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AGGRESSIVE BEHAVIOR AND INTERSPECIFIC KILLING BY FLYING STEAMER-DUCKS IN ARGENTINA

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ABSTRACT.—Flying Steamer-Ducks (*Tachyeres patachonicus*) breeding on small, snow-melt lakes in the Andean foothills show intensive intra- and interspecific aggression toward a wide variety of species not closely related taxonomically, or similar in appearance or food habits. When establishing their territories, newly formed pairs frequently fight and perform mutual vocal and visual displays. We here report first-hand observations and post-mortem evidence of their killing other ducks during this period. Adaptations for intraspecific fighting in this species may have largely eliminated the risk of injury when attacking birds of other species, thereby increasing the probability of benefitting from wider interspecific aggression.

Steamer-ducks (*Tachyeres* spp.) are large, heavy-bodied birds with tough skin and massive heads and necks. The cornified, orange knobs on the proximal part of the carpometacarpus of both sexes are used in territorial fighting and display. In the wild, males are known to be strongly aggressive toward their own and other species (Pettingill 1965, Weller 1976), and they are well-known to aviculturalists for their extreme aggressiveness toward other waterfowl (Delacour 1954). Pettingill (1965) noted that nearly all fully mature male Falkland Flightless Steamer-Ducks (*T. brachypterus*) he collected had battle scars and he mentioned one fight that lasted a full 20 minutes.

Instances of strongly developed interspecific aggression under natural conditions are of interest because they provide a critical test for theories that relate aggression to competition for resources (Orians and Willson 1964). Moore (1978), for example, predicted that Northern Mockingbirds (*Mimus polyglottos*) defending food territories would be most aggressive toward species having similar food habits. Exceptions to this pattern include aggression between individuals of two species that have only recently come into contact (Murray 1981), aggression toward potential predators of eggs or young (Wittenberger 1981), aggression toward same-sex competitors of potentially hybridizing species (Post and Greenlaw 1975, Payne 1980), and cases of mistaken identity (Murray 1971).

Our field observations of frequent interspecific aggression by Flying Steamer-Ducks (*T. patachonicus*) breeding on snow-melt lakes in southern Argentina were especially surprising because they appeared to support none of these hypotheses. Males attacked and even killed individuals of species that were not potential sexual competitors or egg predators and that did not resemble steamer-ducks in food habits or physical appearance.

STUDY AREA AND METHODS

We studied Flying Steamer-Ducks from November 1981 through January 1982 on two snow-melt lakes in the Andean foothills near Calafate, Santa Cruz Province, Argentina. Nuechterlein made additional observations in the 1982–1983 breeding season on three other lakes in the region. Steamer-ducks were especially common on the most fertile of the lakes, Laguna de la Nevada. This lake was unusually rich in snails (*Lymnaea* sp.) which presumably were the primary food of the steamer-ducks. Other waterbirds present included Red Shovelers (*Anas platalea*), Yellow-billed Pintails (*A. georgica*), Red-gartered Coots (*Fulica armillata*), Silvery Grebes (*Podiceps occipitalis*), and Hooded Grebes (*P. gallardoi*). The shovelers were particularly numerous on these lakes, where they undergo the annual wing molt in November and December.

We counted a maximum of 60 adult steamer-ducks on Laguna de la Nevada (17 November). By the end of November, 22 pairs separated and began establishing territories spaced at 50–70 m intervals along the shoreline. Throughout this period, territorial displays and intense fighting were common. We observed the birds' behavior with binoculars and a spotting scope from shore. We recorded their display postures and vocalizations with a Beaulieu 16mm movie camera, 35mm camera, and Uher 4000 Report-L tape recorder. Display terminology is that of Moynihan (1958).

