

burrows sampled in this study had been previously used by Burrowing Owls.

Burrows used for nesting were in soils with a greater sand content than non-nest burrows. Although this difference was statistically insignificant ( $P < 0.14$ ), it may be biologically significant. The significant difference in burrow entrance diameter between nest and non-nest burrows indicates that Burrowing Owls modify prairie dog burrows used as nest sites. Presumably, sandy soil would facilitate enlarging burrow passageways. Coulombe (1971) stated that in California burrow diameters averaged 20 cm, and suggested that owls may modify burrows that have been abandoned by rodents. In addition, sandy soils drain rapidly, which would reduce nest flooding during frequent spring and summer rainstorms.

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#### TERRITORIALITY AND INTERSPECIFIC AGGRESSION IN STEAMER-DUCKS

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Steamer-ducks (*Tachyeres* spp.) are large diving ducks of southern Argentina and Chile, and the Falkland Islands (Murphy 1936). Four species are recognized currently (Humphrey and Thompson 1981): Flying Steamer-Duck (*T. patachonicus*), Magellanic Flightless Steamer-Duck (*T. pteneres*), Falkland Flightless Steamer-Duck (*T. brachypterus*), and White-headed Flightless Steamer-Duck (*T. leucocephalus*). Flying Steamer-Ducks breed in both freshwater and marine habitats; the three flightless species are strictly marine in distribution (Humphrey and Livezey, in press). All members of the genus feed primarily on large molluscs and crustaceans obtained from the bottom by diving and shallow-water foraging, or found exposed during low tide (Murphy 1936; Weller 1972; Livezey and Humphrey, unpubl.).

Steamer-ducks are renowned for their pugnacity; numerous observers have described their intense, sometimes fatal territorial combat (Vallentin 1924; Reynolds in Lowe 1934; Murphy 1936; Pettingill 1965; Cawkell and Hamilton 1961; Weller 1972, 1976). Territoriality in other wa-

terfowl rarely involves combat and generally is shown only toward conspecifics (McKinney 1965, Seymour 1974, Seymour and Titman 1978, Stewart and Titman 1980), although exceptions are known (McKinney et al. 1978, Savard 1982).

Recently, Nuechterlein and Storer (1985) described interspecific aggression of Flying Steamer-Ducks on several freshwater lakes in the Argentine Andes. These authors frequently observed combat between male *T. patachonicus* and regularly noted "mass spooks" of grebes, coots, and ducks when territorial pairs of *T. patachonicus* called or approached. They also witnessed two severe attacks (one fatal) by males on Red Shovelers (*Anas platylea*), and found carcasses of five more shovelers and one Yellow-billed Pintail (*A. georgica*) which were determined to have been victims of steamer-ducks. Nuechterlein and Storer argued that the massive skeletal and muscular morphology of steamer-ducks makes the "costs," or risks, of interspecific aggression negligible, and that this renders "profitable" the attacks on the possibly food-competitive shovelers. They also suggested that such killings may serve as displays of fighting ability in males, and hence be maintained partly by sexual selection.

As part of an ongoing study of the morphology, systematics, and ecology of steamer-ducks, we have observed all four species of *Tachyeres* at a number of ecologically diverse localities: Ushuaia, Tierra del Fuego, Argentina (December 1980-January 1981); Puerto Deseado, Santa Cruz, Argentina (January-February 1981); Puerto Melo, Chubut, Argentina (February 1981, December 1981, January 1982); Andean lakes of Santa Cruz and Chubut (December 1981-January 1982); Puerto Montt and nearby lakes, Region X, Chile (December 1982-January 1983); and Port Stanley and Lively Island, east Falkland Islands (January-

February 1984). While we agree in part with the inferences of Nuechterlein and Storer (1985), our studies prompt us to present a different perspective on territoriality in the genus, and to offer some alternate interpretations of attacks on noncongeners, including protection of broods, adaptive "play," and nonadaptive "inertial" aggression.

