Ecology and behaviour of steamer ducks[1]

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Introduction

Steamer ducks (genus *Tachyeres*) are the largest and probably the most specialized diving ducks of the world, forming a Southern Hemisphere ecological equivalent of northern eiders (especially the genus *Somateria*). Steamer ducks are dominantly slate-grey in colour with white wing specula, prominent orange wing spurs and bills that differ in colour by species and sex. Ruggedly-built, they are well adapted to open waters of the Magellanic coastline or large, windswept lakes of Patagonia. The massive bill with reduced lamellae and heavy nail is well designed for grabbing and crushing large invertebrates taken on bottom substrates.

Few groups of ducks have stimulated more published controversy over their classification. Originally described as two species, one flying and one flightless, they were so similar that some workers believed that only one species existed and that young birds could fly, whereas older, heavier birds were flightless (Cunningham 1871). Numerous papers documented the existence of two species: Abbott 1861; Oustalet 1891; Blaauw 1916; and others. The most conclusive data were presented by Percy Reynolds of Estancia Viamonte in Tierra del Fuego (in Lowe 1934) who also pointed out that Falkland Island and Magellanic flightless forms might be subspecifically different. Murphy's (1936) thorough analysis resulted in acceptance of those conclusions on the two species and the addition of a third full species, the Falkland Island form. This classification has been accepted to-date:

Flying Steamer Duck *Tachyeres patachonicus* (King) 1828.
Patagonia, Tierra del Fuego and the Falkland Islands.
Falkland Flightless Steamer Duck *T. brachypterus* (Latham) 1790.
Falkland Islands.
Magellanic Flightless Steamer Duck *T. pteneres* (Forster) 1844.
Coastal Chile and Tierra del Fuego.

Whereas steamer ducks earlier had been considered relatives of northern diving ducks, Delacour and Mayr (1945) placed them with sheld-geese in the tribe Tadornini because of similarities of downy young, wing speculum, aggressive behaviour, wing spurs and permanent pair bonds. Johnsgard (1965) shifted the steamer ducks to a separate tribe, Tachyerini, on the basis of supporting work and recommendations by Boetticher (1952) and Moynihan (1958). This taxonomic arrangement is a convenience, but the systematic position of steamer ducks in relation to other tribes remains uncertain.

In spite of excellent summaries of general morphological features by previously cited authors, considerable confusion remains over identification, and range maps reflect this uncertainty. Remarkably little has been published on the behaviour and ecology of this group. Observations reported here are not the result of an intensive study of the three forms, but are derived from studies of the waterfowl faunas of the Falkland Islands (Weller 1972) and Tierra del Fuego (Weller 1975a). These observations were made during research funded by NSF Grant GV-21491 to Iowa State University and completed under NSF Grant OPP 76-20058 to the University of Minnesota. I am indebted to Maurice Rumboll, Robert Howard and Doris Weller who assisted materially in some phase of the project, and to many landowners and government officials in the Falkland Islands and Tierra del Fuego.

Observation sites and methods

Both Falkland Flightless Steamer Ducks and Flying Steamer Ducks were observed at several areas of the East and West Falkland Islands; Flying Steamer Ducks and the Magellanic Flightless Steamer Ducks were observed at Estancia Harberton, Isla Grande, Tierra del Fuego; and Flying Steamer Ducks also were observed in the lakes and along the coast of eastern Isla Grande near Estancia Viamonte where Reynolds (in Lowe 1934) made his original observations. My observations were in midsummer during the major hatching and brood-rearing period. Only three nests of the flightless forms were found; two in the Falkland Islands and one in Tierra del Fuego. Steamer duck broods were recorded on maps by habitat type (e.g. type of wetland or coastal features) in relation to activities such as feeding or loafing, so that

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relative uses of various habitats by broods were quantitated.

Behavioural observations were facilitated by the fact that steamer ducks are not hunted in either area, and flightless forms are relatively unwary and easily observed. Flying Steamer Ducks are more secretive, especially with broods, but this may be a product of their habitat selection and their relatively greater ease of movement. Whenever possible, observations and photographs were made of aggressive and parental behaviour, and vocalizations were recorded.

