Escape behaviour of Steamer Ducks
BRADLEY C. LIVEZEY and PHILIP S. HUMPHREY

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, '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 ($X^2 = 20.1, P < 0.005$) on land and water. Pair-wise comparisons of species indicated that T. patachonicus and T. pteneres were similar ($X^2 = 0.4$), and in both species $\frac{1}{2}$ of the initial encounters were of birds on land and $\frac{1}{2}$ on water (Table 1).

$T. leucocephalus$ differed markedly ($P < 0.005$) from the other two species studied and was found on land and water with equal frequency.

Apart from flight, the three species differed ($X^2 = 129.6, P < 0.001$) in frequencies of other escape behaviours used (Figure 1). Closer examination revealed differences in behaviour between T. patachonicus and $T. leucocephalus$ ($X^2 = 103.2, P < 0.001$) and between $T. leucocephalus$ and T. pteneres ($X^2 = 106.3, P < 0.001$). T. pteneres and T. patachonicus were similar in observed frequencies of steaming, swim-
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](image-url)

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 ($X^2 = 27.9$, $P < 0.005$) 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%).

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.

<table>
<thead>
<tr>
<th>Statistic</th>
<th>T. pteneres</th>
<th>T. patachonicus</th>
<th>T. leucocephalus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean number of acts</td>
<td>2.4</td>
<td>3.1</td>
<td>2.2</td>
</tr>
<tr>
<td>$H'$ (acts)</td>
<td>1.45</td>
<td>1.44</td>
<td>1.13</td>
</tr>
<tr>
<td>Swims classed as 'sneaks' (%)</td>
<td>21</td>
<td>14</td>
<td>4</td>
</tr>
<tr>
<td>Initially on land (%)</td>
<td>33</td>
<td>29</td>
<td>52</td>
</tr>
<tr>
<td>Initially on water (%)</td>
<td>67</td>
<td>71</td>
<td>48</td>
</tr>
</tbody>
</table>

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 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 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.

