 25—27 days for the Maccoa Duck. The majority of the White-backed Duck eggs were incubated under broody hens, and hatched in periods from 29 to 33 days (Janet Kear, pers. com.). However, none survived beyond 15 days. The only success in hatching and rearing this species in captivity was that of Ezra (1934), who noted the unusual precocity of the young in its diving abilities, and that both parents cared for the young. Dr. J. M. Winterbottom and Mr. W. R. Siegfried (pers. com.) have informed me that they have observed both parents attending broods under wild conditions. I was unable to stay long enough to observe the ducklings, but Dr. Kear informed me that, judging from sound spectrographic analysis, the distress calls of d o w n y White-backed Ducks are very similar to those of whistling ducks but are totally different from those of the North American Ruddy Duck (Kear, 1967). Although the plumage of the young is admittedly distinct from that of downy whistling ducks, it is also different from that of stiff-tails. Additionally, although the head pattern is somewhat obscured by a tawny suffusion, it does in some respects resemble that of whistling ducks. It has long been recognized that the whistling ducks are unique in the Anatidae in that their skulls have extensions of the lachrymal bones that project backward to enclose the orbits completely (Phillips, 1923). The White-backed Duck, although lacking this trait, has a skull configuration more closely resembling a whistling duck than a stiff-tailed duck (Janet Kear, pers. com.).

In summary, I believe that there is now sufficient evidence to propose that the genus *Thalassornis* be transferred to the Dendrocygnini and regarded as a whistling duck rather than an aberrant stiff-tail.

Black-headed Duck and Musk Duck

I reported earlier (1965a) on certain male displays of the Black-headed Duck, based on limited observations of a single bird at the Wildfowl Trust. I have since seen these same displays performed by males at the Philadelphia and Bronx zoos, and have also observed females at the latter location. Although the female Black-headed Duck's plumage is similar to that of various *Anas* species, its behaviour patterns appear to be *Oxyura*-like. Thus, I heard no Decrescendo Calls nor have I detected any Inciting calls and postures in the three females I observed. Instead, they remained s i l e n t , e v e n w h e n approached by a displaying male. Their most frequent response was a silent gaping threat directed toward the males in a manner reminiscent of female Ruddy Ducks. Thus, the females appeared to lack signals that might facilitate the development of *Anas*-like social courtship groups; indeed, the males appeared to display independently and indiscriminately to any female that came near. 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 most members of this tribe, although Milton Weller (pers. com.) reports the presence of seasonal pair-bonds in Black-headed Ducks. Instead, male stiff-tails may simply defend individual territories and mate with any females that are attracted by the male's display activities. This behaviour is almost certainly true of the genus *Biziura* (Johnsgard, 1965) and there is suggestive evidence for at least one species of *Oxyura* (Clark, 1964). The frequently quoted statement that male North American Ruddy Ducks "assist" (Kortright, 1942) the female in rearing the brood is misleading; little if any attention is paid to the young by the male, which appears to be merely sexually attracted toward the female (Helen Hays, pers. com.). In the North American Ruddy Duck and also the Maccoa Duck the female herself frequently abandons (or is abandoned by) the brood only a few weeks after their hatching. Parental care has been completely lost in the socially parasitic Black-headed Duck (Weller, unpublished MS.), but female Musk Ducks *Biziura lobata* evidently do exhibit prolonged care of their young which usually number only one or two (Lowe, 1966).

Since the publication of my observations (1965b, 1966b) on the Musk Duck, Mr. V. T. Lowe (1966) has produced a similar survey of its behaviour. He is in agreement with most of my observations regarding the display forms and the origins of the various sounds produced by male Musk Ducks. However, he questions the importance of sexual selection in promoting the evolution of the male's remarkable behaviour patterns and the extreme sexual dimorphism of the species, and instead suggests that the male's displays perform a function of recreation and ego-boosting as a substitute for a strong sex interest. Mr. Lowe does support my belief that no pair bond exists at any season in this species. It is significant that Clark's (1964) study of the Maccoa Duck, one of the largest species of *Oxyura*, indicates a situation closely approaching typical Musk Duck behaviour. Thus, during breeding periods individual male Maccoa Ducks patrol small reed-bordered stretches of water where they display and from which they forcibly expel other males, whereas females apparently drift aimlessly from one such territory to another until each chooses "an exceptionally vigorous" male to associate with and in whose territory she may build her nest without interference from other males. In this way more energetic and dominant males might accumulate two or more females simultaneously or consecutively during the prolonged breeding season. It may thus readily be visualized how the similar behaviour of male Musk Ducks, whose overt territorial battles have evidently been largely replaced with visual and auditory displays that serve equally well to delineate territories and attract females, represents a culmination of the trends toward the breakdown of strong pair bonds that can be traced through almost the entire stiff-tail tribe. Therefore, the male Musk Duck's apparently paradoxical subordination of interest in females in favour of a preoccupation with seemingly senseless displays which Mr. Lowe has stressed is no refutation of the influence of sexual selection, for it is only by the complete breakdown of pair bonds and a reduction of the male's attachment to individual females that an effective polygamous or promiscuous mating system can be established.

