Wright (1981: 122) states that "Boreal forest formed a belt perhaps 1000 km broad, starting at or near the [Laurentide] ice front in the north and ending south near a line extending from central Georgia around the southern end of the Appalachian Highlands to Tennessee . . . ." Recovery of remains of predominately boreal small mammals from the lower levels of Cheek Bend Cave and those of four avian species whose present primary northern ranges coincide, coupled with pollen analyses data, suggest that the Nashville Basin was characterized by climatic conditions that included somewhat lower annual mean temperatures than exist today and a climax vegetation dominated by coniferous forest. Although the possibility exists that the former presence of the Hawk Owl, Boreal Owl, Saw-whet Owl, Gray Jay, and Pine Grosbeak at this cave site was the result of southward-wandering vagrants, the small mammal assemblage and the remains of at least two individuals of *A. funereus* and *P. canadensis* suggest a locally established population of these boreal birds during the Wisconsinan.

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Flightlessness in Flying Steamer-Ducks

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Steamer-ducks comprise a single, widely distributed, flying species, *Tachyeres patachonicus* (Falklands and Fuego-Patagonia), and three flightless species, *T. brachypterus* (Falklands), *T. pteneres* (Tierra del Fuego and the southern coast of Chile), and the recently discovered (Humphrey and Thompson 1981) *T. leucocephalus* (coast of Chubut, Argentina). This paper presents data on wing loading and use of flight for escape by Flying Steamer-Ducks and evidence that some individuals are permanently incapable of flight.

Flying Steamer-Ducks occur in freshwater and marine coastal environments in Patagonia, Tierra del Fuego, and the Falkland Islands (Weller 1976, Humphrey and Thompson 1981). They feed on sessile or slow-moving molluscs, crustaceans, and insect larvae, which they often obtain by diving, using hind feet and partly spread wings for propulsion (Murphy 1936: 960; Humphrey and Livezey unpubl. data).

Weller (1976: 47) noted the "hesitancy of . . . Flying Steamer Ducks to fly . . . ." Murphy (1936: 970), writing of Beck's collecting activities, stated that Flying Steamer-Ducks "are capable of getting well into the air within a space of 2 meters, even in a dead calm," and "they rarely dived at the approach of . . . [Beck's] craft, but preferred to take wing. . . . some of them flew heavily, not rising far above the water, while others mounted high into the air and passed quite out of sight." Reynolds (*in* Lowe 1934: 474) wrote that "*Tachyeres patachonicus* is capable of sustained and rapid if somewhat heavy flight. . . . At times *T. patachonicus* may well be taken for a flightless bird, and some of the confusion distinguishing between the two species [*patachonicus* and *pteneres*] is probably due to the unaccountable reluctance to rise so often demonstrated by this species."

During field seasons in 1979 (Humphrey and Max C. Thompson) and 1980–1981 (Humphrey and Livezey), 57 specimens of Flying Steamer-Ducks were collected near Ushuaia, Tierra del Fuego (5–17 November 1979, 24–27 December 1980, 4–6 January 1981), Puerto Deseado, Province of Santa Cruz (10–16 October 1979, 20–26 January 1981), and Puerto Melo,

TABLE 1. Weights, wing areas, and wing loadings of Flying Steamer-Ducks by sex and locality.

Locality and latitude	Sex	Weight (g)			Wing area (cm^2)			Wing loading (g/cm^2)		
		n	Mean	Range	*n*	Mean	Range	*n*	Mean	Range
Puerto Melo, 44°01′	Males	1	2,350	—	1	1,160	—	1	2.03	—
	Females	0	—	—	0	—	—	0	—	—
	Total	1	2,350	—	1	1,160	—	1	2.03	—
Puerto Deseado, 47°46′	Males	16	2,994	2,350–3,350	11	1,307	1,076–1,422	11	2.29	2.03–2.53
	Females	18	2,416	1,950–2,900	14	1,207	1,090–1,290	14	1.95	1.65–2.35
	Total	34	2,688	1,950–3,350	25	1,251	1,076–1,422	25	2.10	1.65–2.53
Ushuaia, 54°48′	Males	10	3,155	2,800–3,480	10	1,272	1,156–1,358	10	2.49	2.21–2.83
	Females	10	2,440	2,150–2,650	8	1,243	1,124–1,369	8	1.98	1.75–2.13
	Total	20	2,798	2,150–3,480	18	1,259	1,124–1,369	18	2.26	1.75–2.83
All localities	Males	27	3,029	2,350–3,480	22	1,284	1,076–1,422	22	2.37	2.03–2.83
	Females	28	2,425	1,950–2,900	22	1,220	1,090–1,369	22	1.96	1.65–2.35
	Total	55	2,722	1,950–3,480	44	1,252	1,076–1,422	44	2.17	1.65–2.83