Distribution and identifying features (Figure 1 and Table 1)

The Flying Steamer Duck ranges from about Concepcion, Chile (Johnson 1965) and the Valdez Peninsula (Jehl, Rumboll and Winter 1973) and Punto Tombo, (Boswall and Prytherch 1972) areas of Argentina southward through Patagonia, Tierra del Fuego and the Falkland Islands without reported variation. The two flightless steamer ducks differ both in size and colouration: The Magellanic Flightless Steamer Duck occurs along all the west coast of Chile from Chiloe Island south to Cape Horn and Staten Island (Johnson 1965), but it is absent from the east coast of Tierra del Fuego (Reynolds in Lowe 1934). Olrog (1968) indicated that it occurs on the east coast of Patagonia in winter, but this needs documentation.

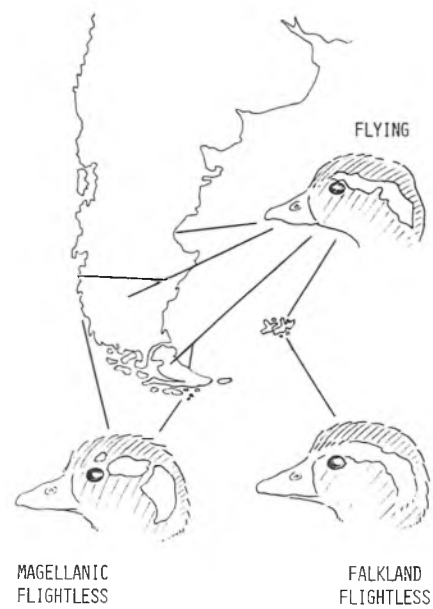

Figure 1. Distribution of steamer ducks and the head patterns of the downy young. The Flying Steamer Duck is widespread on inland lakes and certain coastal waters throughout the Magellanic Region and the Falkland Islands. The Magellanic Flightless Steamer Duck is found mainly on southern and western coasts of Patagonia, whereas the Falkland Flightless Steamer Duck is restricted to those islands.

Table 1. Some characteristic of adult steamer ducks helpful in their identification in the field. All have black nails and light eyerings.

		Flying S.D.	F.I. Flightless S.D.	Magellanic Flightless S.D.
Maxilla				
	♂	Yellow-orange base grading abruptly to olive-grey side at level of the nostrils.	Orange base grading into lighter flesh colored tip.	Completely orange bill, sometimes darker at base.
	♀	Olive-grey with light yellowish base and. culmen.	Olive-grey with yellow base and culmen.	Uniformly orange bill.
Head				
	♂	Whitish; younger males with greyish or brownish face; white eyestripe.	Whitish; younger males with greyish or brownish face; white eyestripe.	Uniform grey; whitish crown in older males.
	♀	Reddish brown face with grey crown and white eyestripe curving down behind eye	Reddish brown face with grey crown and white eyestripe.	Uniform grey; eyeline sometimes apparent.
Neck and body				
	♂ & ♀	Neck grey contrasting with darker grey-brown body. Grey feathers edged with reddish brown.	Neck grey contrasting with darker grey-brown body. Grey feathers edged with reddish brown.	Neck light grey with body slightly darker grey; body feathers light grey, edged with dark grey.

Adults differ in bill, head and body colouration (Table 1), but also in general body form: Flying Steamer Ducks are not only smaller but also less massive in configuration (especially neck, head and bill) and have a rounded back profile resulting from the proportionately larger wings. Preflight flapping is common in the flying species, whereas I have not noticed it in flightless forms. The white wing speculum of the Flying Steamer Duck is said to be longer and more conspicuous (Murphy 1936).