<table>
<thead>
<tr>
<th>Species</th>
<th>Second act</th>
<th>Swim</th>
<th>Steam</th>
<th>First act</th>
<th>Dive</th>
<th>Run</th>
<th>Fly</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>T. pteneres (64)</td>
<td>Swim</td>
<td>—</td>
<td>6 (27)</td>
<td>Swim</td>
<td>3 (60)</td>
<td>0 (0)</td>
<td>—</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>Steam</td>
<td>37 (69)</td>
<td>—</td>
<td>Steam</td>
<td>2 (40)</td>
<td>15 (100)</td>
<td>—</td>
<td>54</td>
</tr>
<tr>
<td></td>
<td>Dive</td>
<td>12 (22)</td>
<td>15 (68)</td>
<td>—</td>
<td>0 (0)</td>
<td>—</td>
<td>—</td>
<td>27</td>
</tr>
<tr>
<td></td>
<td>Run</td>
<td>5 (9)</td>
<td>1 (5)</td>
<td>Swim</td>
<td>0 (0)</td>
<td>—</td>
<td>—</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>54</td>
<td>22</td>
<td>Swim</td>
<td>5</td>
<td>15</td>
<td>—</td>
<td>96</td>
</tr>
<tr>
<td>T. leucocephalus (367)</td>
<td>Swim</td>
<td>—</td>
<td>13 (72)</td>
<td>Swim</td>
<td>25 (96)</td>
<td>126 (68)</td>
<td>—</td>
<td>164</td>
</tr>
<tr>
<td></td>
<td>Steam</td>
<td>276 (87)</td>
<td>—</td>
<td>Steam</td>
<td>1 (4)</td>
<td>58 (31)</td>
<td>—</td>
<td>335</td>
</tr>
<tr>
<td></td>
<td>Dive</td>
<td>34 (11)</td>
<td>2 (11)</td>
<td>Swim</td>
<td>—</td>
<td>2 (1)</td>
<td>—</td>
<td>38</td>
</tr>
<tr>
<td></td>
<td>Run</td>
<td>6 (2)</td>
<td>3 (17)</td>
<td>Steam</td>
<td>0 (0)</td>
<td>—</td>
<td>—</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>316</td>
<td>18</td>
<td>Swim</td>
<td>26</td>
<td>186</td>
<td>—</td>
<td>546</td>
</tr>
<tr>
<td>T. patachonicus (98)</td>
<td>Swim</td>
<td>—</td>
<td>4 (10)</td>
<td>Swim</td>
<td>23 (92)</td>
<td>7 (25)</td>
<td>3 (33)</td>
<td>37</td>
</tr>
<tr>
<td></td>
<td>Steam</td>
<td>53 (52)</td>
<td>—</td>
<td>Steam</td>
<td>0 (0)</td>
<td>3 (11)</td>
<td>2 (22)</td>
<td>58</td>
</tr>
<tr>
<td></td>
<td>Dive</td>
<td>22 (22)</td>
<td>27 (67)</td>
<td>—</td>
<td>3 (11)</td>
<td>4 (44)</td>
<td>—</td>
<td>56</td>
</tr>
<tr>
<td></td>
<td>Run</td>
<td>9 (9)</td>
<td>6 (15)</td>
<td>Steam</td>
<td>1 (4)</td>
<td>—</td>
<td>0 (0)</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>Fly</td>
<td>18 (18)</td>
<td>2 (5)</td>
<td>Swim</td>
<td>15 (54)</td>
<td>—</td>
<td>—</td>
<td>36</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>102</td>
<td>39</td>
<td>Swim</td>
<td>25</td>
<td>28</td>
<td>9</td>
<td>203</td>
</tr>
</tbody>
</table>
three or more. However, both T. patachonicus \((X^2 = 33.3, P < 0.005)\) and T. leucocephalus \((X^2 = 25.7, P < 0.005)\) 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 \((X^2 = 189.3, P < 0.001)\). Separate analyses of T. patachonicus \((X^2 = 10.8, P < 0.05)\) and T. leucocephalus \((X^2 = 127.6, P < 0.001)\) 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-obsuring 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.

**Acknowledgements**

This study was supported by NSF DEB-8012403 to P. S. Humphrey. We thank B. Mayer, Mr and Mrs F. V. T. J. Faurung, Dr O. Kuhnemann, P. Medina, and J. Sesti for warm hospitality and facilities for field work; Dr J. M. Gallardo, Dr J. Navas, R. A. Bockel, and their colleagues in the Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’ for generous assistance; Dr E. O. Gonzales Ruiz and his colleagues, Dirección Nacional de Fauna Sylvestre, Ing. Qea. L. O. Saigq de Chialva, Directora de Proteccion Ambiental, Provincia de Chubut, and Dr D. H. Soria, Director General de Ganaderia, Provincia de Santa Cruz, for permits; Dr A. Tarak and his colleagues, Dirección Nacional de Parques Nacionales, Dr G. A. Giaroli, Subsecretario de Recursos Naturales Renovables y Ecologia de la Nacion, and F. Llobo and F. Villar, Ceremonial, Ministerio de Economia, for arrangements in Argentina; B. Padget for typing and other help; and D. Bennett for drawing the figure.
Bradley C. Livezey and Philip S. Humphrey

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. pteneres* 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.

References

Lowe, P. R. 1934. On the evidence for the existence of two species of steamer duck (*Tachyeres*), and primary and secondary flightlessness in birds. *Ibis* 76:467–96.
Straneck, R., Livezey, B. C. & Humphrey, P. S. Ms. Predation on steamer ducks by killer whale. Submitted to *Condor*.

Bradley C. Livezey and Philip S. Humphrey, Museum of Natural History and Department of Systematics and Ecology, University of Kansas, Lawrence, Kansas 66045, U.S.A.