Escape behaviour of Steamer Ducks

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Introduction

Steamer ducks *Tachyeres* comprise four species of benthic divers limited in distribution to southern South America (Murphy 1936; Humphrey & Thompson 1981): Flying Steamer Duck *T. patachonicus* of marine coastlines and freshwater lakes of Argentina, Chile, and the Falkland Islands; Magellanic Flightless Steamer Duck *T. pteneres* of coastal Chile and the Magellanic Straits; Falkland Flightless Steamer Duck *T. brachypterus* of marine coasts of the Falkland Islands; and the recently described White-headed Flightless Steamer Duck *T. leucocephalus* of coastal Chubut, Argentina. They are named for their habit of 'steaming', a rapid, spray-generating surface locomotion involving wings and feet. The escape behaviours of steamer ducks comprise steaming, diving, typical swimming, concealed swimming or 'sneaking', running and hiding on land, death-feigning, and in one species, flight for escape.

The probable relevance of these diverse escape behaviours to the taxonomy, ecology, and field identification of steamer ducks prompted us to study these behaviours during recent field work designed to clarify the systematics of the genus.

Study sites and methods

We studied three species of steamer ducks in Argentina during December 1980 to February 1981: *T. leucocephalus* at Puerto Melo, Chubut; *T. patachonicus* at Puerto Deseado, Santz Cruz; and *T. patachonicus* and *T. pteneres* at Ushuaia, Tierra del Fuego. Data recorded for pursued birds were: species and sex; location of bird(s) when encountered; sequence of behaviour used; flock size; minimum distance of bird(s) from boat; wind conditions; and occurrence of gunfire. Unless otherwise noted, all observations of escape behaviour were made from boats.

Behaviours used during escape were classified for statistical analyses as: *swimming* surface locomotion powered by feet alone, includes typical 'swimming' with head and neck erect, 'sneaks' or concealing, partially submerged swimming, 'resting' with erect posture, and 'floating' mostly submerged; *steaming* turbulent, spray-generating surface locomotion powered by feet and wings; *diving* subaquatic locomotion accomplished by foot paddling, often aided by strokes of half-folded wings; *hiding* squatting motionless on land, typically with head and neck extended anteriorly; *flight* limited to but not universal in *T. patachonicus* (Humphrey & Livezey 1982). Death feigning, possibly peculiar to *T. pteneres* (Humphrey *et al.* 1970), was not observed.

Contingency tables were designed in accord with Cochran (1954). Analyses of sequences of escape behaviour assumed each behaviour was not immediately repeatable, i.e., termination of one escape mode was defined by the beginning of a different behaviour. Statistical independence of such behavioural transitions was not tested rigorously because of large differences in observed frequencies of different escape behaviours (Lemon & Chatfield 1971).

Results

Frequencies of escape behaviours

T. pteneres, *T. patachonicus*, and *T. leucocephalus* were encountered with different frequencies ($X^2 = 20{\cdot}1$, $P < 0{\cdot}005$) on land and water. Pair-wise comparisons of species indicated that *T. patachonicus* and *T. pteneres* were similar ($X^2 = 0{\cdot}4$), and in both species $\frac{1}{3}$ of the initial encounters were of birds on land and $\frac{2}{3}$ on water (Table 1). *T. leucocephalus* differed markedly ($P < 0{\cdot}005$) from the other two species studied and was found on land and water with equal frequency.

Apart from flight, the three species differed ($X^2 = 129{\cdot}6$, $P < 0{\cdot}001$) in frequencies of other escape behaviours used (Figure 1). Closer examination revealed differences in behaviour between *T. patachonicus* and *T. leucocephalus* ($X^2 = 103{\cdot}2$, $P < 0{\cdot}001$) and between *T. leucocephalus* and *T. pteneres* ($X^2 = 106{\cdot}3$, $P < 0{\cdot}001$). *T. pteneres* and *T. patachonicus* were similar in observed frequencies of steaming, swim-

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ming, diving, and running. *T. leucocephalus* differed from the other two species primarily in its pronounced tendency to swim and steam and lower frequencies of running and diving (Figure 1).