Although there is sexual dimorphism in both body size (Table 2) and voice as discussed later, sexual dichromatism is reduced in comparison with that of most northern Anatinae. The Magellanic Flightless Steamer Duck has almost no dichromatism, and adults are slate grey with slightly lighter necks and head. In Flying Steamer Ducks and Falkland Flightless Steamer Ducks, mature males are white-headed, whereas heads of females are vinous-brown. Thus, there is little chance of confusing adults of the two flightless forms should they ever be found sympatically, or adult Magellanic Flightless Steamer Ducks and Flying Steamer Ducks. Flying Steamer Ducks and Falkland Flightless Steamer Ducks can be difficult to distinguish. Confusion is even greater in yearlings where head colour even of males is female-like and bill colour also is more similar. Field identification then must be based on bill shape and colour and on body form. The hesitancy of even Flying Steamer Ducks to fly adds to the confusion.

Downy young Flying Steamer Ducks (Figure 1) have a white supraorbital line like that of the Falkland Flightless Steamer Duck, but it tends to be more interrupted behind the eye, and the forehead, supraorbital area and chest are darker grey. Magellanic Flightless Steamer Ducks lack a continuous line but have one small supraorbital and two large white post-orbital spots. Young with two spots are illustrated in Lowe (1934), Murphy (1936) and Delacour (1954), but P. Scott correctly illustrated the three spots in Delacour (1964). There is an excellent photograph of the first captive-reared Magellanic Flightless Steamer Ducks in Griswold (1968). Lowe (1934) pointed out that the nail on the bill of downy Flying Steamer Ducks is horn coloured while that of Magellanic Flightless Steamer Ducks is black, but this difference is only obvious in very young specimens and may not be constant. The nail also is smaller in Flying Steamer Ducks.

Data available on weights of adults are shown in Table 2. Because of the variation in presentation of data by different authors, only estimated means can be calculated; these range from 2441 g (5.4 lb) to 6039 g (13·3 lb). The flying form is smallest, the Falkland Flightless Steamer duck is intermediate, and the Magellanic flightless form is the largest. Weights of females of the larger species overlap with the weights of males of smaller species (Figure 2), but if the sex is known, dimorphism in weights is so great within species that there is no overlap between sexes in the recorded samples (Figure 2 and Table

Table 2. Means and ranges of weights reported for steamer ducks.

	Flying S.D.		Falkland Flightless S.D.			Magellanic Flightless S.D.		
Male								
No.	M.	Rg.	No.	M.	Rg.	No.	M.	Rg.
5	3073	2892–3175[1]	3	4350	4200–4650[2]	2	6039	5897–6180[1]
1	3190[3]		2	4312	4256–4368[5]			
2	3033	2891–3175[4]	—	—	—			
—	—	—	5	4334*	4200–4650			
8	3078*	2891–3190						
Female								
6	2616	2438–2835[1]	3	3393	3100–3580[2]	4	4111	3629–4763[1]
1	1665[2]		1	3360[5]				
2	2195	2130–2260[3]	—	—	—			
2	2552	2438–2665[4]	4	3383*	3100–3580			
—	—	—						
11	2441*	1665–2835						

1. Murphy (1936). 2. Weller (unpublished). 3. Zapata (1967). 4. Reynolds in Humphrey *et al.* (1970). 5. Pettingill (1965).
*Estimated mean

2). Sexual dimorphism in weights is greatest in the Magellanic form where females averaged about 68% of the mean of males, whereas Falkland Flightless Steamer Ducks females are 78% and Flying Steamer Ducks are 79% of the males' mean weights.

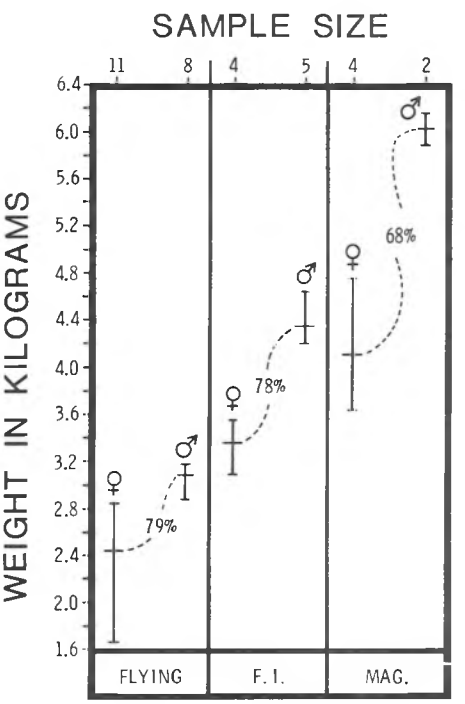

Figure 2. Means and ranges of weights for three steamer ducks, and per cent difference between sexes within taxa.

