



The biology and relationships of the Torrent Duck

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Summary

On the basis of field observations of five of the six described forms of Torrent Ducks, it is concluded that only a single species of *Merganetta* should be recognized, and that probably no more than three sub-species exist, *armata armata*, *colombiana* and *leucogenis*; *turneri*, *garleppi* and *berlepschi* are believed to represent variants of *leucogenis*. The genus *Merganetta* should either be placed in the perching duck tribe Cairinini or given separate tribal status and placed adjacent to the Cairinini.

Although the Torrent Duck *Merganetta armata* occupies a vast geographic range extending some 5,000 miles from the cordilleras of north-western Venezuela to Tierra del Fuego, the species' ecological distribution is limited to the torrential streams that originate in the high Andes and flow downward into the major river systems of both the Atlantic and Pacific drainages. Its altitudinal distribution varies with latitude and local conditions, but the upper limits appear to occur at elevations where the streams become too small to provide adequate foraging opportunities, while the lower limits are probably determined by diminishing stream gradients, since the larger and slower rivers lack the falls, rapids, and emergent rocks which are the heart of the Torrent Duck's habitat requirements. It is not surprising, therefore, that few biologists have seriously attempted to study this remarkable bird, for in most parts of South America its favoured habitats can be reached only with difficulty, and even under the best of conditions the birds are never abundant and are usually extremely wary. As a result, much uncertainty has existed concerning the biology of the Torrent Duck, not only as to its ecology and behaviour, but also regarding the evolutionary relationships of *Merganetta* to other Anatidae and even as to the number of taxonomic sub-units (species or sub-species) within the genus.

Because of these several uncertainties, a trip to South America was made for the primary purpose of investigating as many as possible of the six described populations of *Merganetta*, comparing details of appearance, behaviour and ecology, and attempting to resolve at least some of the more obvious deficiencies in our knowledge of the Torrent Duck. This trip, from 4th July to 28th August, 1965, included stops in Colombia, Peru, Bolivia and Chile, where five of the six populations (all but the Argentine Torrent Duck) were observed. This paper is a summary of the

behavioural and ecological findings of the trip; the taxonomic problems involved are too great to allow anything more than preliminary conclusions at this time. This paper follows the taxonomic interpretation of Delacour and Mayr (1945) and Delacour (1954), which assumes a single species of *Merganetta*. It should be noted, however, that earlier authors accepted as many as five (Phillips, 1926) or six (Salvadori, 1895) species. Conover (1943), who undertook the only thorough specimen analysis to date, concluded that three species (*colombiana*, *leucogenis* and *armata*) and three additional sub-species (of *leucogenis*) should be recognized. He based these conclusions on the considerable differences in the male plumage patterns and on the well-marked geographic separation of the three major population groups, although the latter fact would today be regarded as an argument in favour of considering the forms as sub-species. Phillips and Salvadori regarded the Torrent Duck as a unique form, comprising the sub-family Merganettinae together with the genera *Hymenolaimus* and *Salvadorina* (= *Anas waigiensis*). Delacour and Mayr (1945) separated the genus in a monotypic tribe Merganettini, but Niethammer's (1952) anatomical study convinced Delacour (1954) that *Merganetta* should be included in the dabbling duck tribe Anatini. More recently, however, Woolfenden (1961) has urged that a tribal distinction for *Merganetta* be retained.

Appearance

In life the Torrent Duck is a singularly beautiful bird, without close similarity to any other anatid with the possible exception of the Salvadori's Duck *Anas waigiensis*. Both species are slim-bodied and long-tailed but, while the Torrent Duck's rectrices are distinctly stiffened and slightly decurved and are used for support when climbing on slippery rocks, this adaptation is lacking in the Salvadori's Duck. However, both species doubtless use their long tails for underwater manoeuvring.

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Another unusual feature of the Torrent Duck which is barely indicated in Salvadori's Duck is the presence of a bony spur at the carpal joint, or 'wrist'. Adults of both sexes exhibit this feature, although the spurs are longer on adult males. Unlike the similar spurs of the Spur-winged Goose *Plectropterus gambensis* they are not extensions of the radial bone (Rand, 1954), but rather are somewhat flexibly attached to the first metacarpal. The use to which these spurs are put is still questionable, since through its habitat preference the Torrent Duck is well protected from most terrestrial predators, and no intraspecific fighting among males has been noted to my knowledge. There is no evidence that the spurs are used as an aid in climbing rocks, as has been suggested.

Females of all the populations are similar in appearance, and are a rich ochraceous brown below the grey above, totally lacking the barring of typical female dabbling ducks. The Colombian race differs from the others slightly in that the grey of the head and neck does not extend so far downward, and the body colour may be slightly paler. When swimming, females are often very difficult to see, since only the grey dorsal surface is visible, but when perched on a rock the richly toned brown flanks and under-parts are most conspicuous. As in males, the bright red bill is also highly conspicuous.

Males, unlike the females, differ markedly in different populations, and these plumage variations have been the basis for taxonomic discriminations. In all populations, however, the head patterning is very similar; a black ocular stripe extends back from the eye to the occipital region where it branches and continues down the sides and back of the neck.

This stripe does not actually merge with the crown stripe that extends back from the base of the bill (see photo section), although in the Chilean Torrent Duck the black striping extends down from the eyes and merges with a black throat and neck. This general increase in melanism toward the south is accompanied by a darkening of the legs from a bright carmine similar to that of the bill in the Colombian race to a dusky red, and a blackish culmen area also appears on the red bill in the more southerly forms.