Province of Chubut (29 September 1979), Argentina. We recorded details of escape behavior while each bird was being pursued during 1980–1981; limited data of the same kind were recorded during 1979. We collected 44 Flying Steamer-Ducks for which wing-loading data could be recorded; for 30 of these, we recorded whether or not they flew, and we have information on wind conditions at the time of collection for 21. Each specimen was weighed within 2 h following collection, and additional data were recorded, including: outline of fully extended wing (Raikow 1973: 297), weight of contents of esophagus and gizzard, sex, gonad measurements, weight of pectoral musculature, and molt. Wing area for each

TABLE 2. Mean weights, wing areas, and wing loadings of 22 species of diving-ducks. Sources: (1) Hartman 1961, (2) Magnan 1912, (3) Magnan 1913, (4) Magnan 1922, (5) Meunier 1951, (6) Müllenhoff 1885, (7) Poole 1938, (8) Raikow 1973.

Species	*n*	Weight (g)	Wing area (cm^2)	Wing loading (g/cm^2)	Source
Aythya affinis	20	615	474	1.30	1, 7, 8
A. collaris	3	757	460	1.65	7
A. ferina	1	842	615	1.37	6
A. fuligula	1	741	474	1.56	6
A. marila	1	675	621	1.09	6
A. nyroca	2	510	577	0.88	3, 6
A. valisineria	1	910	701	1.30	8
Bucephala albeola	6	393	341	1.16	7, 8
B. clangula	5	748	539	1.40	4, 6, 8
Clangula hyemalis	2	980	551	1.78	6, 7
Melanitta fusca	4	1,320	866	1.52	2, 5, 8
M. nigra	1	870	679	1.28	4
M. perspicillata	1	827	649	1.27	8
Lophodytes cucullatus	1	630	401	1.57	Present study
Mergus albellus	1	495	431	1.15	4
M. merganser	1	1,470	853	1.72	4
M. serrator	1	818	589	1.39	4
Oxyura dominica	7	363	352	1.03	1
O. jamaicensis	13	530	331	1.60	7, 8
Somateria fischeri	1	1,457	719	2.03	8
S. mollissima	2	2,056	1,210	1.79	5, 8
S. spectabilis	1	1,700	824	2.06	8

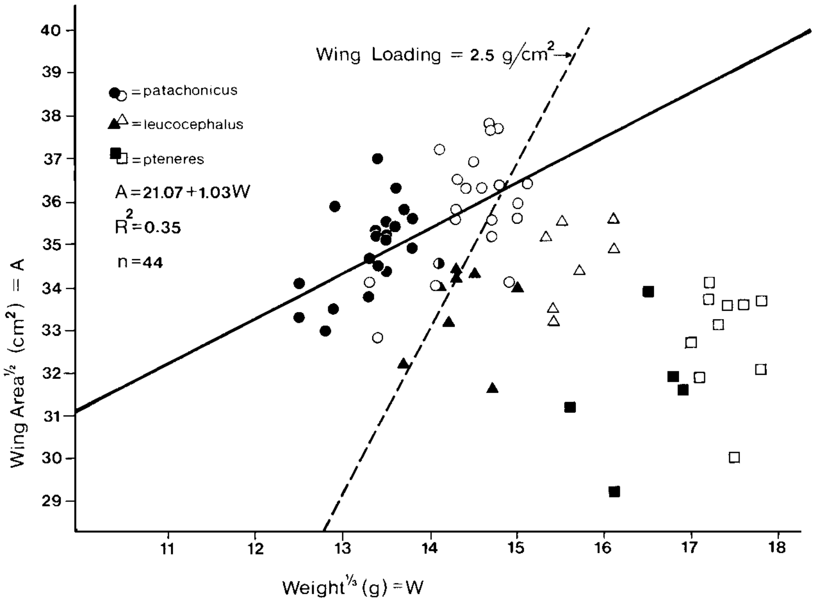

Fig. 1. Regression of cube root of body weight and square root of wing area for 44 Flying Steamer-Ducks. Open symbols represent males, black symbols females. Data for flightless *T. leucocephalus* (15) and *T. pteneres* (15) were not used in calculating the regression equation. Note that, except for four female *leucocephalus*, all points for the two species of flightless steamer-ducks fall to the right of the dashed line representing the threshold of flightlessness and have wing areas below those predicted by the regression equation calculated for *T. patachonicus*.

specimen was measured using a planimeter and doubled to give total wing area. Wing loading in g/cm² was calculated by dividing total weight by total wing area.