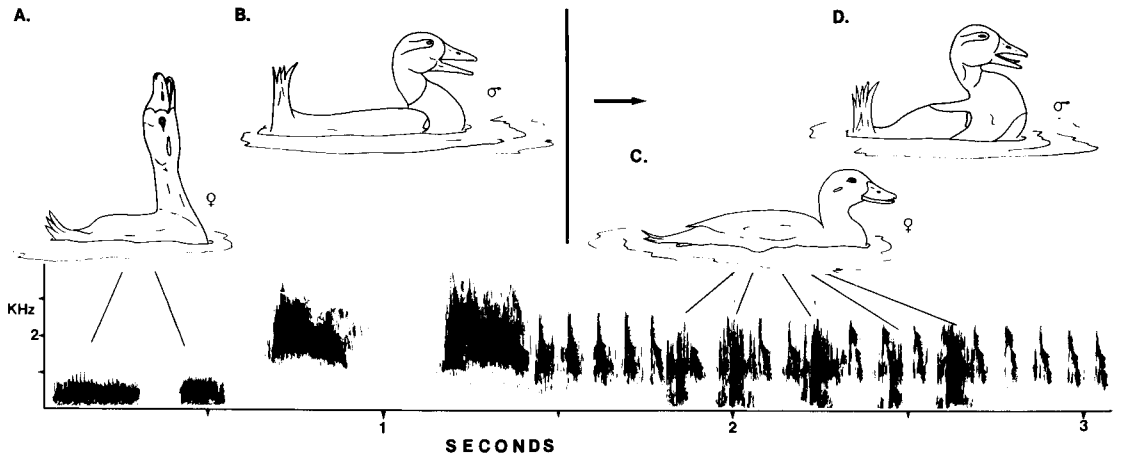

FIGURE 1. Territorial displays and calls of a pair of Flying Steamer-Ducks. The sonogram shows a typical duetting call bout, female calls indicated by lines. Female calls are lower than those of males, containing components in the 0 to 1 kHz frequency range. Females often initiate display bouts by Stretching and Groaning (A). In the Short-high-and-broad posture (B), the male exposes his wing knobs and, in this case, gives two Rasping Grunts, followed by an extended, trill-like Ticking bout. During male Ticking, the female gives five Grunts (C) and the male displays in a more intense Short-high-and-broad posture with the white of the belly exposed.

RESULTS

INTRASPECIFIC AGGRESSION

Females often initiated display bouts by Stretching (Fig. 1a) and giving a low Groaning call, audible only at close range (Fig. 1a, sonogram). Males responded with the most common of their territorial displays, a Short-high-and-broad posture combined with Sibilant or Rasping Grunts (Fig. 1b) and an extended bout of Ticking (Fig. 1c and d, sonogram). During male Ticking, females frequently gave 3–8 low, evenly spaced grunts (Fig. 1c). Upon encountering another territorial pair, males often adopted a stationary, more upright posture with the white of the breast showing above the water (Fig. 1d).

When attacking, males either stretched out low over the water and attack-dived from a Submerged Sneak posture (Fig. 2), or "steamed" (Livezey and Humphrey 1983) across the surface flapping their wings. The mere sight of a bird approaching in a Sneak posture often caused other pairs to retreat rapidly. An attacking bird often made first contact from beneath the water. Both methods were used against other waterbirds also.

Conflicts between paired males on Laguna de la Nevada were frequent, especially during pair formation and territory establishment (2–15 December). Fights usually were between males, who faced each other, charged, grasped their opponent by the head or neck, and beat him with the wing knobs (Fig. 3). While so engaged, males frequently submerged with loud splashing and came up still fighting, 1–30 s later. We timed fights ranging from 15 s to 4.5 min.

INTERSPECIFIC AGGRESSION AND MORTALITY

During our early studies on Laguna de la Nevada, we noted that at infrequent intervals entire flocks of Silvery and Hooded grebes would suddenly cease courting and either dive or skitter across the surface away from a focal point of apparent disturbance. We puzzled over the cause of these "mass spooks" in the otherwise unmolested flocks of grebes, for there were few predators and no source of human disturbance on the lake. Only later did we discover that

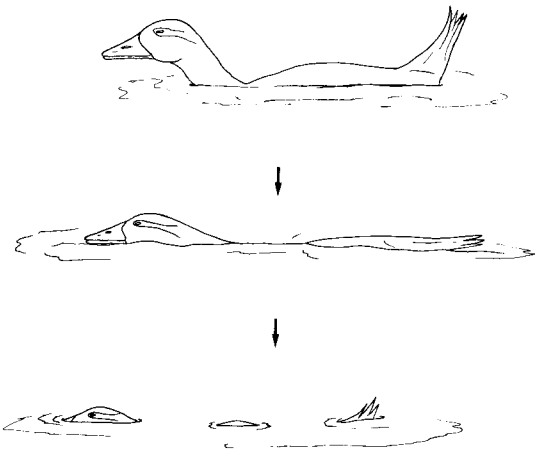

FIGURE 2. Three stages of the Submerged Sneak, a form of underwater attack frequently used by male Flying Steamer-Ducks.