Body plumages of the males differ greatly between populations, and have caused much taxonomic confusion. The Colombian race (*M. a. colombiana*) exhibits the least melanism, having the breast and under-parts nearly a pure white, with only light grey striping, and the edging of the mantle feathers is a light brown. The

Peruvian race (*M. a. leucogenis*) is more distinctly striped below, although at least in eastern Peru near Lake Junin there is distinct variation in the degree of mantle and under-part patterning (Phillips, 1926). In the Cuzcan Andes the Turner's Torrent Duck (*M. a. turneri*) reputedly has the most uniformly dark body of all the races, with black flanks and breast, and black mantle feathers that are brown-edged. However, of at least eleven different males seen by me in the Cuzco area (three skins, eight or more different wild males observed closely), only one bird was almost as dark as the type specimen (illustrated in Phillips, 1926). The remaining birds varied greatly, but most of them could not be readily distinguished from *leucogenis* males (see photo section). These variations in bodily melanism must certainly have minor genetic significance, since the darkest male observed was found in Huarcocondo canyon, where at least four other lighter-coloured males were resident in a six kilometer river distance. In Bolivia (*M. a. garleppi*) the males likewise very closely approach typical *leucogenis*, supposedly differing from it in having white, rather than brownish, edging to the mantle feathers. However, this distinction did not apply to four males observed closely (one of which was collected) on the Río Zongo. Although I did not observe the Argentine race (*M. a. berlepschi*), it is known that males are highly variable in their under-part colouration (Dabbene, 1927). This race is also reported to possess white edging on the mantle feathers, which, if true, would help to distinguish it from *leucogenis*, and suggest some affinities with the Chilean race (*M. a. armata*), although there is a considerable geographic gap between these populations (Johnson, 1963). This last race is the most distinctive of all, with definitely white-edged mantle feathers, brown flanks, and black under-parts extending up the throat to the bill and eyes. In short, it would appear that there exists a light-coloured and fairly uniform northern population (*colombiana*), a melanistic and fairly uniform population (*armata*), and several highly variable intermediate populations with varying degrees of under-part melanism and white to brown mantle edging. Conover (1943) recognized this intermediate group as a distinct species (*leucogenis*) consisting of four sub-species, but considering the individual variation I observed in the Cuzco area and reported elsewhere by Dabbene and Phillips, I would suggest that only a single race, *leucogenis*, should be recognized. Besides the marked gap separating this central group from the Chilean

race, there is probably also a gap in northern Peru and Ecuador separating it from *colombiana* (Conover, 1943).

This unusual degree of individual and sub-specific male plumage variation is unique among ducks, and deserves some attention. It would seem that the absence of closely related, sympatric forms would reduce selective pressures for male uniformity to ensure species recognition by females, and would provide at least a partial explanation for this variability. More important, the fact that Torrent Ducks are confined in their movements within river systems, and may be completely isolated from adjoining populations by lack of connecting river drainages, would tend to result in much local genetic variation. Finally, Torrent Ducks appear to be highly sedentary and monogamous, with relatively permanent pair bonds, further reducing gene flow and increasing variability even within potentially interbreeding populations.

Environmental Conditions

As suggested above, water conditions are of critical importance in determining Torrent Duck distribution. In every location where Torrent Ducks were found, the river could be characterized as having rapids and falls (up to 20 feet high), interspersed with stretches of more placid water. The width of the river appeared to be of little importance; ducks were observed on high mountain streams no more than six feet across (e.g., near Pisac, Peru), as well as such streams as the Rio Petrohué, which is over 200 feet wide. All, however, had numerous slightly submerged and emergent rocks which produced the falls, rapids, and pools that appear to be of crucial importance for Torrent Ducks. The surrounding vegetation appeared to be of no significance; Torrent Ducks were observed in such diverse vegetational zones as the moist alpine páramo of Colombia, the dry alpine puna zone of Peru, upper and lower montane rainforests of Colombia, coastal xerophytic desert of Peru, and temperate rainforest of Chile.

All of the rivers supporting Torrent Ducks were distinctly cold (the Rio Chisbar had an average temperature of 12°C) and thus the water was capable of retaining much of the oxygen to which it is exposed when passing over falls and rapids. Such high oxygen tensions would clearly be of importance in supporting the aquatic animal life upon which the Torrent Duck is dependent.

The altitudinal distribution of *Merganetta* appears to be as varied as its ecological distribution. In Colombia Tor-

rent Ducks were found between the elevations of 1,500 and 2,500 meters on the Rio Cauca, Rio Chisbar, and Rio Grande, near Popayán. However, Dr. F. Lehmann (pers. comm.) has observed them as low as 200 meters on the Pacific slope of the Farallones mountains, near Cali. In Peru we observed *M. a. leucogenis* on the Rio Lurin above Santa Cruz de Luya, at approximately 2,000 meters, and Phillips (1953) found them on the nearby Rio Cañete at 2,500 meters. Dr. Maria Koepche (*in litt.*) has observed Peruvian Torrent Ducks at altitudes between 800 meters (Rio Chancay) and 3,600 meters (Quebrada Yanganuco, Cordillera Blanca). Near Cuzco we observed *M. a. turneri* along the Vilcanota, Urubamba river system from a point just above Yaucat (near Tinta, the type locality of *turneri*), at 3,386 meters, to a few kilometers above Machu Picchu, at about 2,040 meters. Chapman (1921) reports Torrent Ducks in the Urubamba valley at elevations of 9,100 feet (2,270 meters), 10,000 feet (3,050 meters), and 11,000 feet (3,350 meters). In Bolivia on the Rio Zongo we observed *M. a. garleppi* from a short distance above Cuticuch station (2,697 meters) to a point two kilometers above the lowest accessible point, Chururaqui station, at 1,830 meters. Niethammer (1953) states that they are found between 1,200 and 3,600 meters in Bolivia, and Phillips (1925) reports that specimens have been taken as high as 15,000 feet (4,500 meters). In Chile, we found *M. a. armata* on the Rio Teno above Los Queñes, at 1,200 meters, and also on the upper Rio Petrohué, at 160 meters. Mr. A. W. Johnson (pers. comm.) informs me that there is a definite latitudinal, altitudinal gradient of Torrent Duck distribution in Chile, and that in the extreme north *M. a. turneri* occurs near Arica (lat. 18°S) only at elevations above 4,000 meters. The Chilean race occurs at similar heights as far north as latitude 27°S, but that from that point south the birds occur at gradually lower altitudes, eventually reaching close to sea level in the provinces of Aisen and Magallanes.

As an indication of the typical stream gradients that support Torrent Ducks, a few examples might be mentioned. In Peru, the Huarcoondo canyon enters the Urubamba valley above Ollantaitambo, and the stream which flows through this canyon supports a good population of Torrent Ducks. From the village of Huarcoondo (3,320 meters) to Pachar station (2,800 meters), a distance of 19 kilometers, there is an average stream gradient of 27 meters per kilometer. The middle third of the canyon, from a point six kilometers below

Huarocondo to approximately six kilometers above Pachar station, supported at least five and possibly six pairs of Torrent Ducks during July of 1965, suggesting a maximum population of about one pair per kilometer. Mr. John O'Neill (*in litt.*) observed eleven Torrent Ducks in the lower thirteen kilometers of this canyon in January, 1965, indicating a similar population at that time of year.

