NOTES ON THE BEHAVIOR OF THE FLYING STEAMER DUCK

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THE steamer ducks of the genus *Tachyeres* are a small group of three closely related species of diving ducks, confined to the colder southern part of the neotropical region. They are all dull grayish or brownish birds, very massive and heavy, with short wings and heavy bills; superficially similar to the large eiders of the northern hemisphere in general proportions and ecological adaptations. Their common name derives from their practice of "steaming" along the surface of the water, using their wings as paddles and churning up the water like the old-fashioned side-wheel steamers. Two of the species are so heavy and short-winged that they are essentially flightless. They can raise the body partly out of the water during steaming; but they cannot leave the surface completely. The third species is lighter and capable of "real" sustained flight in the air for short periods.

One of the flightless species, *brachypterus*, is confined to the Falkland Islands; while the other, *pteneres*, is found in the magellanic region of continental South America, Tierra del Fuego, and some of the adjacent islands. The Flying Steamer Duck, *patachonicus*, is more widely distributed, and is found throughout the ranges of both the flightless forms.

Some of the habits of the steamer ducks have been described in previous publications (see Murphy, 1936); but very little has been recorded about their special social signal behavior patterns. It may be of interest, therefore, to describe and analyze some of the hostile and sexual reactions of Flying Steamer Ducks which I observed during November and December of 1956, along the east coast of Tierra del Fuego, near Viamonte, Argentina, and the north coast of the same island, near Porvenir and Gente Grande, Chile. This may help to reveal or explain some of the basic factors regulating such behavior, and may also clarify the systematic position of the group. It has been found that some hostile, sexual, and associated patterns, especially the "ritualized" patterns or "displays", *i.e.* those behavior patterns which have become specialized (standardized and/or exaggerated in physical form) in order to subserve a social signal function, may provide reliable indications of phylogenetic relationships (see Lorenz, 1951–53). (Those patterns apparently ritualized, I indicate with capitalized names.)

Most of my observations of the Flying Steamer Duck were made in the open, without cover; but it was sometimes possible to use an empty building or some natural obstruction as a "blind". I was able to watch

the birds in a variety of environments, on small rivers and lakes and along the ocean beaches.

The period of my study was rather late in the breeding season, and I may not have seen all the hostile and sexual reactions of the species; but those patterns that were observed were probably "typical".

PURELY HOSTILE BEHAVIOR

The term "hostile behavior" is used here to include all the patterns produced by a tendency to attack and/or a tendency to escape, *i.e.* the attack and escape "drives".

(1). *Escape behavior.*

Simple "pure" escape reactions, behavior patterns which appear to be expressions of the escape drive alone, are relatively rare in the Flying Steamer Duck. They are most common as a reaction to the sudden appearance of a "potential predator", *i.e.* any large or strange object or animal (such as human beings, dogs, cars, etc.). A disturbed bird may simply swim, or "steam", or fly away from such stimuli.

These "pure" escape reactions apparently are produced when the escape drive of the disturbed bird is relatively very much stronger than the attack drive or any other counteracting motivation; (there are indications, in this and other species, that the attack and escape drives are always activated simultaneously—although one of the drives may be so much weaker than the other that it fails to express itself in overt behavior). The actual strength of the escape drive in these simple reactions would seem to vary considerably; swimming retreats being followed by steaming and then flying as the escape tendency increases.

(2). *The alert posture.*

Most birds escaping by swimming assume an erect alert posture during the retreat (see figure 2c). This posture is rather conspicuous; but it does not seem to be rigid or exaggerated enough to be ritualized.

Most of the alert postures must also be produced by a relatively very strong escape drive; but some of them occur in somewhat more aggressive situations, and may contain a slightly stronger attack component than most of the other escape reactions. The alert posture is also combined with certain display patterns (see below) which are definitely more aggressive.

(3). *Tail-raising.*

Flying Steamer Ducks swimming or floating on the water usually raise the elongate and curled central tail feathers to some slight extent.