Most of the aggression shown by steamer-ducks is distinctly territorial (*sensu* defense of an area; Noble 1939), although we observed some aggression among birds in non-breeding flocks or feeding on highly tidal waterfronts where no static territory was obvious. Territoriality in steamer-ducks has been interpreted as defense of nest site, food supplies, brood, and/or loafing site, and probably serves most or all of these functions (Vallentin 1924; Weller 1972, 1976). Both sexes regularly are involved in territorial disputes, although males are the primary combatants (Cawkell and Hamilton 1961, Pettingill 1965, Schmidt 1969). Methods of attack are described by Nuechterlein and Storer (1985). Defended areas generally are contiguous, regularly spaced segments of shoreline and adjacent water, and marine territories of at least *T. brachypterus* are defended all year, and perhaps for life (Vallentin 1924; Cawkell and Hamilton 1961; Pettingill 1965; Weller 1972, 1976). Territorial dispersion of nesting pairs evidently affects some regulation of local population densities of steamer-ducks, in that large flocks of non-breeding birds, which are excluded from territories and loiter at communal loafing sites, have been observed for *T. brachypterus*, *T. leucocephalus*, and marine *T. patachonicus* (Murphy 1936; Pettingill 1965; Weller 1972, 1976; pers. observ.).

Steamer-duck aggression is most intense among congeners. During late summer, we observed numerous intraspecific territorial disputes in both sexes of *T. brachypterus*, several of which culminated in prolonged physical combat. Also, 12 of 18 territorial encounters of continental steamer-ducks for which we have field notes were intraspecific: seven between *T. pteneres* and *T. patachonicus*, four within *T. pteneres*, and one within *T. leucocephalus*. Invariably, in territorial encounters involving two species of *Tachyeres*, the individual of the larger flightless species was dominant.

We found mended fractures in 22 of 170 complete postcranial skeletons of steamer-ducks (13 of 89 males, 9 of 81 females; 13% overall); the count of fractures excludes one bird with a mended humerus that obviously was broken by a .22-caliber bullet. Tiemeier (1941) found that 33 of 256 (13%) assorted anatid skeletons contained healed fractures, but these included six that obviously had been caused by gunshot. Based on our discussions with local residents, steamer-ducks are not considered good eating and are hunted seldom if at all. Hence, most of the fractures we found must have resulted from fights, falls, or predators. Elements of the wing and pectoral girdle comprised 21 of the 25 "naturally" broken bones, and six of these were in the carpometa-carpus, which supports the wing knobs that are used in fighting. This finding strongly suggests that the majority of fractures suffered by steamer-ducks resulted from combat.

Unlike most anatids (McKinney 1965), steamer-ducks frequently attack other (non-congeneric) species, often fatally (Table 1). Species from seven taxonomic orders have been attacked, involving birds in the wild and in aviaries; captive victims may have been less able to escape than those in natural habitat. In addition, a captive female *T. brachypterus* killed a wild rat (*Rattus* sp.; Sea World personnel, pers. comm.), and a captive pair of *T. brachypterus* with young attacked a 1.5-m catfish (*Silurus glanis*), which later died (Schmidt 1969).

Competition and the defendability of food supplies are minimal prerequisites for the evolution of food-related territoriality (Brown 1964, Nudds and Ankney 1982). We suggest that the large size, physical strength, and aggressive tendencies of steamer-ducks evolved in part because of

the structurally simple, open, almost linear nature of their littoral habitat and the associated sessile, predictable, and defendable food resources. In the three flightless species and marine populations of *T. patachonicus*, these habitat characteristics occur in combination with a relatively benign maritime climate which permits year-round residency. Together, these conditions may have favored the evolution of birds capable of year-round sequestering of food, i.e., with intense territoriality and morphological weapons. We hypothesize that this evolutionary trend was selectively maintained through intrageneric competition for food and that, as at present, steamer-ducks had few or no non-congeneric food competitors. These selection pressures probably affected marine populations of steamer-ducks most intensely, primarily because of the year-round defendability of food supplies. This general adaptive regime, however, probably also applies to freshwater *T. patachonicus*, because the feeding and nesting ecology, general features of breeding habitat, sympatric water birds, and probable marine wintering areas of lake-nesting *T. patachonicus* are similar to those of marine steamer-ducks.

The selective advantage of intrageneric territorial behavior and associated morphology in steamer-ducks is enhanced through the defense of preferred nesting and brood-rearing sites, and perhaps, to a lesser extent, through the protection of nesting females from attack and/or rape by other males. We know of no observation of rape in *Tachyeres*, however, and we suspect that males have relatively little need to defend their mates because of the fighting abilities of the females, the low mobility of males, probably long-term pair bonds, and the localized activity of birds during nesting. Territoriality and large size probably co-evolved with other "K-selected" traits of steamer-ducks: increased longevity, late sexual maturity, and the importance of competitive interactions (relative to environmental factors) in reproductive success.