It would thus appear that the Black-headed Duck might in many ways be regarded, both behaviourally (Johnsgard, 1965; Weller, MS.) and anatomically (Woolfenden, 1961), as the most generalized of the stiff-tailed ducks and as one derived rather directly from the presumed dabbling duck-like ancestor of the tribe, whereas the Musk Duck can be considered the predictable evolutionary end-product of the behavioural trends that may be first detected in the Black-headed Duck and may be clearly observed in the genus *Oxyura.*

Typical stiff-tails *Oxyura*

For some time it has been my hope to obtain a detailed account of the displays of Masked Ducks *Oxyura dominica,* in several respects apparently the least specialized species of *Oxyura.* This lack of specialization is certainly indicated by its bill structure (" *Nomonyx* " refers to the ordinary appearance of the bill's nail), and by its skeletal anatomy (Woolfenden, 1961). Thus, perhaps the species might be regarded as closest to an ancestral *Oxyura* type (Johnsgard, 1965b) and which in turn may have been derived from a *Heteronetta*-like ancester. Milton Weller (pers. com.) agrees with this view and believes, like Woolfenden, that generic distinction is warranted. Bond's (1961) description of the downy young indicates that Scott's illustration (in Delacour, 1959) is misleading in various details, e.g., the pale areas are actually yellowish buff rather than white, and the light superciliary stripe extends over the lores to the bill. These two mentioned features would seemingly bring the Masked Duck's downy plumage closer in appearance to that of *Heteronetta.* Furthermore, Wetmore (1965) has stated that the male Masked Duck's oesophagus has an elongated and apparently inflatable middle portion, and that the trachea has two air sacs, including a smaller one leading from the anterior ventral surface and a larger one opening from the dorsal surface. So far as is known, the male of no other *Oxyura* species has both an inflatable oesophagus and well developed tracheal air sacs. The male Masked Duck in breeding condition does exhibit black spiny papillae around the base of the intromittant organ (Wetmore, 1965), a feature apparently characteristic of many or all species of *Oxyura* (Helen Hays, pers. com.).

Since my own attempts to locate and study Masked Ducks have thus far been unsuccessful, I am able here to add little information regarding the behaviour of this most interesting of the *Oxyura* species. The only person I have located who has observed Masked Duck display is L. Irby Davis, who informed me (pers. com.) that his observations date from more than 20 years ago and his notes have been lost or mislaid. However, he recalls that the male definitely cocked its tail during display, that the throat or neck was enlarged, and that a sound was produced by the male as it performed movements similar to those made when preening the neck feathers. The occurrence of frequent quick rushes over the water surface by the male was another of the display features which he clearly remembers. These observations would suggest a great deal of similarity between Masked Duck displays and those of the other typical stiff-tails, but it may be hoped that more concrete information on the species' visual and auditory displays will eventually become available for purposes of comparison.

The remaining five species of *Oxyura* also pose considerable problems in understanding their behaviour and relationships. The only male displays which have been reliably reported in all of them involve neck inflation and tail-cocking. In all but the White-headed Duck *O. leucocephala* a display involving repeated bill-dipping followed by lateral head-shaking (" bill-flicking ") or head-rolling on the scapulars has been reported. This sequence serves as a precopulatory display in the North American Ruddy Duck, probably also in the Maccoa Duck (Clark, 1964), and possibly in the Argentine Ruddy Duck, but in the Australian Blue-billed Duck these same movements occur at the end of a display sequence called Sousing (Johnsgard, 1966). This display, first described as such for the Australian species, is clearly identical to one of the displays described by Clark (1964), for the Maccoa Duck, even to the preliminary head-pumping and the following bill-dipping and head-shaking. Furthermore, Dr. Martin Moynihan has recently shown me sketches he made of display in the Argentine Ruddy Duck *O. vittata* and which indicate the occurrence of Sousing in that species too. Considering the complexity and frequency of this display sequence in the Australian Blue-billed Duck it may well be regarded as the species' primary " courtship " display, in the same manner that the Bubbling sequence may be so regarded for the