This is so common that it is very difficult to interpret. I did notice, however, that it is often absent when birds are feeding normally, or otherwise perfectly "relaxed". This might suggest that all or most of the slight tail-raising is a very low intensity, generalized, indication of hostility, resulting from weak activation of the hostile drives.

(4). *Extraneous comfort movements.*

Both sexes may perform a number of apparently extraneous comfort movements in obviously hostile situations. (The term "comfort movements" may be applied to all movements which help to care for the body surface or plumage, such as preening, scratching, shaking, etc. A movement may be considered "extraneous" when it seems to be "irrelevant"; *i.e.* apparently out of its usual context; see Moynihan, 1955a). Among the extraneous comfort movements of the Flying Steamer Duck are head-shakes or head-flicks (vigorous lateral movements, perhaps including a slight rotary component), general swimming shakes, both with and without wing-flaps, and tail-wags, which may occur by themselves alone before or after general shakes.

Such movements appear to be unritualized in physical form, and many of them may be "autochthonous". (This term is used in the same sense as Tinbergen, 1952, meaning that some of the movements are probably "genuine" or "normal"—produced by their usual motivation, the same "care of the body surface and plumage" motivation as the similar movements in non-hostile situations.) There does, however, seem to be a definite tendency for all these movements to become more frequent when birds are mildly alarmed, *i.e.* when both the attack and escape drives are weak, but the escape component is stronger than attack. (McKinney, oral communication, has noted similar movements by other ducks in what he calls "the pre-flight situation". See also the comments in Weidmann, 1956.)

The tail-wags, and especially the head-shakes, are certainly hostile in some circumstances. They may also occur in conjunction with some of the higher intensity displays. Tail-wags may be performed by males in the Submerged Sneak Posture (see below) after vigorous aggressive chases. Head-shakes may also occur in the same situation; but they are even more characteristic of Grunting disputes. Both males and females usually perform many head-shakes during all types of Grunting; and head-shakes reach a peak of frequency during the Grunting of males in the Short-high-and-broad Posture (see below).

The motivation of these tail-wags and head-shakes is probably the same as, or very similar to, the motivation of the display patterns with which they are combined at the time.

(5). *Extraneous drinking movements.*

Another type of extraneous activity in hostile situations is "False Drinking", which is rather more conspicuous than most of the comfort movements. It is almost certainly ritualized.