Only 11% of *T. patachonicus* flew when pursued. This reflects, in part, heavy wing loadings and the resultant difficulty of take-off (Humphrey & Livezey 1982). In addition, 10 specimens of *T. patachonicus* were flightless because of moult of remiges. Birds in wing moult were usually encountered in flocks and, like the flightless species, resorted to swimming, steam-

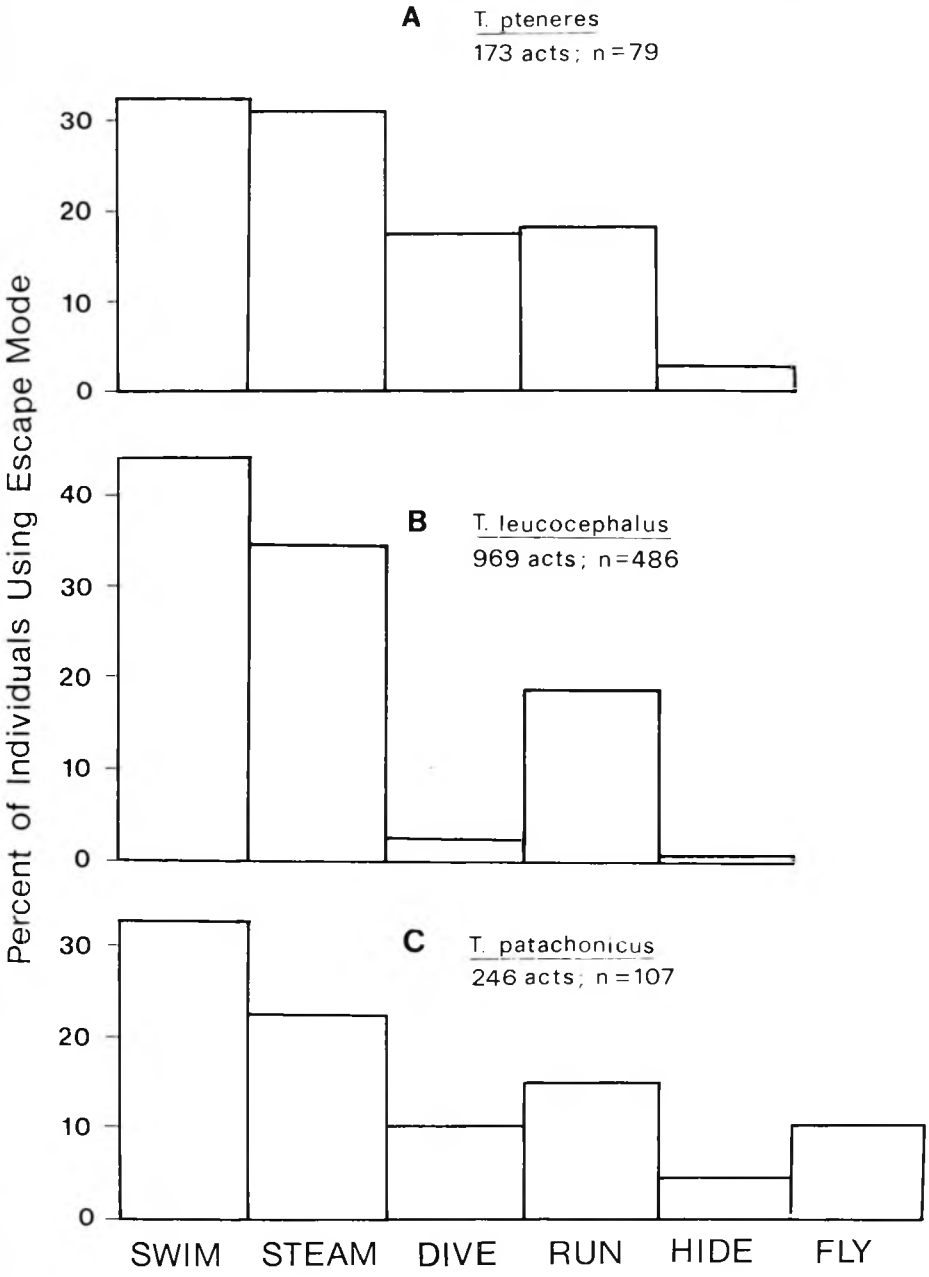

Figure 1. Relative frequencies of escape modes observed at three localities in Argentina during December 1980–February 1981.

ing, diving, running and hiding for escape.