North American Ruddy Duck (Johnsgard, 1965a). If this is the case, one might conclude that two species of *Oxyura (jamaicensis* and *leucocephala)* probably have as their primary male displays the Bubbling sequence and that the three strictly southern hemisphere species *(maccoa, vittata* and *australis)* presumably utilize Sousing as a characteristic display. This dichotomy would fit in well with the postulated taxonomic relationships which I earlier (1961b) proposed on the basis of the more limited information available. It would further seem probable that each species using Sousing as a display has an inflatable oesophagus whereas those which perform Bubbling may possess tracheal air sacs. Unfortunately, the male tracheal and oesophageal structures of the White-headed Duck and the Maccoa Duck are still undescribed, although Clark (1964) suggests that a tracheal air sac may be present in the Maccoa Duck.

Sound production through splashing movements is evidently a basic part of *Oxyura* displays. Thus, a rapid forward Rush through the water by the male (called Motor-boating in *O. australis*) has been reported for nearly all the *Oxyura* species, and a Ringing Rush (or Display Flight) just over the water surface accompanied by a rattling sound produced by the wings and/or feet striking the water has been noted in all of the species except the poorly studied White-headed Duck, Masked Duck, and Argentine Ruddy Duck. However, an actual display call by males is evidently much more restricted in occurrence. It is apparently best developed in the Maccoa Duck, which produces a "purring" or "vibrating trumpet call" with its tail erect, head forward and beak open, and with the crown feathers raised except for a central groove running from front to back (Clark, 1964). Except for the call, this description exactly fits the posture assumed by the North American Ruddy Duck as it utters its weak belching note at the termination of the Bubbling sequence. A similar posture and presumably an associated call is assumed at the end of the corresponding displays in White-headed Ducks (Mountfort, 1958). Apparently the male Masked Duck also produces one or more vocal sounds, variously rendered as "Kurikirro" or like "a short note from a motor horn," although possibly this latter note is produced by the female. Lord William Percy (in Barber's *Birds of Cuba*) stated that "the male has a curious habit of responding like a cock pheasant to such noises as the banging of a punt pole on the water or an explosion in the distance," suggesting the significance of male vocalizations in territorial establishment and maintenance. It would seem, however, that male vocalizations in most stiff-tails have been subordinated to non-vocally produced noises that may serve these same functions.

As a means of summarizing our still relatively primitive state of knowledge about stiff-tail behaviour, the accompany-

Table II. Summary of some male displays and display structures in the species of *Oxyura*.
An "X" indicates presence and a dash indicates apparent absences of the indicated feature.

	Masked Duck	N. Amer. Ruddy Duck	White-headed Duck	Maccoa Duck	Argentine Ruddy Duck	Blue-billed Duck
Tail cocking	X	X	X	X	X	X
Bill-dipping and water-flicking	?	X	?	X	X?	X
Forward Rush in water	X	X	X	X	?	X
Ringing Rush over water	?	X	?	X	?	X
Sousing sequence	?	-	?	X	X	X
Bubbling sequence	?	X	X	-	-	-
Calling during tail-cocking	X?	X	X	X	?	-
Inflated Neck Display	X	X	X	X	X	X
By oesophagus	X	-	?	?	X	X
By air sacs	X	X	?	?	-	-