Patterns of habitat use

Because of their mobility, only Flying Steamer Ducks can use inland waters. Flightless forms normally are restricted to seashores, although they occasionally walk short distances overland to freshwater lakes. Both taxa drink fresh water when available.

Observations on habitat use by pairs with broods is presented in Table 3. I have not surveyed all types of habitat, and it is difficult to equate conditions in diverse habitats such as lakes and coastal waters, but the pattern is obvious: Flying Steamer Ducks favour freshwater areas for breeding territories whereas Flightless Steamer Ducks use marine waters. However, Flying Steamer Ducks regularly use estuaries along the Beagle Channel for rearing young. Reynolds (in Lowe 1934) reported that broods are common in marine situations, but he did not clarify whether they were most often in estuaries. Adults often use protected marine channels and bays for feeding (Weller 1975a). The Flying Steamer Duck is the only species occurring along the east coast of Tierra del Fuego where extreme tides would strand flightless adults or young and modify available foods. Brood rearing has not been documented in such situations, but broods are reared on nearby lakes.

Brood-rearing areas also are significant in denoting possible food types. Flightless Steamer Ducks of both forms tend to use silt-free shorelines of gravel or small stones. Such areas are rich in small isopods and gammarids used at least by young Falkland Flightless Steamer Ducks. Most Flying Steamer Duck broods that I have observed (Table 3) have been in lakes with clay, silt or fine gravel substrate holding populations of

Table 3. Habitat distribution of steamer ducks pairs with broods, Falkland Islands (1970–71) and Tierra del Fuego (1972). Percentage in parentheses.

	Flying S.D.			Flightless S.D.	
	F.I.	T. del F.	Total	F.I.	Mag.
Fresh water ponds—					
Bog	1 (14)	0	1 (6)	0	0
Clay-gravel	4 (57)	4 (40)	8 (47)	0	0
Streams	0	0	0	0	0
Estuary	2 (29)	5 (50)	7 (41)	0	0
Marine coastal—					
Silt-sand	0	0	0	1 (4)	0
Gravel	0	1 (10)	1 (6)	23 (96)	9 (100)
Boulder	0	0	0	0	0
Rock	0	0	0	0	0
Cliff	0	0	0	0	0
	7 (100)	10 (100)	17 (100)	24 (100)	9 (100)

snails or fingernail clams. Others have been in or near silting estuaries. One pond on the Falkland Islands, where Flying Steamer Ducks were reared in two consecutive years, held only rich populations of small gammarids possibly produced by enrichment from a colony of Magellanic Penguins *Spheniscus magellanicus*.

Food utilization of adults is less closely related to habitat types. Johnson (1965) and Humphrey et al. (1970) presented the rather sparse data on food habits of Magellanic Flightless Steamer Ducks, which eat at least mussels, clams and crabs. Prey items of Falkland Flightless Steamer Ducks ranged in size from isopods, gammarids and kelp snails of about 5 mm to marine crayfish *Munida* sp. having minimal dimensions of 35 mm (Weller 1972). The use of deep and open waters, and benthic rather than free-swimming organisms, seems typical of both flightless forms. Foods of Flying Steamer Ducks need detailed study in freshwater areas, but they also feed by diving.

Because Flightless Steamer Ducks walk and climb awkwardly, another habitat feature of possible significance in determining distributions of pairs is shoreline topography. Although females will nest on rocky outcrops, pairs tend to frequent shorelines with easy access to the uplands. Access for broods going to the sea may be even more significant. In the Falkland Islands, pairs that are regularly seen in areas lacking such access seem to be less mature than those that hold successful breeding territories.