In Bolivia, the Río Zongo provided another basis for estimating stream gradients suitable for Torrent Ducks. Between Cuticucho station and Chururaqui station there is a linear distance of nine kilometers, with an average stream gradient of 96 meters per kilometer, or four times as steep as the Huarocondo location. In this distance two pairs plus three additional males were seen, but owing to the impossibility of an adequate inventory of this precipitous and thickly vegetated canyon, many additional birds may have gone unnoticed.

Torrent Ducks are particularly abundant in the lake district of southern Chile (Johnson, 1963). We observed at least four males in a two kilometer stretch of the Río Petrohué, between Lake Esmeralda and the first extensive rapids. The Río Petrohué drops from an initial height of 180 meters to sea level in approximately 40 kilometers, with an average gradient of 4.5 meters per kilometer. However, Torrent Ducks are probably restricted to the upper portion of the river, where the gradient is considerably higher than this. Mr. Johnson tells me (*pers. comm.*) that the largest number of Torrent Ducks he has ever seen was at Los Queñes, where in the month of August he observed seven males and four females in an approximate ten kilometer river distance.

In summary, it would appear that Torrent Duck populations rarely exceed one pair per kilometer, and usually would be much less than this.

General behaviour

By far the most impressive and unforgettable aspect of Torrent Duck behaviour is their incredible ability to negotiate the most impossible rapids, making headway upstream against an overpowering current, or turning and careening downstream through the tumultuous rapids, barely avoiding the rocks and nearly disappearing from sight amid the spray and froth. I have observed adults dropping over falls several feet high, particularly when they are attempting to escape danger. When not disturbed, however, they usually stop short of such falls, climb out on a rock, then fly down to the next stretch of calmer water.

While swimming, the body is often totally submerged, with only the head and neck visible as the bird moves up or downstream. When swimming upstream in very rapid water, both adults and young sometimes 'run' over the water surface in the manner of frightened fledgling ducklings. When frightened, a typical manoeuvre is to swim 10 or 20 yards upstream from the observer, then dive and be swept downstream by the current some 50 yards or more, finally emerging and flying away or continuing downstream with only the head above water. Although this is a typical adult response, we also saw two groups of downy young, no more than two weeks old, perform the same tactic. In one case they manoeuvred about 30 yards downstream through two stretches of rapids before emerging again. Although I was not able to ascertain this point positively, adults appeared to hold their wings open slightly when swimming under water, probably for steering purposes rather than propulsion. In general, birds took flight when frightened only as a last resort, usually flying no more than a few hundred yards before landing in the water again and generally hiding among the shoreline rocks. In three cases where pairs with downy young were found, the male conspicuously flew away from the group, often calling loudly. The females always stayed near the young and led them to shore where they hid among the rocks.

One remarkable and previously unnoticed escape device was observed that warrants description. In the Río Chongo, above Pisac, Peru, a pair had been under observation for several days and it was believed that the female might be nesting. On one afternoon the male was observed foraging alone in the river several hundred yards above the presumed nest site. At our approach he began to swim downstream, then turned and, swimming underwater, went rapidly back upstream to the base of a small waterfall about 2 feet high, and disappeared from view in the spray of the fall. The river was sufficiently shallow to see that he had not gone back downstream, and we concluded that he must be hiding at the base of the fall. To find out we threw several large rocks into the water near the point where he disappeared, but to no effect. We were about to abandon the search when the male suddenly appeared on a rock at the base of the fall, saw us, and disappeared again. This time we approached the fall, threw several more rocks into the spray, and even reached back into the recesses of the rocks as far as possible. Still failing to dislodge the bird, we began to walk away, whereupon the

male emerged flying from the very spot we had searched, moving downstream some 150 yards to the next waterfall of similar size. It landed just above the brink, swam over it, and again disappeared in the white water below. Later, in Bolivia, we observed a female with young hide in exactly the same manner after the young bird had retreated from us to the rocks on the opposite shore. In this case she remained hidden for over half an hour before she finally emerged and flew downstream to her mate, who had remained in sight during most of this time.

One difference in general behaviour of the Torrent Duck that sets it apart from such stream-dwelling species as the Salvadori's Duck and the Harlequin Duck *Histrionicus histrionicus* is the fact that Torrent Ducks do not 'nod' the head when swimming or walking as these species typically do. Furthermore, unlike the Salvadori's Duck, the Torrent Duck rarely raises its tail from the water and never cocks it vertically during normal swimming. When standing on a rock and watching some object in the distance or about to dive into the water, Torrent Ducks do frequently move their heads up and down, or from front to back, possibly as a distance-estimating technique. These may also serve as diving intention movements.

Torrent Ducks take flight without any obvious pre-flight movements or calls, and can spring out of a rapid torrent with the agility of a teal. They fly low over the water, rarely higher than 20 feet, and methodically follow the course of the river. While most flights are of short duration and only long enough to put them out of the observer's view, on one occasion we flushed a pair that must have flown at least three kilometers. This occurred on the Rio Lurin, near Lima, and as we followed the birds upstream, we met several groups of natives who informed us that they had seen the birds fly past. Finally, some three kilometers upstream, we abandoned the search.

The wingbeats of Torrent Ducks in flight are unusually shallow and rapid, although the speed of flight does not appear to be great. On the basis of some short motion picture scenes, the rate of wing beats during sustained flight is about twelve per second.

Foraging behaviour and food

The foraging of Torrent Ducks is no less remarkable than their escape behaviour. Typically the birds forage from a large, rounded rock near the middle of a stream, from which they repeatedly dive. When

diving the bird usually drops head-first directly into the current in front of or beside the rock, and completely disappears from view until it suddenly appears scrambling up the smooth rock surface near the point where it entered the water. In Chile on the Rio Petrohué some measurements of diving and resting times were taken of a male foraging in the fastest rapids of this then-raging river. During a period of 3 minutes and 22 seconds the male made seven dives, ranging in length from 12 to 18 seconds (average 16.0), and rested on a rock for seven periods ranging from 9 to 18 seconds (average 12.6). I estimated the surface velocity of the river at that point to be approximately 10 feet per second; thus, a bird simply maintaining its submerged position in the water for 16 seconds would have to perform the equivalent effort of swimming 160 feet underwater! The repeated performance of this feat would appear to be almost impossible, and thus I believe that during these dives the bird must go directly to the bottom, foraging upstream along the river floor where the water velocity is greatly reduced, and then returning to the surface at nearly the exact point of entry.