In all species of *Tachyeres*, it is evident that failure to acquire and hold a territory precludes breeding. We believe that this territorial "arms race" (Dawkins and Krebs 1979) is the cause, in part, of weight-related flightlessness in steamer-ducks, which includes 25% of the males of marine *T. patachonicus* at two localities in Argentina (Humphrey and Livezey 1982). In addition, such selection probably affects males more than females, and undoubtedly contributes to the relatively great sexual dimorphism in the genus (Livezey and Humphrey 1984). We suspect that from this several-faceted, mostly intrageneric regime of selection emerged a heavy-bodied, hyperaggressive, predominantly sedentary, and largely flightless genus of waterfowl, which is preadapted for aggression toward other species. African Black Ducks (*Anas sparsa*), which inhabit linear, well-defined territories on rivers that permit year-round residency, show a similar combination of life-history characteristics: long-term pair bonds, year-round territoriality in both sexes, absence of rape, frequent physical combat, and aggression toward several other species (Ball et al. 1978, McKinney et al. 1978).

Although we believe that Red Shovelers are not serious competitors for food with steamer-ducks on fresh or salt water, we agree with Nuechterlein and Storer (1985) that the risks or costs incurred by steamer-ducks in interspecific aggression are negligible, hence, making such attacks competitively neutral or marginally favorable. The likelihood of interspecific aggression probably is especially great because the simple structure of the habitat permits good visibility and allows for some ecological overlap (Orians and Willson 1964). Marginal competition for food, however, is not a sufficient explanation for attacks by steamer-ducks on other species, even other anatids, because a variety of species have been attacked on salt water, where dietary overlap is insignificant.

Many instances of interspecific aggression by steamer-ducks can be most readily interpreted as defense of duck-

TABLE 1. Records of attacks by steamer-ducks on non-congeners, including birds that were pursued but not engaged physically, birds that were killed, and the circumstances of the attacks, if known. Species of *Tachyeres* are abbreviated: *pat* = *patachonicus*, *bra* = *brachypterus*, *leu* = *leucocephalus*.

Species attacked (no., age, sex)	Bird(s) killed	Attacking steamer-duck(s)					Sources
		Species	Sex	Paired	With brood	Captive	
<i>Podiceps major</i> (1, ad)	No	<i>pat</i> <sup>a</sup>	♂	Yes	No	No	Pers. observ.
<i>Diomedea</i> sp. (1)	Yes	<i>bra</i>	—	—	—	Yes	Todd 1979
<i>Phalacrocorax olivaceus</i> (1)	No	<i>pat</i> <sup>b</sup>	♂	Yes	Yes	No	Pers. observ.
<i>Phalacrocorax</i> sp.	Yes	<i>bra</i>	♀	No	No	Yes	Hubbs-Sea World personnel
<i>Nycticorax nycticorax</i>	Yes	<i>bra</i>	♀	No	No	Yes	Hubbs-Sea World personnel
<i>Chloephaga hybrida</i> (1)	No	<i>bra</i>	♂	—	—	No	Pettingill 1965
<i>Cygnus</i> sp.	Yes	<i>bra</i>	—	—	—	Yes	Todd 1979
<i>Anas sibilatrix</i>							
(2, ad, ♂♀)	No	<i>pat</i> <sup>a</sup>	♂	—	No	No	Pers. observ.
(2, ad)	No	<i>pat</i> <sup>a</sup>	♂	—	No	No	Pers. observ.
(2, ad) <sup>c</sup>	Yes	<i>bra</i>	♂	No	No	Yes	D. Crompton and J. Kear, pers. comm.
<i>A. strepera</i> (1, ad) <sup>d</sup>	Yes	<i>bra</i>	♂	No	No	Yes	D. Crompton and J. Kear, pers. comm.
<i>A. platyrhynchos</i> (2, ad, ♀♀) <sup>d</sup>	Yes	<i>bra</i>	♂	No	No	Yes	D. Crompton and J. Kear, pers. comm.
<i>A. georgica</i> (1, ad) <sup>e</sup>	Yes	<i>pat</i> <sup>a</sup>	—	—	—	No	Nuechterlein and Storer 1985
<i>A. platalea</i> (1, ad) <sup>f</sup>	Yes	<i>pat</i> <sup>a</sup>	♂	Yes	No	No	Nuechterlein and Storer 1985
(1, ad, ♂) <sup>f</sup>	No	<i>pat</i> <sup>a</sup>	♂	Yes	No	No	Nuechterlein and Storer 1985
(5, ad) <sup>g,s</sup>	Yes	<i>pat</i> <sup>a</sup>	—	—	—	No	Nuechterlein and Storer 1985
(1, ad) <sup>e</sup>	Yes	<i>bra</i>	♂	No	No	Yes	D. Crompton and J. Kear, pers. comm.
<i>Lophonetta specularioides</i>							
(1)	No	<i>pat</i> <sup>b</sup>	♂, ♀	Yes	No	No	Pers. observ.
(1)	No	<i>leu</i>	♂, ♀	Yes	Yes	No	Pers. observ.
<i>Netta erythrophthalma</i>	Yes	<i>bra</i>	♀ <sup>h</sup>	Yes	No	Yes	D. Crompton and J. Kear, pers. comm.
(5, downy)							
<i>Netta</i> sp. (several, ad)	Yes	<i>bra</i>	♂, ♀	Yes	No	Yes	Delacour 1954, Schmidt 1969
<i>Fulica americana</i> (several)	Yes	<i>bra</i>	♀	No	No	Yes <sup>i</sup>	Hubbs-Sea World personnel
<i>Larus dominicanus</i> (several)	No	<i>bra</i>	♂, ♀	Yes	Yes	No	Pettingill 1965, Weller 1972