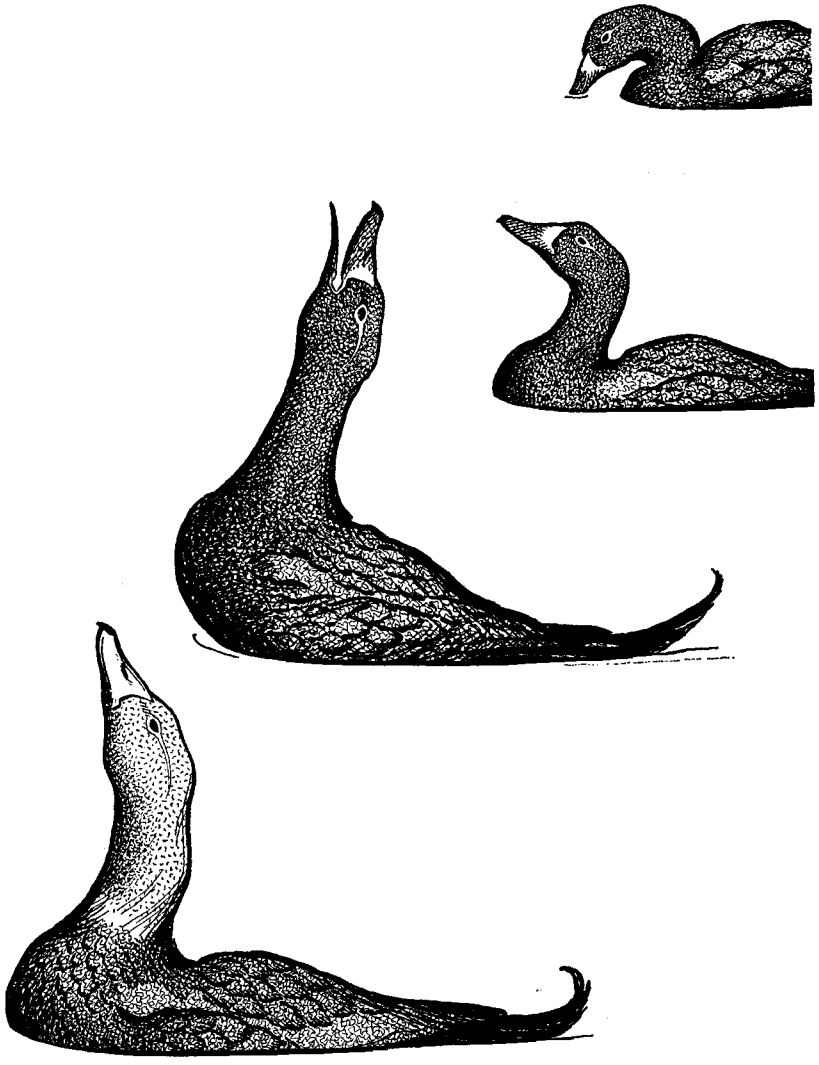

FIGURE 1. False Drinking and Stretch patterns of the Flying Steamer Duck. From top to bottom: a. the preliminary bill-dipping of False Drinking; b. the usual lifting of the head and neck after dipping; c. an extreme Stretch posture; d. the extremely vertical posture occasionally assumed by males at the climax of the second phase of False Drinking.

The first movement of False Drinking is a dipping of the bill into the water (see figure 1a). This may occur by itself alone; but such cases are relatively rare, and are obviously incomplete. The head is usually lifted after the bill-dipping, and the bill is pointed diagonally upward (see figure 1b). This is accompanied by slight swallowing movements of the bill and throat, just as in "normal" drinking in non-hostile situations. The whole False Drinking pattern, in fact, is very similar to genuine drinking in physical form. It is my impression, however, that the neck is usually stretched further, and the head and bill pointed more strongly upward, during the second phase of the hostile performance. This is certainly true of some hostile Drinking, which is almost as exaggerated as the Stretch (see figure 1d).

The motivation of False Drinking appears to be similar to that of most of the independent extraneous comfort movements—but somewhat stronger on the average. The False Drinking is usually performed by obviously alarmed birds, which are swimming, or have just swum, away from a disturbing stimulus, a potential predator or a threatening opponent during territorial disputes.

The presence of an activated escape drive in this performance is thus evident. (It should also be mentioned that False Drinking is more often performed by females than by males; and females are usually more timid, retreating more rapidly than males. Some females tend to turn away from their mates when False Drinking; and this may be another indication of their moderately strong escape tendency.) The presence of a simultaneously activated but weaker attack drive in False Drinking is less obvious, but is suggested by the fact that the Drinking is often associated, or alternated, with other hostile activities (such as Grunting) which contain an unmistakable aggressive component.

(6). *The Stretch.*

This pattern is certainly ritualized; and is apparently confined to females. It resembles the second phase of False Drinking in physical form.

Without any preliminary bill-dipping, the neck is stretched upward, and sometimes slightly backward, while the head and bill are also pointed straight up or upward and slightly backward. The stretch of the neck is very extreme, and the breast may be pulled partly out of the water by the vigor of the movement (see figure 1c). The Stretch is apparently always accompanied by a single brief opening and closing of the bill at the apex of the movement. This may be accompanied by some sound, (and the bill movements themselves are reminiscent of Grunting movements); but I have never actually heard any noise during the performance. If there is any sound, it must be very much weaker than any of the Grunts described below. The whole Stretch performance is very rapid; the performing bird relaxes almost immediately after the bill movements.