Three other methods of foraging were observed. At times the birds would swim on the surface, with only the head submerged and directed upstream, apparently picking up food as it was swept past in the current. An extension of this method was to be almost totally submerged except for the tail, feeding in the pools and eddies behind large rocks. Finally, a bird would sometimes swim to the foot of small fall a foot or two high, crawl behind the main flow of water, and probe among the rocks with the bill as the water flowed over its back and head in an almost unbroken sheet.

It is clear that Torrent Ducks rely largely on food of animal origin, judging from published records. Niethammer (1952) noted that three Bolivian and one Peruvian Torrent Duck he examined contained almost entirely stone-fly and caddis-fly larvae. A nesting female Colombian Torrent Duck collected by Holman, near Cali, contained caddis-fly larval cases, and three Peruvian Torrent Ducks collected by Lord W. Percy near Lake Junin contained primarily larvae of caddis-flies and mayflies, with only a trace of vegetable materials (Phillips, 1926). Pemberton (in Phillips) reported that in southern Argentina the Torrent Ducks ate 'mollusks including gastropods', while Conover found that two collected in the same general area contained insects and their larvae.

Although it has not been reported in the

literature, it is possible that at least in some areas small fish may contribute to the diet of Torrent Ducks. Dr. F. C. Lehmann tells me that biologists in Bolivia report considerable damage to planted trout fingerlings by Torrent Ducks. In Peru we were told by a local hunter who knew the birds well that one male he had shot in March had a full crop of 'sardine-sized' fish. I examined the male we collected on the Rio Zongo, and found that the gizzard contained only well-ground vegetable matter and a few very small stones.

It is worth noting that, except in Chile, we never failed to find the White-capped Dipper *Cinclus leucocephalus* on every stream where we found Torrent Ducks. Indeed, the best 'indicators' of Torrent Ducks proved to be the presence of Dippers and white droppings on the larger rocks in the rivers. Since the quantity of droppings produced by *Merganetta* is considerably greater than that of *Cinclus*, it was a simple matter to distinguish them. In Chile, however, we were south of the Dipper's range, and the winter rains quickly washed away droppings on the rocks, so that we were not able to use these clues. In any case, it is probable that Dippers and Torrent Ducks have nearly identical habitat requirements and probably are dependent on the same sources of food.

Breeding Seasons

Although very few Torrent Duck nests have been found (two of the Chilean race and two of the Colombian race are known to me), it is possible to make a few observations about breeding periodicity. On the Rio Chisbar near Popayán, 11th July, we found a pair with two young less than a week old. We were told by natives that two other pairs with young of similar age were seen a few days previously on the Rio Blanca, near Paletara. Conover (1943) reports downy young of this race taken in October, eggs taken in November, and immatures taken in January, March, April and September. Thus, it is clear that the breeding season in Colombia is a very extended one, as might be expected near the equator.

In the Cuzco area of Peru, Chapman (1921) reported a pair with two downy young in Huarcocondo canyon in late July. On 26th July we located two pairs with downy young in this same canyon. One of the broods, with two young, was estimated to be no more than two weeks old, while the other brood of three appeared slightly older. We also had reason to believe that a female on the Rio Chongo, near Pisac, was nesting at this time. These sightings would suggest that breeding in

the Cuzco area occurs during the dry season.

In Bolivia, Niethammer (1953) reported collecting a pair of Torrent Ducks with enlarged gonads near Pojo in early August, leading him to conclude that the ducks breed prior to the rainy season, when the water is clear and not flowing too swiftly. Our observation of a pair on the Rio Zongo with a single downy young (two or three weeks old) on 3rd August, supports this view, although the male we collected only ten kilometers upstream had inactive testes.

It is clear that in Chile and southern Argentina seasonal temperature variations are of greater importance than farther north, and that breeding occurs during the southern spring. Johnson (1963) found a nest in an old burrow of the Southern Ringed Kingfisher *Megaceryle torquata stellata* with three nearly fresh eggs at Llifén, on 11th November. He has also observed (pers. comm.) broods somewhat later than this, usually numbering two or three young, but as many as five (twice). Therefore, the nesting season in Chile occurs at the end of the wet winter, and young emerge during the mild and relatively dry spring.

Judging from our observations of four broods in Colombia, Peru and Bolivia, no specific brooding habitat requirements exist. However, in two cases the brooding area was bounded below by fairly steep canyons and high falls, which perhaps represented the original nesting sites. Likewise, the presumed nesting area near Pisac, Peru, was a steep-walled canyon with falls and rapids both above and below. Both of the broods found in Huarcocondo canyon were seen on or near low, rocky islands on which shrubs and low trees were growing; presumably these islands served as relatively safe resting and sleeping areas.

Vocalizations

Previous accounts of Torrent Ducks have offered little information regarding vocalizations, which is not surprising considering the problems of hearing calls above the noises of rushing water. Scott (1954) reported a call, described as a 'keech', uttered by Bolivian Torrent Ducks repeatedly when the birds were nervous, and Niethammer (1952) mentioned a shrill whistle uttered by the male and possibly also the female.

We heard vocalizations from males of the Colombia, Turner's, Bolivian and Chilean races. In all these races the calls appeared identical, and most commonly consisted of a sharp, clear whistle, dropping

slightly in pitch toward the end. This was uttered at several second intervals by males to other males, their mates, or their families, apparently as a warning note. It was usually uttered as the bird stood on a rock, but was also produced by swimming and flying birds. On one occasion, on the Rio Chongo, the male swam up the canyon in which we believed his mate to be nesting, uttering a series of eight to ten soft and rapidly repeated whistling notes. At this time the female remained hidden, but on the next day when the same call was given, the female emerged from the rocks above the river and joined the male, then both flew downstream together.

We did not hear any definite calls from females, but Mr. H. Lüthi (pers. comm.) heard an unusual sound from a group of four Torrent Ducks (two pairs) in May. This was a rough, guttural sound, prolonged and on the same pitch, which may well have originated from the females. Mrs. A. W. Johnson (pers. comm.) remembers that when they captured a nesting female it uttered a high and strange squealing note, quite different from the usual calls of female ducks, and that only once did it produce anything resembling a 'quack'. Mr. Johnson also recalls hearing a 'weak quack' from this bird.

The 'lost' calls of the downy young, which we heard on several occasions, are single-noted peeping whistles, much like the distress note of downy Mallards *Anas platyrhynchos*.