Behaviour and social structure

Flightless Steamer Ducks are well known for their strong and seemingly permanent pair bonds and for a territory defended most if not all year. During the breeding season, pairs do not leave their territories for long. Males defend the area when the female is on the nest, and females with broods later appear in places where lone males earlier defended territories. Males do not always accompany broods, but they are rarely far away.

Large flocks of nonbreeding birds are common in areas not used by breeding pairs. These birds enter the wing moult earlier than do breeding birds. One flock of Falkland Flightless Steamer Ducks numbered 192 individuals. On the basis of plumage colour and behaviour of Falkland Island birds, I suspect that there are at least four age classes: yearlings in large flocks, birds two years or older in smaller groups or roving pairs, still older nonbreeding birds with some white on the head of males resident on suboptimal territories and white-headed males that are successful breeders. I have too few observations to judge whether this pattern also is true of Flying Steamer Ducks, but variation in head and bill colour of males suggests this possibility. The precise ages of these classes need to be established by study of marked birds because the social structure seems to be one of long-lived and permanently paired birds restricted in density by the availability of suitable territories.

Territory

The territorial spacing of pairs of Falkland Flightless Steamer Ducks to specific areas has been well described by several workers (Cobb 1933; Pettingill 1965). In Port Stanley, Falkland Islands, virtually all townspeople know the 'Government House Pair,' or the 'East Jetty Pair.' If these pairs are not on shore in the territory, they are loafing or feeding in view of the shore and return quickly when any disturbance or challenge occurs. Regular surveys of several kilometers of uninhabited and virtually undisturbed shoreline near Fitzroy revealed the same pattern. Pettingill (1965) noted a pair of steamer ducks every 300 yards (= 274 m) except for a site used by nonbreeders. I suspect that topographic features such as coves and bays are vital in separating territories, but that breeding pairs will be spaced along uninterrupted shorelines at perhaps greater distances.

From limited observations, mostly in the Falkland Islands, Flying Steamer Ducks defend whole lakes or portions of large lakes. Young may dabble in the shallows of lakes, but they are active divers, and there is less obvious use of shorelines than occurs in the flightless forms.

Because inland lakes often freeze in Tierra del Fuego and Patagonia, Flying Steamer Ducks must either move to the sea in winter or shift to ice-free lakes. Flightless forms spend the entire year along one shoreline, which seems to be the focal point of their linear territory; they spend considerable time loafing there. The amount of adjacent water defended is uncertain. Food size and gathering efficiency may be factors in the high percentage of time spent in loafing; i.e., flightless forms take large food items in brief but intense feeding periods, whereas Flying Steamer Ducks seem to feed more continuously on smaller items.

Ian Strange, a competent naturalist who resides in Port Stanley, Falkland Islands, told me of one pair of Flightless Steamer

Ducks in front of his house that successfully defended a shoreline against intrusions of a flock of about 340 full-grown steamer ducks in the post-rearing period in April. Although many individuals in this flock may have been immatures of that breeding period, it is obvious that such a flock also needs a loafing site, and the defensive pressure and energy demand on such a pair must be very great.

Linearity of territory also is conspicuous because of the use of gravel beds for feeding areas by broods. Such territorial defense seems to insure nest sites, resting sites and food for both adults and young. Most workers agree that the territory is defended all year in the flightless marine species, which suggests that release of such a territory would involve greater fighting and danger of losing the territory than holding it year-round.

An issue of evolutionary significance is whether a lone female with a brood can maintain a territory without a male. In repeated surveys of the broods of the Fitzroy area, several females were seen without males. Whether they were truly alone is uncertain. Residents of Port Stanley refer to the occasional situation of a hen that loses a newly hatched brood when, for some reason, the male is not present. It seems logical that the male is vital to long-term maintenance of a territory, that his presence enhances breeding success and that the territory is important in providing food resources for young and adults.