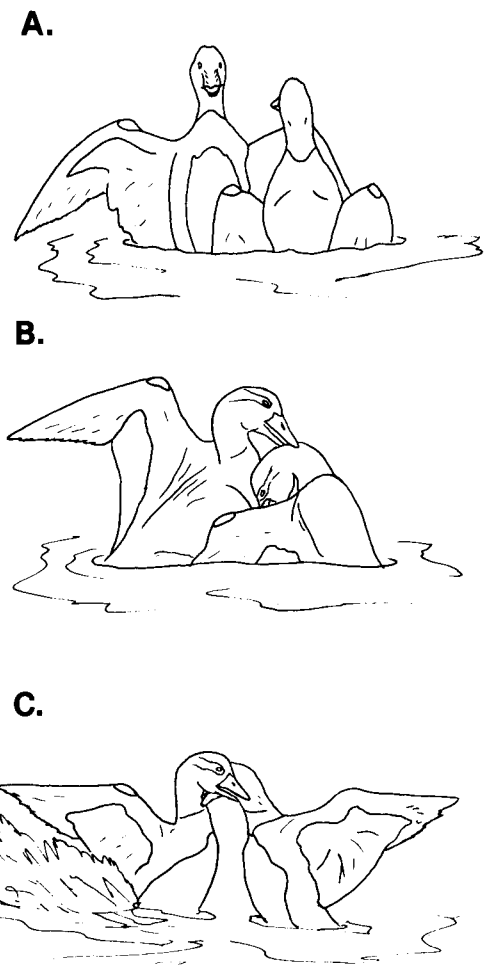

FIGURE 3. Three stages of a territorial fight between two males. After facing off with wing knobs protruding (A), the birds lunge at one another in an attempt to grasp the neck or body of their opponent (B). The birds then repeatedly beat each other with their wings (C).

these "spooks" were caused by pairs of territorial steamer-ducks, which approached such flocks in the Submerged Sneak posture. Similar alarm reactions were frequent in the large flocks of shovelers, pintails, and coots on the lake.

During the first two weeks of December, alarm responses also occurred when Silvery and Hooded grebes were nesting on artificial platforms which we constructed to attract grebes closer to shore. At least eight of eleven such reactions were immediately preceded by the approach of a calling, territorial pair of steamer-ducks. The grebes appeared to react especially to the Ticking and Grunting calls (Fig. 1) of the steamer-duck pair. They readily distinguished such displaying pairs from those that were merely swimming or feeding nearby. When we played this territorial call from a tape recorder near the platforms, the grebes immediately assumed an alert posture.

On 11 November, Storer found two fresh carcasses of female Red Shovelers on the southern shore of Laguna de la Nevada; both were exceedingly fat and showed no obvious outward cause for mortality. One bird was in full wing molt. Then, on 25 November, at a nearby lake named Laguna Blanchillo, Nuechterlein observed a male steamer-duck catch and kill a molting adult shoveler. In this attack, which lasted over 3.5 min, the steamer-duck grabbed the shoveler by the neck and pounded its body with his wing knobs. As in intraspecific fights, the steamer-duck was nearly stationary and upright in the water, with wings spread (Fig. 3a). Several meters away, a female steamer-duck displayed excitedly, calling and Stretching (Fig. 1a) repeatedly. At intervals, the male steamer-duck pulled the shoveler beneath the surface, then raised it up again and renewed the wing-beating. After approximately 2 min, the male steamer-duck was distracted by the female and displayed with her. Within 30 s, he returned to the shoveler, grabbed it by the neck, and again beat it another 15–20 times with its wings. He then released the limp body of the shoveler, pecked at it, and released it again. Turning to the female, he joined her in calling repeatedly while she Stretched. A full minute later, after the steamer-ducks had left, the shoveler raised its head and began struggling toward shore. As the shoveler moved, the steamer-duck pair again approached within 2 m, the female in the lead, but then swam off. The crippled shoveler eventually reached shore, where it died 15 min later. Examination of the specimen disclosed several broken bones, hemorrhages in the lower neck region, and massive internal bleeding at the base of the right leg. The skin was not broken, but there was obvious subcutaneous evidence of bites on the head, back, tail and left hip. The bird was fat, weighed 675 g, and was in full wing molt.

On 20 December, Nuechterlein observed another male steamer-duck "steam" across the water and catch a male shoveler by the back of the neck. The shoveler struggled free and attempted to escape, but was in full wing molt and unable to fly. The steamer-duck rushed at the shoveler again, caught him by the nape, and began beating with his wings. This time the shoveler wrenched free, dived, came up briefly 5 m away, and dived again to safety. The male steamer-duck turned back and called to his female, who Stretched repeatedly.

Steamer-ducks approaching flocks of pintails or shovelers often assumed the Submerged Sneak posture. On one occasion a male steamer-duck made three separate rushes from this posture toward different members of a

small pintail flock, all of whom flew off unharmed. We never saw a steamer-duck catch either Hooded or Silvery grebes, possibly because of their superior underwater abilities and wariness toward underwater attack. Most grebe species frequently use similar submerged attack tactics.