The Stretch may have been derived, at least in part, from the extraneous False Drinking. This hypothesis is supported by certain similarities in the usual circumstances of the two patterns. The Stretch tends to appear in much the same situations as the False Drinking, but it is always much rarer. This rarity, plus the extreme morphological exaggeration of the pattern, might suggest that the Stretch is produced by a similar combination of relatively strong escape motivation and weaker attack motivation, with both drives being stronger than they ever are in the Drinking (of females). There are also indications that the Stretch tends to appear whenever False Drinking movements become particularly common and vigorous—which would seem to support the same conclusion.

The signal functions of both the Stretch and False Drinking remain obscure. The physical form and motivation of these patterns are reminiscent of many appeasement displays (see Moynihan, 1955b) in other species; but I was never able to prove that they were actually appeasing in this species.

(7). *Grunting.*

The generic term "Grunting" may be applied to a whole group of rather varied but closely related vocal performances, which take different forms in the two sexes.

The Grunting of the female is simpler than that of the male. A single Grunt given by a female swimming on the water, or standing or walking on land, is always brief and moderately loud. Such Grunts are always deeper in pitch and more sonorous than any of the Grunts given by males. Single Grunts are relatively rare, as a female usually gives a series of these sounds, the successive notes being similar but separated by definite pauses. The number of notes in a series varies tremendously. In extreme cases, the series may last over a minute and include 20 or 30 individual Grunts. These series of Grunts may be uttered on land or water, and similar or identical series are sometimes given by flying females. The notes in a long series of Grunts, on the water, may become very rapid, and show a tendency to run together. This is somewhat reminiscent of the Ticking Grunt performances of the male (see below), but it is never so extremely rapid. The bill is usually opened and closed with each note; but some single notes and series of Grunts can be given with the bill apparently completely closed, or the bill may be kept wide open throughout a particularly long and rapid series of notes.

The Grunts of the female on water or land are usually given from unritualized postures, (with the neck perhaps stretched slightly upward), except when they are combined with certain other displays, which appear to be fundamentally distinct patterns and frequently occur by themselves alone (see below). The Grunts given by females in the air are apparently always given from a normal unritualized flying posture.

The hostile and ambivalent motivation of all these Grunts is particularly clear. A female may Grunt during intra-specific disputes, usually

territorial disputes between neighboring pairs, and as a response to the approach of a potential predator. In the former case, on the water, her Grunts are usually alternated or combined with both overt escape behavior, more or less precipitate retreats in the alert posture, and obviously aggressive or overt attack behavior, pecking intention movements and chases, as well as False Drinking and Stretches. All these Grunts would appear to be produced by moderately strong and approximately equal attack and escape drives. The relative strength of attack and escape may vary from time to time; but I could not detect any morphological difference between more and less aggressive Grunts. It is obvious, however, that the single notes are lower intensity than the series of notes, and that the length of a series increases as the strength of motivation, both attack and escape, increases. The longest series of notes are most common during the longest and most vigorous hostile encounters, the most violent territorial disputes. The loudness of the notes may be another indication of the strength of motivation, as the loudest Grunts I heard were given by females during particularly violent attacks or flying away from a disturbing stimulus. The particularly rapid series of Grunts seem to be the highest intensity of all. They are always rare, and seem to be absolutely confined to the most vigorous territorial disputes. All these Grunts are apparently threat (see Moynihan, 1955b). Their intimidating effect on other birds on the ground or water is usually unmistakable.

The Grunting of the male can be divided into three main types, which may be called Rasping Grunts, Ticking Grunts, and Sibilant Grunts. They are all rather different from any of the Grunts given by females, as they are all, in varying degrees, rather whistle-like, and are particularly difficult to describe in words. The best descriptive term for them might be "Whistling Grunts"; but this is preoccupied by such terms as "Grunt-Whistle" used by Lorenz (1951: 174-176) for certain displays of dabbling ducks and related forms, displays which are probably not strictly homologous with these sounds of the Flying Steamer Duck.