Proportions of swims classed as 'sneaks' differed ($X^2 = 27{\cdot}9$, $P < 0{\cdot}005$) among the three species (Table 1). *T. pteneres* and *T. patachonicus* both sneaked relatively frequently (21% and 14% of all swims, respectively); *T. leucocephalus* rarely sneaked (4%).

swimming. In *T. leucocephalus* swimming was also generally followed by steaming, but steaming, if terminated, most often gave rise to more swimming. Also, the relatively land-loving *T. leucocephalus* escaped as frequently by running followed by swimming.

Sequences of escape behaviour initiated

Table 1. Mean numbers of acts, behavioural diversities (H′), percentages of swims classed as 'sneaks', and percentages of birds initially encountered on land and on water.

Statistic	*T. pteneres*	*T. patachonicus*	*T. leucocephalus*
Mean number of acts	2·4	3·1	2·2
H′ (acts)	1·45	1·44	1·13
Swims classed as 'sneaks' (%)	21	14	4
Initially on land (%)	33	29	52
Initially on water (%)	67	71	48

T. pteneres and *T. patachonicus* were also more similar to each other than to T. *leucocephalus* in diversity of escape behaviour. Both numbers of acts and the Shannon-Weaver index (H′) suggested low behavioural diversity in *T. leucocephalus* compared to the other two species studied (Table 1).

Behavioural sequences

Tabulation of frequencies of changes from one escape mode to another, provides further evidence that *T. leucocephalus* differed from *T. patachonicus* and *T. pteneres* (Table 2). In the latter two species, swimming gave rise more frequently to steaming, steaming to diving, and diving to more

on land differed between the otherwise similar *T. pteneres* and *T. patachonicus*, although neither species was typically first encountered ashore. Flightless *T. pteneres* always ran to water and immediately steamed. Beached *T. patachonicus* most frequently ran to almost immediate flight (54%); running was less commonly followed by swimming (25%), steaming (11%) or diving (11%).

Effects of flock size

Data for *T. pteneres* showed no significant differences in escape behaviour among single birds, birds in pairs, or flocks of

Table 2. Two-act sequential analyses of escape behaviour. Cells contain number (%) of various escape modes that were followed by other escape modes.

Species	Second act	First act: Swim	Steam	Dive	Run	Fly	Total
T. pteneres	Swim	—	6 (27)	3 (60)	0 (0)	—	9
(64)	Steam	37 (69)	—	2 (40)	15 (100)	—	54
	Dive	12 (22)	15 (68)	—	0 (0)	—	27
	Run	5 (9)	1 (5)	0 (0)	—	—	6
	Total	54	22	5	15	—	96
T. leucocephalus	Swim	—	13 (72)	25 (96)	126 (68)	—	164
(367)	Steam	276 (87)	—	1 (4)	58 (31)	—	335
	Dive	34 (11)	2 (11)	—	2 (1)	—	38
	Run	6 (2)	3 (17)	0 (0)	—	—	9
	Total	316	18	26	186	—	546
T. patachonicus	Swim	—	4 (10)	23 (92)	7 (25)	3 (33)	37
(98)	Steam	53 (52)	—	0 (0)	3 (11)	2 (22)	58
	Dive	22 (22)	27 (67)	—	3 (11)	4 (44)	56
	Run	9 (9)	6 (15)	1 (4)	—	0 (0)	16
	Fly	18 (18)	2 (5)	1 (4)	15 (54)	—	36
	Total	102	39	25	28	9	203

three or more. However, both *T. patachonicus* ($X^1 = 33{\cdot}3$, $P < 0{\cdot}005$) and *T. leucocephalus* ($X^2 = 25{\cdot}7$, $P < 0{\cdot}005$) showed different escape behaviour depending on flock size. Lone birds and pairs of *T. patachonicus* hid, dived, and flew more frequently than conspecifics in larger flocks, but larger flocks were somewhat more prone to steam. Steaming was also more frequent in larger flocks of *T. leucocephalus*.