Pair bonds and social behaviour

In contrast to most ducks, the Torrent Duck does not appear to be gregarious and has never been reported as occurring in flocks. This solitary nature may simply be a reflection of limited food supplies and the sedentary tendencies of the species, although some altitudinal movements may occur at various seasons. We observed birds almost exclusively in pairs or presumed pairs; the only exception occurred in Chile, where no females were observed. However, according to Johnson (1963), female Chilean Torrent Ducks become much less conspicuous in winter than males.

There can be little doubt that Torrent Ducks are monogamous and have relatively permanent pair bonds, which would explain the greatly extended breeding season in northern South America, and might possibly allow for more than one brood per year. This prolonged pair bond would also account for the lack of an 'eclipse' plumage in males. Other South American species which are similar in this latter regard are the Ringed Teal *Callonetta*

leucophrys, Brazilian Teal *Amazonetta brasiliensis* and Chiloe Wigeon *Anas sibilatrix*.

There is little opportunity for contact between Torrent Ducks and other waterfowl under most conditions. We observed at least three pairs of Sharp-winged Teal *Anas flavirostris oxypteryum* in Huarcocondo canyon and the adjacent Urubamba River, occupying relatively calmer stretches of these rivers. In southern Chile there may be occasional contacts with the Bronze-winged Duck *Anas specularis*, although we did not encounter this species.

Sexual behaviour and displays

The published observations of Phillips (1953), Scott (1954) and Johnson (1963) comprise the sum total of previously available information of Torrent Duck displays, and these three accounts show remarkably little similarity. Undoubtedly, the fact that pair bonds are relatively permanent largely accounts for the rarity with which display has been observed in this species, and thus it might be expected that most displays serve in maintaining, rather than establishing, pair bonds. The absence of sympatric, closely related species also reduces the need for elaborate pair-forming displays.

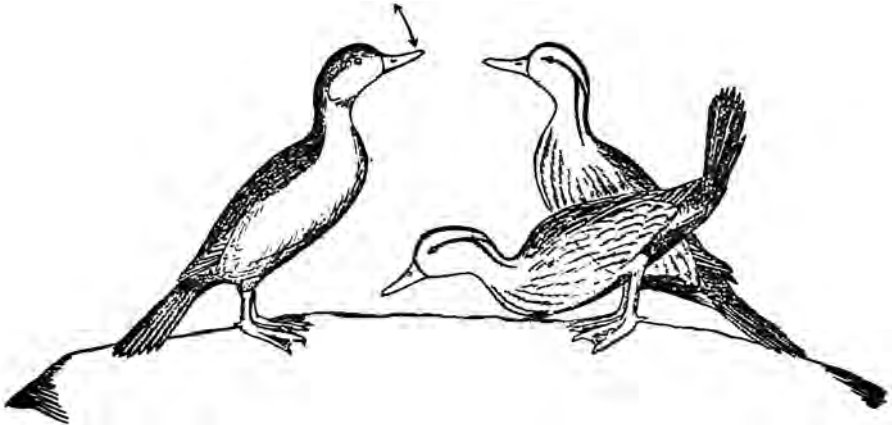
Of the available accounts, Scott's (1954) appears to be the one which most probably represents pair-forming display in Torrent Ducks. His observations on the Bolivian Torrent Duck, made in late March, were of a group of two females and three males. The male displays he describes show no similarities to those of typical dabbling ducks or any other anatids, but such singularity in male pair-forming displays might be expected.

Phillips' (1953) accounts of display in the Peruvian Torrent Duck were obtained during January on the Río Cañete. He describes seeing a male on a rock 'bowing deeply and at the same time pushing the tip of its tail upward to a height exceeding that of its vertically extended head and neck. The entire action appeared to be pendulum-like, with the feet serving as inverted fulcrums. After each such four- or five-second performance, it would resume its normal stance which was marked only by an occasional turn of the head. It would then advance 6 to 12 inches and perform again.' A female was later found to be standing on part of the same large rock.

Wright (1965) has recently reported on some apparently aggressive behaviour he observed in Peruvian Torrent Ducks. He describes two drakes facing one another in a stiffly upright posture, with the body, neck and head all held nearly vertically.

While in this upright posture the males rhythmically bobbed their heads and remained about half a meter apart, in the presence of a single female. One male finally flew away, while the other remained with the female.

My own observations of display were made on the Colombian and Chilean races, and are remarkably similar to those of Phillips. On 8th July on the Río Grande, we watched a pair of Torrent Ducks foraging some 100 yards away. The male soon climbed a large rounded rock, and was shortly joined by the female who stood within 2 feet of him and facing him. She stood quite erect, with her tail propped on the rock, and began to perform rapid vertical bill movements toward him. The male, also standing erect and facing the female, suddenly began a series of increasingly strong downward and forward thrusts with his head, each one more pronounced than the one before, until his bill nearly touched the rock, and with each thrust raising his hindquarters and cocking his tail (see accompanying sketch). After



about six of these fairly rapid, teeter-totter movements the bird assumed a normal posture, appeared to shake his wings, and repeated the sequence. At least four such sequences were performed in a half minute or less. The female responded to the male with much less conspicuous vertical head movements. Both birds then jumped into the water, swam downstream through several series of rapids, and resumed foraging. A few days later a less elaborate version of the same display was observed in another pair. In this instance as a male approached a resting female on a large rock, he made several 'bowing' movements without cocking the tail, then sat down beside her and tucked his bill under the scapulars.

On 19th August, on the Río Petrohué in Chile, I observed what clearly was the same display. In this case a male performed the display apparently to another male which had just flown off the rock. In this instance the male preceded the display by standing very erect and nearly motionless for several seconds, and followed the display with the same rapid wing-shaking movement that was observed in the Colombian race. In both instances the distances were too great to photograph the activity or to determine whether any calls were associated with it. It is significant, however, that the same display should occur in the three populations which represent the most morphologically distinctive forms, indicating that the taxonomic interpretation of a single species of *Merganetta* is a reasonable one.

Although no female was definitely present in the last encounter mentioned, I believe that this is basically a pair-maintaining display, and thus is probably a basic and important display in the species. It is similar in form to the mutual

displays of such perching ducks genera as *Cairina* and *Pteronetta*, although in these forms there is no tail-cocking associated with the head-thrusting movements (Johnsgard, 1965). In these species the display occurs in 'triumph ceremony' situations as well as during aggressive encounters.