The various types of male Grunts tend to occur together, in a fairly rigid sequence. They are sometimes accompanied by conspicuous ritualized postures and movements, and sometimes not. In the latter case, the typical "complete" performance, on the water, is as follows.

The male swims in his usual unritualized swimming posture, or with his head and neck stretched slightly upward (see figure 2a), giving a few "introductory" notes. These are usually Rasping Grunts. Each Rasping Grunt note sounds almost exactly intermediate between the usual Grunts of the female and a pure whistle. The successive notes are separated by definite intervals, and the bill usually opens and closes

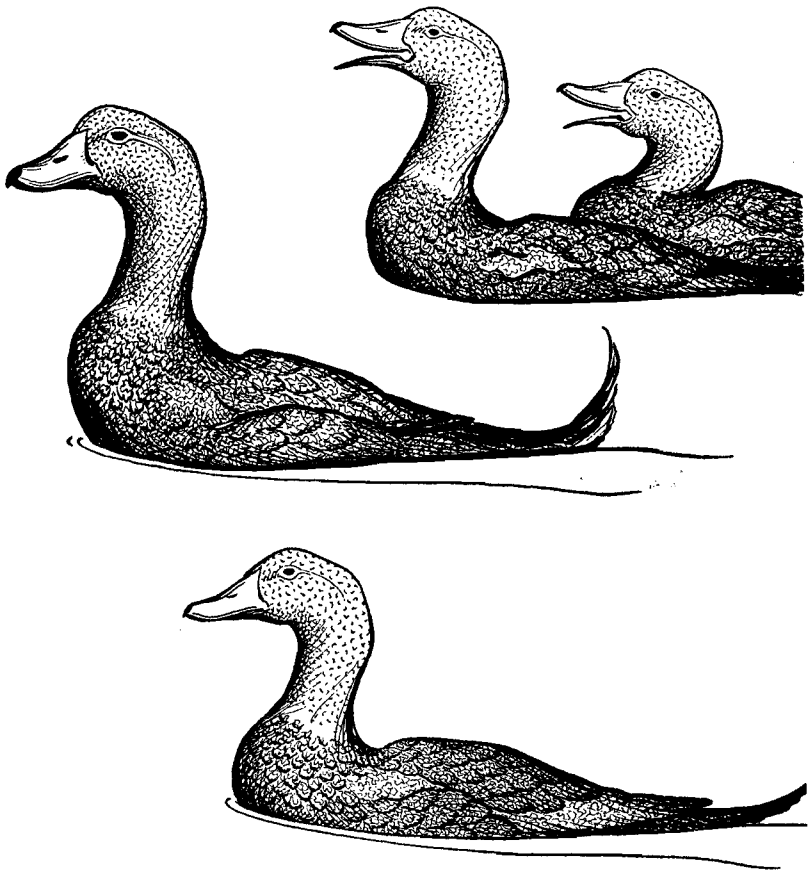

FIGURE 2. Alert and Grunting Postures. a. Top right, the unritualized posture which often accompanies the introductory Rasping Grunts of the Flying Steamer Duck. b. Top left, the erect posture which often accompanies the Sibilant Grunts of the Flying Steamer Duck. c. Center, the alert posture of the Magellanic Flightless Steamer Duck. d. Bottom, the alert posture of the Flying Steamer Duck.

with each note. This is followed by a more or less prolonged burst of Ticking, given from the same posture. A burst of Ticking sounds like a series of abbreviated single Grunts (either Rasping or Sibilant) uttered so very rapidly as to sound absolutely mechanical, like some sort of child's noise-maker. The bill is kept wide open throughout the burst of Ticking, while the tongue is raised and vibrates rapidly. (The bright yellow-orange bill of the male is conspicuous in all types of Grunting; but the Ticking also reveals and emphasizes the bright pinkish-orange color of the tongue and the inside of the mouth.) Ticking is followed

by a few Sibilant Grunts. These are similar to the Rasping Grunts; but they are even more whistle-like, the grunting quality being hardly more than an undertone. They are often accompanied by the same bill movements as the Rasping Grunts, although the last one or two Sibilant notes tend to be given with the bill almost or completely closed. The male frequently assumes a very erect posture (see figure 2b) rather like the alert posture when he begins the Sibilant Grunts, and relaxes again as soon as they are over.