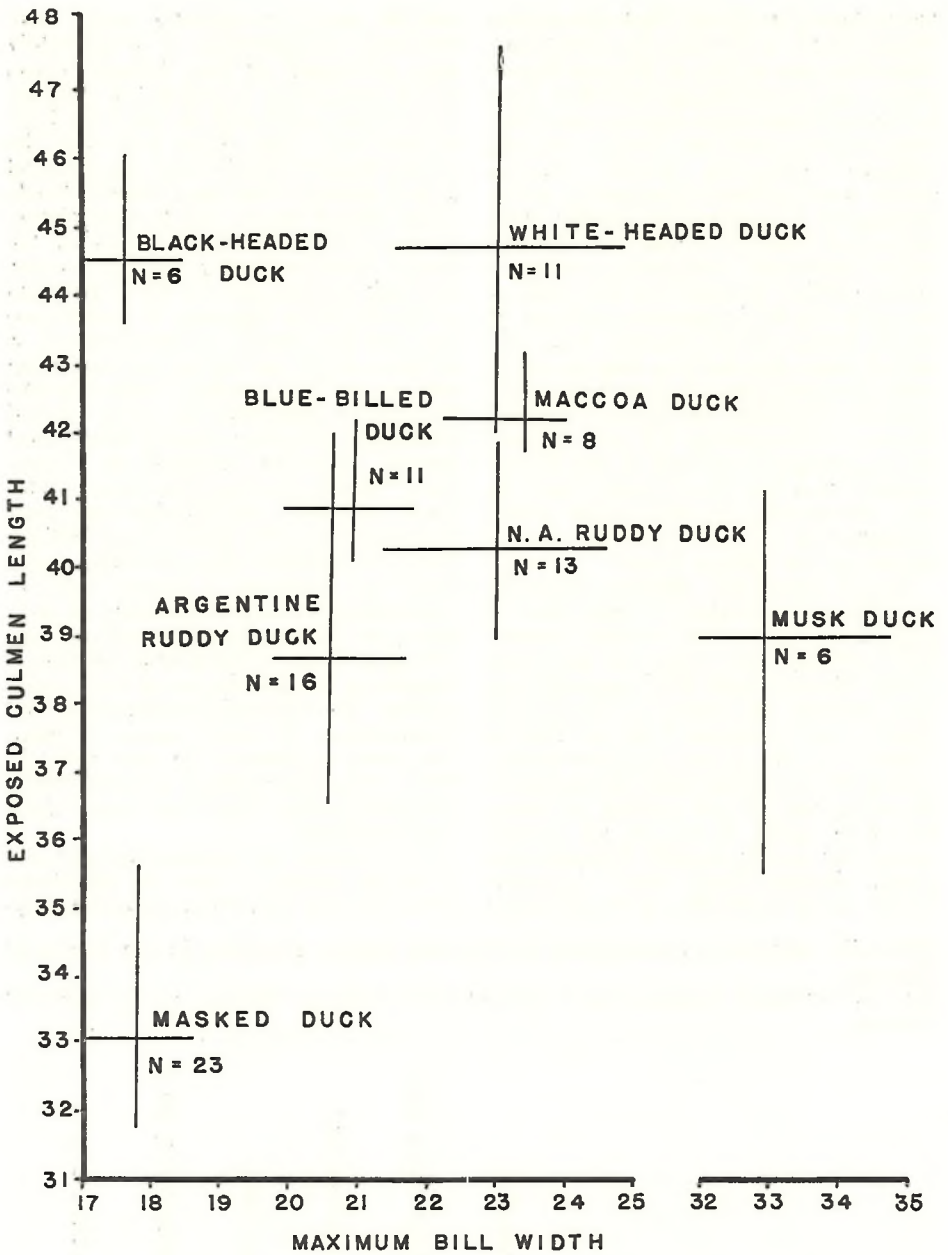

Figure 2. Measurements (in millimetres) of bills of adult male stiff-tailed ducks. The lines intersect at the mean of each sample.

ing Table II lists the apparent distribution of these various male behavioural and structural features in the *Oxyura* species. Additionally, a diagram (Fig. 2) showing interspecies variation in exposed culmen lengths and maximum culmen widths of adult male stiff-tail species has been prepared, since these measurements appear to be among the most useful for characterizing the various species. It may be seen that in the genus *Oxyura* a fairly constant ratio between culmen width and length is maintained throughout the genus, with the Masked Duck differing from the others only by virtue of its considerably smaller size. On the other hand,

the Black-headed Duck's bill is relatively long and narrow, much like that of an *Anas* species, whereas the massive bill of the Musk Duck is unusually short and broad, and is evidently adapted to crushing rather than filtering foods.

Acknowledgements

These observations were made with the financial support of a National Science Foundation research grant (G.B. 1030). I also wish to thank the Wildfowl Trust for the opportunity of again utilizing the collection at Slimbridge. Additionally, unpublished observations were provided by Dr. Janet Kear, Mr. S. T. Johnstone, Miss Helen Hays, Dr. Milton Weller, Mr. L. I. Davis, and Mr. W. R. Siegfried, to all of whom I am very grateful.

References

BOETTICHER, H. VON. 1952. *Gänse- und Entenvögel aus aller Welt.* Die Neue Brehm-Bücherei, Heft 73. Ziemsen, Wittenberg Lutherstadt. 96 pp.