Of all aspects of behaviour, none is more uniform within taxonomic groups and more indicative of evolutionary relationships than that associated with copulation. Although I did not witness such behaviour, a detailed account has been provided by Johnson (1963) for the Chilean Torrent Duck. Precopulatory behaviour consisted of the two birds swimming round each other, making repeated bill-snapping and thrusting movements of the head, as if

catching flying insects, and mutually rising in the water in a grebe-like manner. Similar mutual thrusting movements occur during precopulatory display in some perching ducks (*Aix galericulata* in particular), but the grebe-like posturing appears to be unique among the Anatidae.

Evolutionary relationships and taxonomic conclusions

It appears that Torrent Ducks have little or nothing in common with typical dabbling ducks in their sexual behaviour patterns, and may more closely approach the perching ducks in this regard. Some aspects of their general behaviour, such as their hole-nesting, apparently reduced female vocalizations, and obvious climbing and perching abilities might also suggest affinities with the perching ducks, but the possibilities of evolutionary convergence must be carefully considered here.

Niethammer's (1952) conclusion that the sternum and trachea of *Merganetta* indicate dabbling duck affinities appears to be an over-simplification, since Woolfenden (1961) reports numerous unique skeletal features of the genus which are not suggestive of this relationship. The tracheal bulla has the same general configuration as that found in the dabbling ducks, perching ducks, and shelducks, but it is no more similar to that of *Anas* than, for example, is that of *Pteronetta hartlaubii*.

If the distinct morphological similarities between Torrent Ducks and Salvadori's Ducks are simply the result of convergence, then inclusion of *Merganetta* in the tribe Anatini is certainly not warranted. Unless a separate tribe Merganettini is

recognized I would favour including *Merganetta* in the perching duck tribe Cairinini.

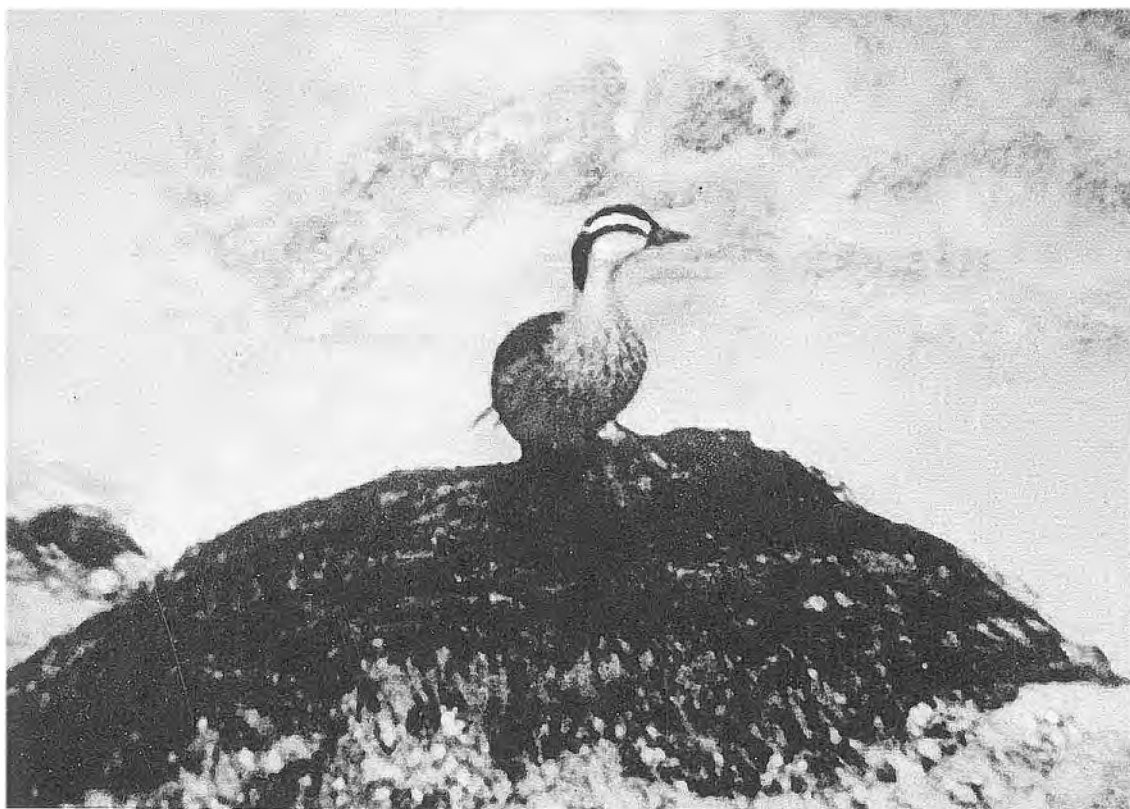
The fact that at least the Chilean, Peruvian and Colombian forms of Torrent Ducks possess identical head-thrusting and tail-cocking displays may be regarded as evidence supporting the view that only a single species of *Merganetta* should be recognised. Further, because of the unusually great male plumage variation occurring in Peru, Bolivia and northern Argentina, I believe that the races *turneri*, *garleppi* and *berlepschi* should not be recognised, and that the entire population from northern Peru to the Tucumán area of Argentina should be regarded as *M. a. leucogenis* until a more thorough study of these regions can be made. This procedure would also avoid the present inexplicable situation of four alternately light-bodied and dark-bodied races geographically replacing one another in a north-south direction.