Vocalizations

Male Falkland Flightless Steamer Ducks give a clear, high-pitched, rasping whistle that carries long distances and may be syllabylized as '*pe-ough* or '*pe-e-ough*'. Its initiation is sharp and, although its duration may vary, it rarely exceeds 2 seconds. It is used in alertness and in post attack. The same call in Magellanic Flightless Steamer Ducks tends to be more slurred, seems also to more regularly have the extra syllable, but is the same in form and function: '*pse-e-ough*' or '*pse-e-e-ough*'. The call of the Flying Steamer Duck male is similar but higher pitched. Males of all three taxa give intense, high-pitched calls resulting from a series of short notes given in rapid sequence '*pew-pew-pew*'. When confronted on shore with a brood, female Falkland Flightless Steamer Ducks hiss aggressively while exposing their wing spurs. Major calls of females are croaking grunts of diverse forms. A deep, vibrant croaking '*gurr-r-r*' is given slowly as a warning to intruders. A grunting '*gurrk*' is given singly with the stretch posture (Figure 2), or in a series '*gurrk-gurrk-gurrk*'. Still shorter notes rapidly given in series may be syllabilized '*groink-groink-groink*'. There is concurrently a clicking sound which I believe is produced by the female.

In both flightless forms, territorial defense involves the whistling '*pe-ough*' by the male. The '*gurrk*' call of the female normally is synchronized between the whistle note of the male. When the male intensifies its calling to the higher, pitched '*pew-pew-pew*,' the female may duet with the '*goink-goink-goink*' call. Mutual vocalization is characteristic of the aggressive behavior of sheldgeese and may provide further evidence of relationship to the Tadornini as Delacour (1954) suggested.

Aggressive behaviour

Aggressive behaviour of all species is similar, and detailed photographic analyses would be required to demonstrate differences. In Falkland Island Flightless Steamer Ducks, pairs or lone males defend territories by patrolling and calling. Pairs in adjacent territories may intensify calling, make pseudoattacks and then return to their territories. Duetting by pairs is common in such circumstances. The motivation to attack may occur when pairs are several hundred meters apart, and the attacking male may leave the female behind. However, she may continue more slowly and eventually may fight with the opposing female. A victorious male returning to hens still in battle may aid his female. Young may be abandoned during these battles, at least when they are old enough to feed independently.

The opponent-oriented actions form a continuous sequence that Moynihan (1958) divided into displays in Flying Steamer Ducks. The total action involves varying degrees ranging from *threat* to *attack* (or aggressive steaming). The major display is given with the *pe-ough* call before or after the attack or between charges and is called the *short-high-and-broad* by Moynihan (1958), but perhaps is better described by the term used for sheldgeese by Johnsgard (1965) as *high-and-erect*. This posture involves head up and back, tail erect and spread, slightly opened wings showing the specula and wing spurs, and with the concurrent vocalization, *pe-ough*. The display resembles the *bubbling display* of the North American Ruddy Duck *Oxyura jamiacensis* except that the wings are spread. Bill shakes are common. Seemingly dependent on intensity, the call may become the rapid series *pew-pew-pew* eventually

settling into the slower and the lower pitch and *pe-ough*.

Calling by opponents induces an aggressive posture with the head slightly forward, tail low, and involving such rapid swimming that rippling sounds may be a significant part of the display. A *threat* posture involves the head outstretched over the water while swimming or walking. This may grade via a further lowering of the head into a *sneak*, with the bill and neck on the water. Full *attack* involves head forward, bill open, flapping of wings on the water and paddling toward the opponent. Perhaps in situations of uncertainty of response or change of tendencies, males may stop, give the *short-high-and-broad* with calls and then continue the *attack*. However, the *short-high-and-broad* display often is given after the attacker turns toward his territory. The resultant white tail flash and white wing speculum may mark the territorial boundary.

In the *submerged sneak*, the bird disappears under water at full speed, and may swim out of sight for 30 to 100 m. The opponent usually is *alert* and nervously swimming in circles on the surface, or it also may dive. When contact is made, usually from under water, violent battles may result which last up to 20 minutes. Cawkell and Hamilton (1961) reported that males have been killed in such battles; Reynolds (in Lowe 1934) reported Indians catching fighting male steamer ducks by hand; Pettingill (1965) noted that many males have battle scars on the head.