Wing loadings of 44 Flying Steamer-Ducks averaged 2.17 g/cm² (Table 1). Based on major reviews of wing loading (Müllenhoff 1885, Banks 1933, Poole 1938, Savile 1957, Hartman 1961, Greenewalt 1962, Raikow 1973), Flying Steamer-Ducks have among the highest wing loadings recorded for flying birds.

The relationship between means of wing area and body weight in 23 species of diving-ducks, including *T. patachonicus* (Tables 1 and 2), is expressed in the power equation:

$$\text{Wing Area} = 7.36\ \text{Weight}^{0.65}\ (R^2 = 0.85,\ n = 23)$$

and thus approximates the expected, wherein the allometric coefficient is 0.67, given that wing area increases as the square and body weight as the cube. The relationship between wing area and body weight for Flying Steamer-Ducks is negatively allometric:

$$\text{Wing Area} = 147.4\ \text{Weight}^{0.27}\ (R^2 = 0.36,\ n = 44).$$

Wing areas of two species of flightless steamer-ducks (*T. pteneres, T. leucocephalus*) are below those expected from the linear regression of the square root of wing area on the cube root of weight calculated for Flying Steamer-Ducks (Fig. 1). In addition, wing loadings of flightless steamer-ducks are for the most part much higher; wing-loading values of heavy male *T. patachonicus* overlapped those of female *T. leucocephalus* with low body weights (Fig. 1).

Weights and wing loadings of Flying Steamer-Ducks differed between sexes and among the three localities of collection (Table 1). Males averaged heavier than females at Puerto Deseado ($t = 6.19$, $P < 0.001$) and Ushuaia ($t = 7.94$, $P < 0.001$). Extreme weights of males and females overlapped at Puerto Deseado but not at Ushuaia (Table 1). Weller (1976: 47) found no overlap in weight between sexes of three species of steamer-ducks. Males also exceeded females in wing area at Puerto Deseado ($t = 2.88$, $P < 0.005$) but not at Ushuaia ($t = 0.87$, $P < 0.20$). Also, male Flying Steamer-Ducks were heavier ($t = 1.75$, $P < 0.05$) at higher-latitude Ushuaia than at Puerto Deseado, in agreement with Bergmann's Rule (James 1970, McNab 1971); females, however, were similar in weight at the two localities ($t = 0.24$, $P > 0.40$).

Of 22 male specimens (not in wing molt) collected in 1979 and 1980–1981, six had wing loadings of 2.5 g/cm² or greater, the limit beyond which Meunier (1951: 430) estimated aerial flight to be impossible. The highest wing loadings of birds known to have flown were 2.25 and 2.43 g/cm^2; both birds were males and were collected on windy days. We collected seven birds, all males, with wing loadings of 2.25 g/cm^2 and greater that swam, steamed, or dived but did not fly when pursued by a noisy motorboat. Two of the birds had slight amounts (34 g, 35 g) of food in esophagus and gizzard and the rest only clean grit (average 15 g, range 9–22 g). Of the latter, two had wing loadings above 2.6 g/cm^2; both had little fat, flightworthy remiges, and pectoral musculature at or near maximum weight (17% of body weight; pers. data). One was collected on a calm day and the other in a strong wind when other steamer-ducks were flying. We believe these birds were incapable of flight.

Assuming the validity of Meunier's (1951) flightlessness threshold of 2.5 g/cm^2, 50% of the nonmolting males we collected near Ushuaia were flightless, as were 8% of those collected near Puerto Deseado. The higher incidence of flightless males in the south is related to greater body weights and resultant higher wing loadings. Nevertheless, at both localities most male Flying Steamer-Ducks with wing loadings below 2.5 g/cm^2 are close to the threshold of flightlessness (Fig. 1).

We weighed the contents of gizzard and esophagus of all specimens collected in 1980–1981; maximum weight of gizzard and esophageal contents of Flying Steamer-Ducks was 176 g, and mean weight (n = 32) was 32 g. Because our measure of weight of ingested food did not include intestinal contents, the maximal weight of food ingested per feeding bout is probably twice (or more) the 176 g measured for contents of esophagus and gizzard, or 350+ g.