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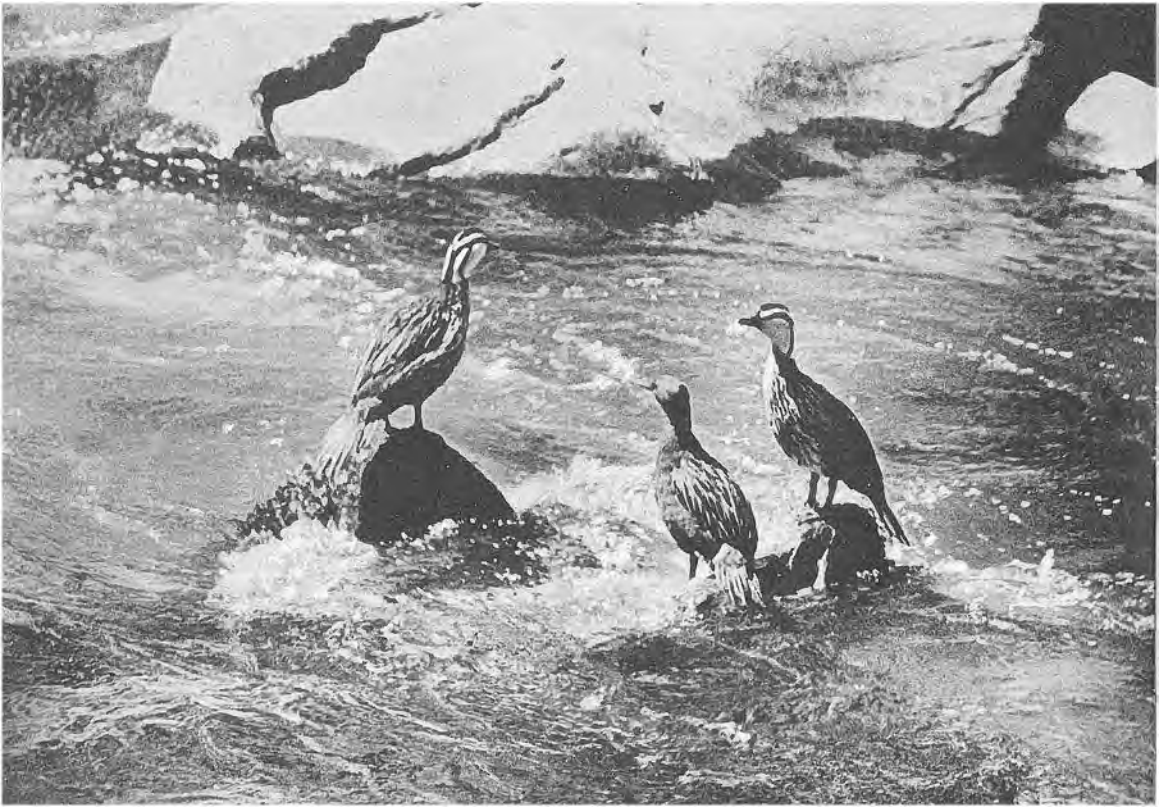
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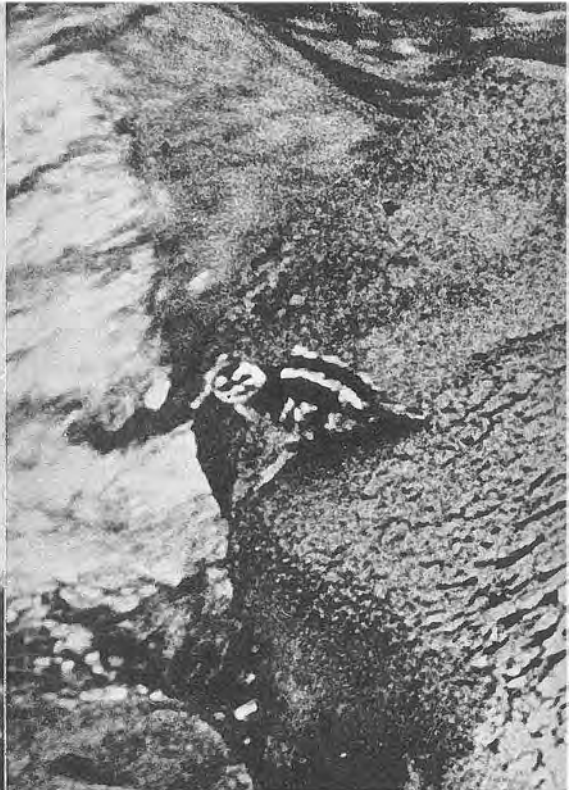
TORRENT DUCKS *Merganetta armata* (See pages 66 to 74). With the exception of the upper photograph on the next page, taken by and reproduced with the permission of H. Luthi, the photographs in this section were taken by PAUL A. JOHNSGARD. Their poor technical quality is regretted.

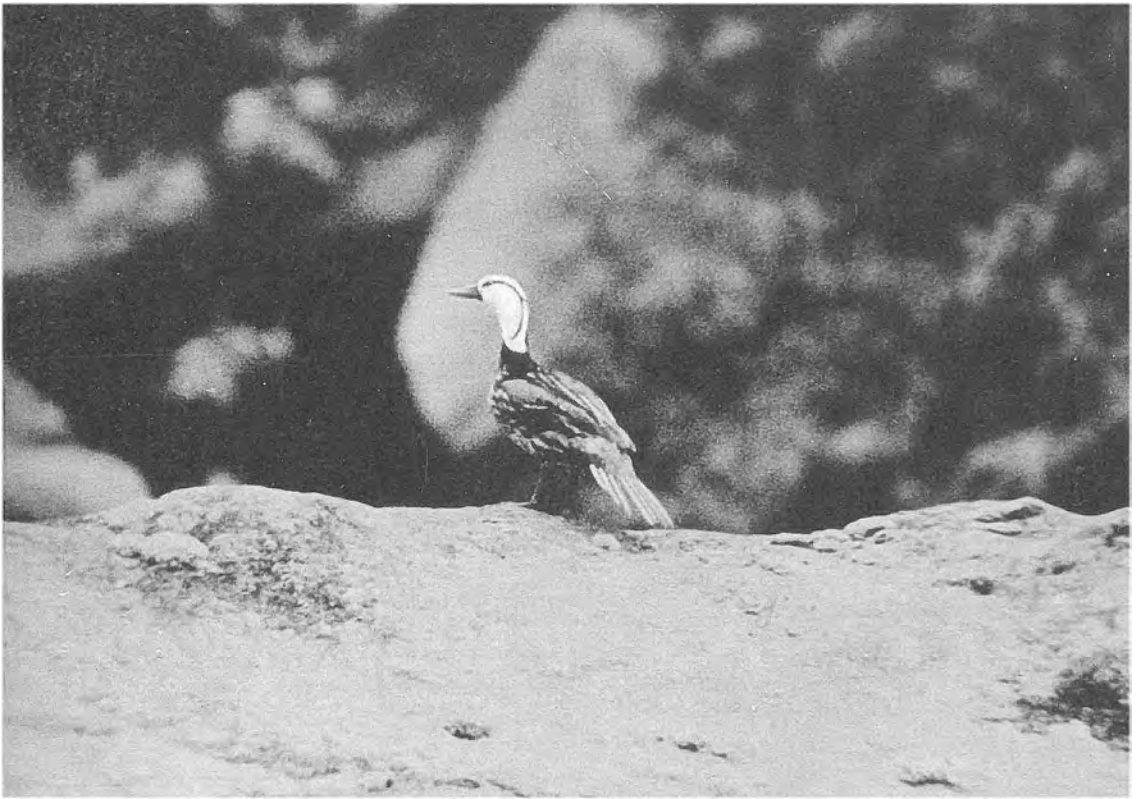
(Above) 31 male and (below) 32 female Colombian Torrent Ducks, Rio Chisbar, Popayán.