In situations of less intense territorial border patrolling, males shift toward or away from their territories each with opposing postures. The silent attacker may give the *threat* or *sneak*, while the slowly retreating bird gives the *short-high-and-broad* with white undertail coverts flashing. If the charging bird turns and assumes the *short-high-and-broad* display, the retreating bird may turn and give the swimming *threat*.

In addition to overt attack, females regularly give a bill-up posture called the *stretch* (Moynihan, 1958), which included the *gurrk* call. He also reported *false drinking*, which is similar to the *stretch* but involves dipping of the bill in the water first; it also is given by male Flying Steamer Ducks. The *stretch* and associated call are given in disturbance, alertness or conflict and may have the same function as inciting in dabbling ducks. It also may be given as a triumph display after battle when the male gives the *short-high-and-broad* and associated call. The *stretch* and call also may be given as the female leads the brood from potential danger. Its use seems similar in both Falkland Island and Magellanic Flightless Steamer Ducks. The tail is slightly raised during the *stretch*.

Experimental playback of recorded calls

That the major territorial call is the whistled *pe-ough*, and that males react violently to intruders in their territories giving this call, was demonstrated by playback of recorded calls—even calls of the defending male itself. Territorial male Falkland Flightless Steamer Ducks *threatened* and attacked from 150 m across open water and toward the speaker. Males even charged on shore with head back, spread wings, tail up as in the *short-high-and-broad* display. The graded series of displays did not involve *submerged sneak* as the bird was moving toward shallow water along shore, but it reflected the continuous nature of aggressive response from *short-high-and-broad* display, and *swimming threat* to *attack*. In one case, the pair *attacked* side by side, and stopped and duetted between charges. Males also responded to playback call at night, and one swam under a jetty on which we were playing calls.

Interspecific aggression

The habitat distribution of Falkland Island Flightless Steamer Ducks and Flying Steamer Ducks reduces overlap and potential interaction. But in Tierra del Fuego, use of adjacent habitats seems more common, and Reynolds (in Lowe 1934) states that Flightless Steamer Ducks chase the smaller Flying Steamer Ducks. Near Estancia Harberton I saw three situations in which the two species fed close together, but none involved pairs with broods. However, avoidance of Flightless Steamer Ducks by Flying Steamer Ducks suggested that the smaller species is dominated by the larger.

Brood behaviour and parental care

Whereas males of most Northern Hemisphere ducks desert their females Southern Hemisphere males often assist in care of broods. Figures on size of steamer duck broods are given in Table 4, and data on brood care are shown in Table 5. Of the three species, the loyalty of male Flying Steamer Ducks to the brood seems weakest. This may be expected because adults are more mobile and the habitats are less stable. Nevertheless, 72% of the broods were attended by males. In most cases, males played an important role in defense of the brood. Although males often

Table 4. Sizes of broods of all ages of steamer ducks observed in the Falkland Islands (1971–1972) and Tierra del Fuego (1972–1973).

	Flying S.D.			Mag. Flightless S.D.			F.I. Flightless S.D.		
	No.	Rg.	M ± S.D.	No.	Rg.	M ± S.D.	No.	Rg.	M ± S.D.
Falkland Isl.	7	1–6	4·0 ± 2·2	—	—	—	72	1–9	4·4 ± 2·2
T. del Fuego	10	1–6	3·1 ± 2·1	9	1–6	3·7 ± 1·50	—	—	—
TOTAL	17	1–6	3·5 ± 2·2	9	1–6	3·7 ± 1·50	72	1–9	4·4 ± 2·2

Table 5. Brood care by the three steamer ducks based on observations sometimes involving repeated observations of the same broods.

	Flying S.D.		Flightless S.D.			
			Magellanic		Falkland Isl.	
	No.	% attended	No.	% attended	No.	% attended
T. del Fuego	10	80%	9	100%		
Falkland Isl.	15	66%			72	91%
Total	25	72%				

loafed some distance away as the female and brood fed, they charged quickly to the brood when potential predators such as gulls approached.