<sup>a</sup> On fresh water.

<sup>b</sup> On salt water.

<sup>c</sup> Pinioned birds.

<sup>d</sup> Full-winged birds.

<sup>e</sup> Diagnosed post-mortem.

<sup>f</sup> In full wing molt.

<sup>g</sup> Four birds in wing molt.

<sup>h</sup> 10-month-old bird.

<sup>i</sup> Duck was free at time of killings.

lings against potential avian predators, made effective by morphological refinements for combat. Attacks by steamer-ducks on albatrosses, herons, and gulls (Table 1) can be explained most simply as anti-predator actions (Humphrey and Livezey, in press). This explanation also may apply to attacks on grebes and coots; related species in both groups are known to attack ducks and broods (Gullion 1953, Kirby 1976).

We agree with Nuechterlein and Storer (1985) that ritualization of interspecific attacks is likely in steamer-ducks. The marginal or neutral competitive importance of the aggression, the behavior of females during attacks by their mates on other species, and the intensity of attack suggest that these acts are sexually selected to some extent.

Interspecific attacks by steamer-ducks may also serve as adaptive learning experiences or practice for combat. The incessant fighting among young birds that we observed in wandering, non-breeding flocks of *T. brachypterus* probably represents, in part, informative bouts in which dominance hierarchies are established, fighting skills are improved, and pair bonds are formed. Other species, particularly other anatids, also may be safe targets for improvement of the steamer-ducks' complex combat skills that are essential for reproductive success. Such practice

would be especially important for young birds and may be considered an example of "functionalist" animal play (Fagen 1974). The killing of five downy African Pochards (*Netta erythrophthalma*) by a ten-month-old male *T. brachypterus* (Table 1) conforms well to this interpretation.

Nuechterlein and Storer (1985) rejected the hypothesis that interspecific killing by Flying Steamer-Ducks results from mistaken identification of the attacked birds as conspecifics, a view proposed for birds generally by Murray (1971, 1981). We suggest that the aggressive adaptations of steamer-ducks and the associated low cost of interspecific attack make it likely that most sizable birds encountered on defended waters are attacked *as if* they were predators of ducklings, or competitors for food, nest sites, or mates. For steamer-ducks, there probably is little selective pressure for discrimination of targets for interspecific aggression.

In conclusion, we view interspecific aggression in steamer-ducks as a suite of secondary adaptations for protection of young, defense of food resources from marginal competitors, sexually selected ritualized behavior for assessment of males by females, and practice for intrageneric combat. Some attacks may represent nonadaptive, "inertial" aggression. Consequently, we suggest that much of

the aggression of steamer-ducks toward other birds is not directly related to competition for food, in contrast to the findings of several authors from studies of interspecific aggression in other avian species (e.g., Simmons 1951, Kruuk 1967, Cody 1968, Dow 1977, Savard 1982). We emphasize, however, that the presumed low proximate costs of this varied interspecific aggression were made possible only by the extensive and costly competition-related adaptations of steamer-ducks for intrageneric combat, which in turn are related to predictable, defensible food supplies. These adaptations for aggression are presumably costly throughout life, in terms of energy and materials. In addition, they probably have had important influence on other aspects of the life history and morphology of steamer-ducks, including sexual dimorphism, flightlessness and associated low mobility, and budgeting of energy reserves for territorial behavior, nesting, and brood-rearing.

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