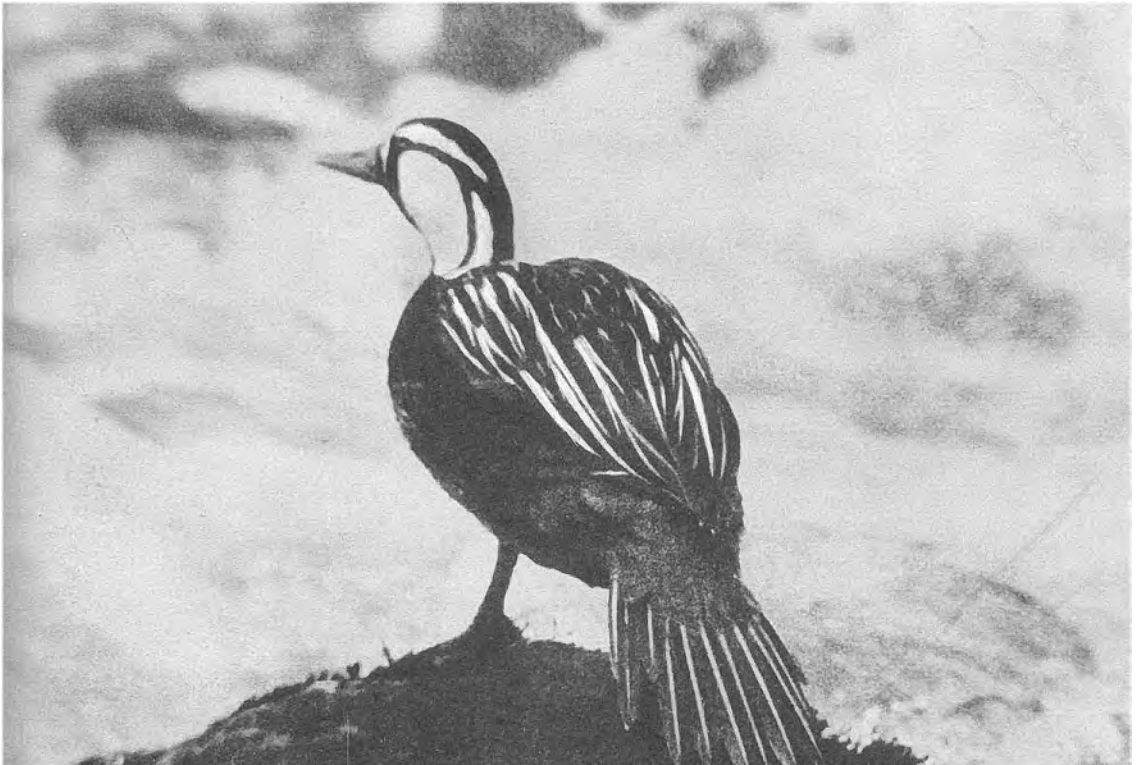


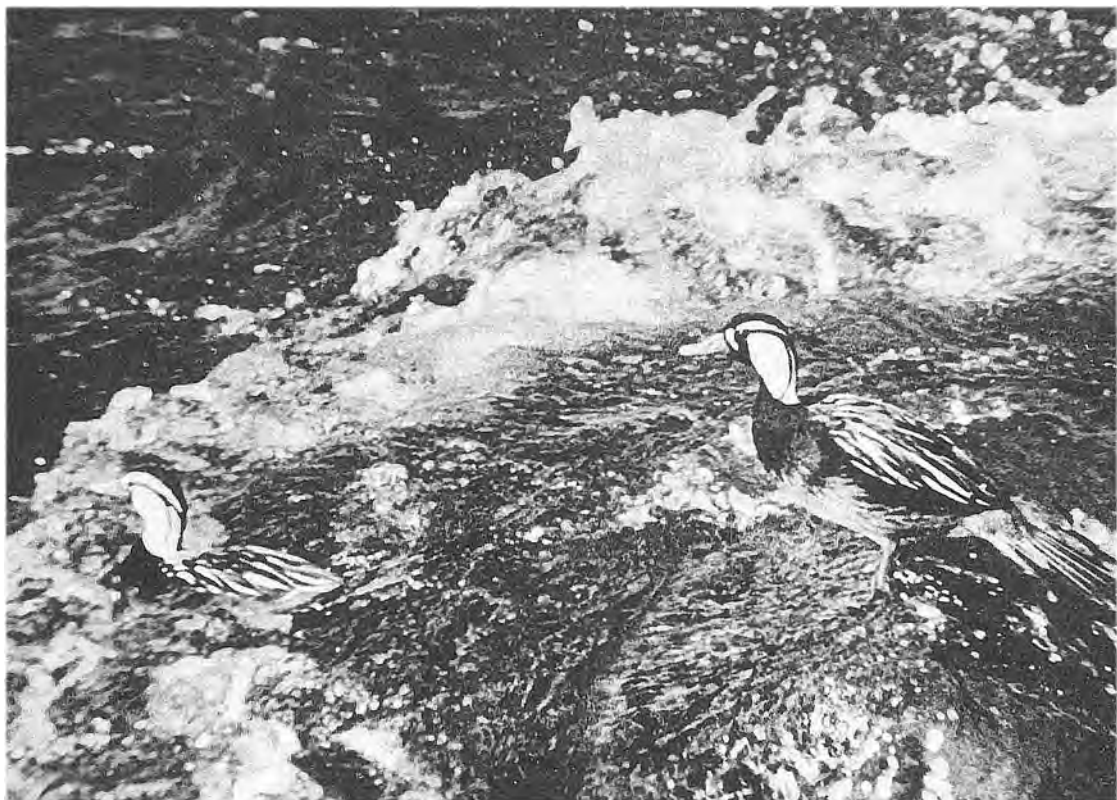
(Above) 33. Two male and a female Peruvian Torrent Duck, Rio Lurin. (Below) Turner's Torrent Duck, Huarcoondo Canyon. (Left) 34. A light-coloured male. (Right) 35. A downy young.





(Above) 36. Male Bolivian Torrent Duck, Rio Zongo. (Below) 37. Male Chilean Torrent Duck, about to dive, Rio Petrohue.





38, 39. Chilean Torrent Ducks.