Discussion

Thoughts on origins

This endemic genus obviously is an ancient one, and even tribal level relationships are uncertain. The Flying Steamer Duck logically represents something similar to an ancestral, flying, freshwater form that successfully adapted to saline waters. Perhaps via isolation during ice ages, the flying lake form was separated in the Patagonian plains from the coastal populations west and south of the heavily glaciated Andes. Large size and flightlessness were suitable adaptations to a benthic diver in cold water restricted by severe climate to a coast where all needs are met in a linear, coastal territory defended all year. The habitat strategy of the flying bird demands mobility, because it often must shift from breeding lakes that become unavailable via winter freezing to estuaries that remain open all year and are rich in foods.

The differentiation of two flightless forms seems logical because of the spatial separation of the Magellanic and Falkland Island regions, but it raises the question of the origin of the latter form. Did flightlessness originate once or twice; i.e., was dispersal to the Falkland Islands via a flying or swimming form? The Falkland Flightless Steamer Duck is more like the presumed ancestral plumage (i.e., more like the flying form) in both downy young and sexually dichromatic adults. Suitable environmental conditions would have influenced the chronology of migration and establishment of either form on the Falkland Islands. The possibility that flightless birds swam to the Falkland Islands seems unlikely. However, during several previous ice ages, sea level changes may well have provided island complexes or shallows whereby movement of flightless ducks from South America to the Falkland Islands may have been an easier trip than it seems now. Crawshay (1907) reported pairs 15 miles (24 km) at sea, so they obviously can move significant distances in open water. Although a benthic feeder, its habit of feeding on kelp snails may have provided a suitable food source when crossing part of the 322 km (200 miles) to the Falkland Islands.

Movement of Flying Steamer Ducks to the Falkland Islands would have been relatively simple. However, I suspect that, although marine conditions long have been present for steamer ducks, suitable freshwater habitats may have only recently evolved. Lakes on the Falkland Islands even now are marginal habitats for Flying Steamer Ducks because of their acidity and relatively low productivity, and Flying Steamer Ducks are the rarest waterfowl (Weller, 1972). These lakes probably lacked suitable food resources under colder, postperiglacial conditions. For example, food resources in lakes in South Georgia, which is in the Antarctic Convergence 1238 km (800 miles) east of the Falkland Islands, would not support large, diving birds (Weller, 1975b). Moreover, the

number of suitable estuaries on the Falkland Islands is limited compared with those in Tierra del Fuego.

The presence of sexual dichromatism in Flying Steamer Ducks may be explained by the fact that they, like northern hemisphere Anatinae, often inhabit lakes that are unavailable in winter because of freezing. This forces seasonal movements and may influence time and duration of courtship and pairing in comparison with seemingly permanent pairs and territories of Magellanic Flightless Steamer Ducks.

Also difficult to explain is the presence of fairly distinct dichromatism in the sedentary Falkland Flightless Steamer Duck. If the speculation on recency of establishment of steamer ducks in the Falkland Islands is true, it would seem possible that the presence of dichromatism is a relatively more primitive character resulting from a flying ancestor. Either there has been little selective pressure for change, or the event has occurred too recently.

Summary

The three steamer ducks (genus *Tachyeres*) range through parts of Patagonia, Tierra del Fuego and the Falkland Islands. Criteria for separating adults of all three taxa are reviewed. The flightless forms feed and rear their young on the seacoast, whereas Flying Steamer Ducks use mainly lakes or estuaries. Their vocalizations and territorial behaviour are similar, and all are very aggressive. Flightless adults seem to maintain permanent territories on marine coastlines while Flying Steamer Ducks often must shift when inland lakes freeze. Whether Flying Steamer Ducks are permanently paired is uncertain, but general observations suggest that permanent pairing is regular among flightless taxa. Males assist in care of the brood, but males of Flying Steamer Ducks are less regular (72% attendance) than are flightless forms (100% in Magellanic and 91% in Falkland Island forms). It is suggested that origin and dispersal of the three taxa were influenced by the limiting environmental conditions of these harsh climatic regimes.

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