BOND, J. 1961. *Sixth supplement to the check-list of birds of the West Indies* (1956). Academy of Natural Sciences of Philadelphia. 12 pp.

CLARK, A. 1964. The Maccoa Duck (*Oxyura maccoa* (Eyton)). *Ostrich,* 35 : 264-276.

D'EATH, J. O. 1965. In search of two interesting African ducks. *Avic. Mag.,* 71 : 16-20.

DELACOUR, J. 1954, 1959. *The Waterfowl of the World.* Country Life, London. Vols 1 and 3.

DELACOUR, J. and E. MAYR. The family Anatidae. *Wilson Bulletin.* 57 : 3-55.

EYTON, T. C. 1838. *A Monograph of the Anatidae, or Duck Tribe.* London. 178 pp.

EZRA, A. 1934. Deux oiseau africains éleves pour la première fois en captivité. *Oiseau,* 4 : 188-9.

HELLMAYR, C. E. and H. B. CONOVER. 1948. Catalogue of the Birds of the Americas. Pt. 1, No. 2. *Pub. Field Mus. Nat. Hist., Zool. Ser.,* Vol. 13. 434 pp.

JOHNSGARD, P. A. 1960. Comparative behaviour of the Anatidae and its evolutionary implications. *Wildfowl Trust 11th Ann. Rep.* : 31-45.

JOHNSGARD, P. A. 1961a. The tracheal anatomy of the Anatidae and its taxonomic significance. *Wildfowl Trust 12th Ann. Rep.* : 58-69.

JOHNSGARD, P. A. 1961b. The taxonomy of the Anatidae — a behavioural analysis. *Ibis,* 103a : 71-85

JOHNSGARD, P. A. 1965a. *Handbook of Waterfowl Behavior.* Cornell University Press, Ithaca, N.Y. 378 pp.

JOHNSGARD, P. A. 1965b. Observations on some aberrant Australian Anatidae. *Wildfowl Trust 16th Ann. Rep.* : 73-83.

JOHNSGARD, P. A. 1966a. The biology and relationships of the Torrent Duck. *Wildfowl Trust 17th Ann. Rep.* : 66-74.

JOHNSGARD, P. A. 1966b. Behavior of the Australian Musk Duck and Blue-billed Duck. *Auk,* 83 : 98-110.

JOHNSON, A. W. 1965. *The Birds of Chile and adjacent regions of Argentine, Bolivia and Peru.* Vol. 1. Buenos Aires. 398 pp.

JOHNSTONE, S. T. 1966. The Collections in 1965. *Wildfowl Trust 17th Ann. Rep.* : 10-13.

KEAR, J. 1967. The calls of very young Anatidae. *Die Vogelwelt.* In press.

KORTRIGHT, F. H. 1942. *The Ducks, Geese and Swans of North America.* Wildlife Management Institute, Washington, D.C. 476 pp.

LEHMANN, F. C. 1946. Two new birds from the Andes of Colombia. *Auk,* 63 : 218-223.

LOWE, V. T. 1966. Notes on the Musk Duck. *Emu,* 65 : 279-290.

MACKWORTH-PRAED, C. W. and C. H. B. GRANT. 1952. *Birds of Eastern and North Eastern Africa.* Vol. 1. Longman, Green and Co., London. 836 pp.

MOUNTFORT, G. 1958. *Portrait of a Wilderness.* Hutchinsons, London. 240 pp.

PHILLIPS, J. C. 1926. *A Natural History of the Ducks.* Houghton Mifflin, Boston. Vol. 4. 489 pp.

RIDGWAY, R. 1880. Revision of nomenclature of certain North American birds. *Proc. U.S. Nat. Mus.,* Vol. 3 : 15-16.

SIEGFRIED, W. R. 1964. Parasitic egg laying in South African Anatidae. *Ostrich,* 35 : 61.

WETMORE, A. 1926. Observations on birds of Argentine, Paraguay, Uruguay and Chile. *Bull. U.S. Nat. Mus.,* Washington, No. 133. 448 pp.

WETMORE, A. 1965. The birds of the Republic of Panama. Pt. 1. *Smith Misc. Coll.,* Vol. 150. 483 pp.

WOOLFENDEN, G. E. 1961. Postcranial osteology of the Waterfowl. *Bull. Florida State Museum, Biological Sciences,* 6(1) : 1-129.