In the first week (2–8 December) of pair formation and territory establishment by steamer-ducks on Laguna de la Nevada, we picked up the carcasses of eight additional ducks (seven shovelers, one pintail). Two were too far decomposed to determine the cause of death but the other six probably were killed by steamer-ducks. None of the birds had suffered external breaks in the skin, yet all showed obvious subcutaneous bruises, usually on the neck, base of tail, and back. Three of the Red Shovelers were in full wing molt, and all were in good condition with excess fat. In all cases, death appeared to be caused by massive subcutaneous and intra-muscular hemorrhaging, especially on the neck (five birds) and basal joints of the wings (two) or legs (two). Drowning was another possible proximal factor causing death in these birds, but this could not be assessed.

DISCUSSION

Why has such strong interspecific aggression evolved in Flying Steamer-Ducks? We propose that the large body size, thick skin, and massive head and neck of steamer-ducks have made the risk of injury from other species they encounter on the breeding grounds almost negligible, such that for them the costs of intense interspecific aggression are greatly reduced. Even a small benefit may therefore be sufficient to release aggressive behavior, and interspecific aggression may appear to be nearly indiscriminate.

In studies on interspecific aggression, most authors have emphasized primarily the benefits that may derive from such aggression (e.g., from reduced resource competition). Predictions that result from examining the cost side of the equation have been largely ignored. The two major costs of aggression usually cited are: (1) wasted time and energy, and (2) risks of injury and predation (Wittenberger 1981). To assess their relative importance in terms of natural selection, such costs must be measured or converted to the same units (e.g., units of fitness) and interpreted with respect to their effects on reproductive success. Such a quantitative approach to the costs of aggression is beyond the scope of this paper. For most species, however, the costs of risking injury during fights are probably considerable.

Steamer-ducks may represent an extreme example of a species in which the probability of defeat, injury, or predation during fights with virtually any waterbird they encounter on the breeding ground is negligible—hence the only cost is in the investment of time and energy. This means that for steamer-ducks the threshold for intense interspecific aggression is greatly lowered.

Without data on diet and prey abundance, we can only speculate on the possible benefits that male steamer-ducks gain through interspecific aggression. One possible benefit, suggested by the presence and behavior of females during interspecific fights, may be related to sexual selection. By approaching and Stretching, females frequently seemed to instigate a fight. Possibly males victimize birds of other species in order to display their belligerency and fighting abilities to their females. Birds in full wing molt were especially vulnerable to Sneak attacks. After capturing a victim, male steamer-ducks treated it like a conspecific male and fought vigorously—more than would seem necessary to defend the territory. Yet we find it difficult to believe that male steamer-ducks repeatedly mistake their opponents for conspecifics, at least not for species as diverse as those we found.

A second possible benefit of the aggression is that it reduces competition for food. Although Red Shovelers on the lake feed primarily by straining small invertebrates from the surface, they probably also ingest snails (M. Weller, pers. comm.). Steamer-ducks feed primarily within their territories, and a flock of several hundred molting shovelers could substantially reduce the food supply of a pair. We were impressed with the ease by which territorial steamer-duck pairs kept molting flocks away from their territories following the first week of extreme interspecific aggression. Possibly observational learning is important, and holding a "public beating" enhances the effectiveness of their territorial displays.

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RECENT PUBLICATIONS

Bird navigation: the solution of a mystery?—R. Robin Baker. 1984. Holmes and Meier Publishers, Inc., New York. 256 p. $32.50 cloth, $24.50 paper. Limiting himself to birds instead of the animal kingdom, Baker has here examined migration more intensively than in his previous encyclopedic work (noted in Condor 81:121). He argues for the solution to the "mystery" mechanism(s) of bird navigation as a combination of a memorized landscape map (including smells), sun and magnetic compasses, and compasses based on stars and the moon for night-flying birds. He discusses the major hypotheses of bird navigation, the controversy surrounding them, and the systematic methodology required to prove them. While he has not solved this "whodunit," he has certainly written a useful text for teaching the scientific method. References, indexes.—J. Tate.

Falkland Island birds.—Robin W. Woods. 1982. Anthony Nelson, England. 79 p. Hard paper covers. $15.00. Source: P.O. Box 9, Oswetry, Shropshire, SY11 1BY. This is a pocket-sized version of the author's *The birds of the Falkland Islands* (no longer available). An introduction to the habitats is followed by bird lists for the islands, and the main text, in a field guide format. Illustrated with over 50 excellent photographs by Cindy Buxton and Annie Price referenced to the text. An authoritative and handy field guide. Endpaper map, index.—J. Tate.