Sixteen male Flying Steamer-Ducks had wing loadings of less than 2.5 g/cm^2. We calculated the weight increase needed for each of these birds to have a wing loading of 2.5 g/cm^2. The mean increase required was 304 g, and for 11 birds the increase needed was less than 350 g. Therefore, we hypothesize that approximately 64% of male Flying Steamer-Ducks at Puerto Deseado and 80% at Ushuaia that are not already functionally flightless for other reasons (wing molt, wing loading of 2.5 g/cm^2 or greater) could become temporarily flightless because of weight gained from ingested food.

A strategy that would avoid substantial temporary increases in weight from feeding would be to eat small amounts of food at any one time and to feed often during the day. Weller (1976: 49) stated that "flightless forms [*pteneres, brachypterus*] take large food items in brief but intense feeding periods, whereas Flying Steamer Ducks seem to feed more continuously on smaller items."

We conclude that the threshold of flightlessness in Flying Steamer-Ducks is at wing loadings of approximately 2.5 g/cm^2. Roughly 25% of male *T. patachonicus* exceed this threshold and approximate the wing loadings of the lightest of their flightless congeners. Depending on the availability of wind, Flying Steamer-Ducks may be reluctant to fly with wing loadings as low as 2.3 g/cm^2; they are unable to fly with wing loadings of 2.5 g/cm^2 and above. Wing loadings and incidence of flightlessness in Flying Steamer-Ducks are higher in males and in birds from higher latitudes.

We are now investigating factors that affect weight, wing area, and wing loading of steamer-ducks and testing hypotheses concerning the morphology, adaptive significance, and evolutionary origins of flightlessness in *Tachyeres*.

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Observations on migratory Turkey Vultures and Lesser Yellow-headed Vultures in northern Colombia

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Turkey Vultures (*Cathartes aura*) breed from southern Canada to Tierra del Fuego, while Lesser Yellow-headed Vultures (*Cathartes burrovianus*) occur from México through Central America to northern Argentina and Uruguay (Meyer de Schauensee 1966). It has long been known that Turkey Vultures breeding in the northern parts of their range are migratory, and data are available on their arrival at or departure from their breeding grounds in spring or fall (Bent 1937). Likewise, parts of their migration routes and winter ranges in Central America are well documented (Chapman 1933, Wetmore 1965, Smith 1980). Migrating Turkey Vultures were observed in northwestern Colombia by Dugand (1947), Haffer (1959), and Olivares (1959), but there are no data on their abundance or ecology. Because seasonal changes in their abundance in Panamá have been observed, it is believed that the northern Lesser Yellow-headed Vultures are also migratory (Ridgley 1976).

A tight flock of at least 150 soaring Turkey Vultures was observed on 14 October 1978, some 16 km to the east of the town of Barranquilla, Colombia. Such an unusually large number suggested migrating birds. A closer view confirmed this; none of the vultures showed the whitish or dull yellow bands across the backs of their necks that characterize the resident race, *Cathartes aura ruficollis*. Although similar in general appearance and size to the Turkey Vulture, some birds of the flock had conspicuous orange-yellowish heads and dirty-whitish wing patches that identified them as Lesser Yellow-headed Vultures. The results presented here are based mainly on observations and line-transect counts made along the Caribbean coast between the ports of Barranquilla and Santa Marta in northern Colombia. They give a first account of the magnitude and ecological aspects of vulture migrations in South America.

Counts of vultures were made by driving along the Troncal del Caribe highway between Puente de la Barra, near the town of Cienaga, and Los Cocos, near the port of Barranquilla on the Magdalena River. This area includes most of Isla de Salamanca National Park. A detailed description of this region, including a portrayal of its flora and fauna, is found in Franky and Rodriguez (1976). Visibility along most of the highway was not impaired by vegetation, so nearly all roosting or soaring vultures could be counted within a broad corridor of up to more than 500 m on each side of the highway. Twenty-eight line transects, each covering a distance of 44 km, were made between 1000 and 1500 from 17 October 1978 to 17 January 1980. One person drove, holding the speed at a constant 70 km, while a second person, using a hand-operated counter, counted vultures with the naked eye. Due to similarities in their plumage coloration and silhouettes, Turkey Vultures and Lesser Yellow-headed Vultures, when soaring or roosting, were difficult to separate at a distance. Separate counts for resident Turkey Vultures and the race of migrating Turkey Vultures were even more difficult.

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