Effects of nearness of boat

Frequency data revealed no differences in escape behaviour related to distance of approach. However, when we surprised feeding steamer-ducks at close range, the birds typically dived to escape us. When birds detected us at a distance they generally steamed, swam, or flew away. This disagreement between our impression in the field and the statistical results may be because escape behaviours were affected by when the ducks detected us rather than simply the closeness of our approach.

Effects of gunfire

Our limited data show marked differences in escape behaviour before and after gunfire for the three species pooled ($X^2 = 189{\cdot}3$, $P < 0{\cdot}001$). Separate analyses of *T. patachonicus* ($X^2 = 10{\cdot}8$, $P < 0{\cdot}05$) and *T. leucocephalus* ($X^2 = 127{\cdot}6$, $P < 0{\cdot}001$) demonstrated marked differences in escape modes employed before and after shots were fired; small sample sizes prevented a separate analysis for *T. pteneres*.

T. patachonicus swam less but steamed and dived more frequently after gunfire. *T. leucocephalus* most often swam before gunfire, but afterwards showed marked increases in steaming, diving, or going to land.

Discussion

Interspecific differences in escape behaviour are presumably adaptive and may reflect differences in relative risk from aquatic, aerial, and terrestrial predators.

Submarine predators of steamer ducks include southern sea lions *Otaria byronia* and killer whales *Orcinus orca*, and possibly several others (Straneck *et al.* Ms). We suspect that steaming functions primarily as a rapid, target-obscuring method for escaping underwater predators, especially in flightless species.

Diving is probably employed as an escape behaviour by steamer ducks mostly to avoid aerial predators. The threat of aerial attack by Kelp Gulls *Larus dominicanus*, Skuas *Catharacta skua*, and Giant Petrels *Macronectes giganteus* is substantial for downy young of *Tachyeres* (Pettingill 1965). Diving ability is acquired early, and we observed short feeding dives in class-I ducklings of *T. pteneres* and *T. patachonicus*.

Foxes *Dusicyon* spp. are predators of adult *T. patachonicus* and *T. pteneres* on mainland South America (Reynolds *in* Lowe 1934) and occurred formerly on the Falklands (Clayton 1776). The utility of running to avoid canids is obvious, especially for flightless species during nesting. The usefulness of death-feigning is not clear in that most terrestrial predators are also scavengers.

Flightlessness in waterfowl is generally associated with island faunas, presumably as a response to a lack of predators (Weller 1980). However, all *T. pteneres*, *T. leucocephalus*, and some *T. patachonicus* are permanently flightless and coexist with several predators along continental coastlines. The success of these flightless populations on the mainland suggests that predation on adult steamer ducks is insignificant or that locomotor behaviours other than flight are collectively effective for escaping predators.

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Summary

This paper presents results of field work during December–February 1980–81 at three sites in Argentina on the escape behaviour of White-headed Flightless Steamer Ducks *Tachyeres leucocephalus*, Flying Steamer Ducks *T. patachonicus*, and Magellanic Flightless Steamer Ducks *T. pteneres*. The three species studied differed in use of escape modes, not including flight. *T. leucocephalus* differed substantially from the generally more similar *T. ptereres* and *T. patachonicus* in frequency of escape modes, diversity of escape behaviour, and two-act behavioural sequences. Escape behaviour of pursued *T. Leucocephalus* and *T. patachonicus* were affected by flock size and gunfire. We speculate that escape diving is used primarily to elude aerial predators (especially by ducklings) and that steaming functions as a target-obscuring method for escape from underwater predators.

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