There are numerous variations of this pattern—even when the more conspicuous display movements and postures are absent. The performance may end after Ticking; or Rasping Grunts may take the place of the Sibilant notes. Both the Rasping and Sibilant Grunts can also occur by themselves alone; and the number of Rasping or Sibilant notes in a series may vary from one or two to seven or eight. (I have heard a few Grunts of all types given by males on the ground, and once heard Ticking uttered by a flying male—all from unritualized postures. Such cases are very rare in comparison with the Grunting performances on the water.)

The Grunting of the male tends to occur in the same social situations as that of the female, in association with many of the same additional hostile patterns (and Submerged Sneaks). The masculine Grunts must also be produced when the attack and escape drives are moderately strong and roughly similar in strength. It is most unlikely, however, that all the Grunting sounds are produced by exactly the same motivation. The precise balance of attack and escape must be very slightly different in different types of Grunting. This is indicated by the characteristic orientation of each type, and its usual association with other hostile patterns.

The Rasping Grunts are the most aggressive of the three types. They seem to be produced when the attack drive is at least slightly stronger than escape. They are commonly uttered by males advancing toward, or chasing, an opponent during territorial disputes. They are often accompanied by the extreme Short-high-and-broad Posture or the Submerged Sneak.

The Ticking is less aggressive; probably produced when the attack and escape drives are almost exactly equal. It is seldom or never given by a male actually advancing toward an opponent. It is almost equally rare during escape. It is most common, during territorial disputes, when a male turns around, after chasing or advancing toward an opponent, and returns to his territory (and his mate, if present). It may then be accompanied by a declining Short-high-and-broad Posture, if the preceding Rasping Grunts were accompanied by an extreme version

of this posture. It is apparently never combined with the Submerged Sneak.

The Sibilant Grunts are probably the least aggressive of the three types; appearing when the escape drive is slightly stronger than attack. This is indicated by their frequent association with a very erect posture (like the alert posture) and Head-flagging (a more or less ritualized avoidance movement—see below). Sibilant Grunts are never given by a male advancing toward an opponent, and they are never combined with the Submerged Sneak. They only occur with very weak and declining Short-high-and-broad Postures after Ticking after Rasping Grunts, long after a male has turned away from his opponent. More significant still, the most conspicuous and prolonged series of Sibilant Grunts by themselves alone are given by males retreating before a potential predator (a human observer).

(8). *The Short-high-and-broad Posture.*

This is by far the most elaborate display posture of the Flying Steamer Duck. It seems to be confined to males; and only performed on the water. I have seen only one low intensity "intention movement" of this posture given by a male on land.

A male assuming the extreme Short-high-and-broad Posture stretches his neck upward and slightly backward (even raising his breast slightly out of the water), holds his head horizontal or points the bill slightly upward, raises his tail very high (sometimes raising it so far that it actually inclines forward toward his head), spreads the tail feathers, and partly spreads his wings (the carpi and primaries are usually trailed under water). The wing and tail movements reveal and emphasize the conspicuous white specula on the secondaries and the striking contrast between the dark tail feathers and the white under tail-coverts. The raised neck and tail give the body a shortened effect, and the wings are held so as to form a broad low arch. Figure 3b shows a fairly typical version of this extreme posture.

The extreme Short-high-and-broad is apparently always accompanied by Rasping Grunts. I have only seen it during intra-specific disputes, when it is assumed by aggressive males advancing toward their opponents during the most intense and prolonged territorial hostilities. Males may begin Grunting in the usual unritualized swimming posture, and then assume a more and more exaggerated Short-high-and-broad Posture as they continue to advance.

This would suggest that the Short-high-and-broad is also produced when the attack drive is stronger than escape, and both the attack and

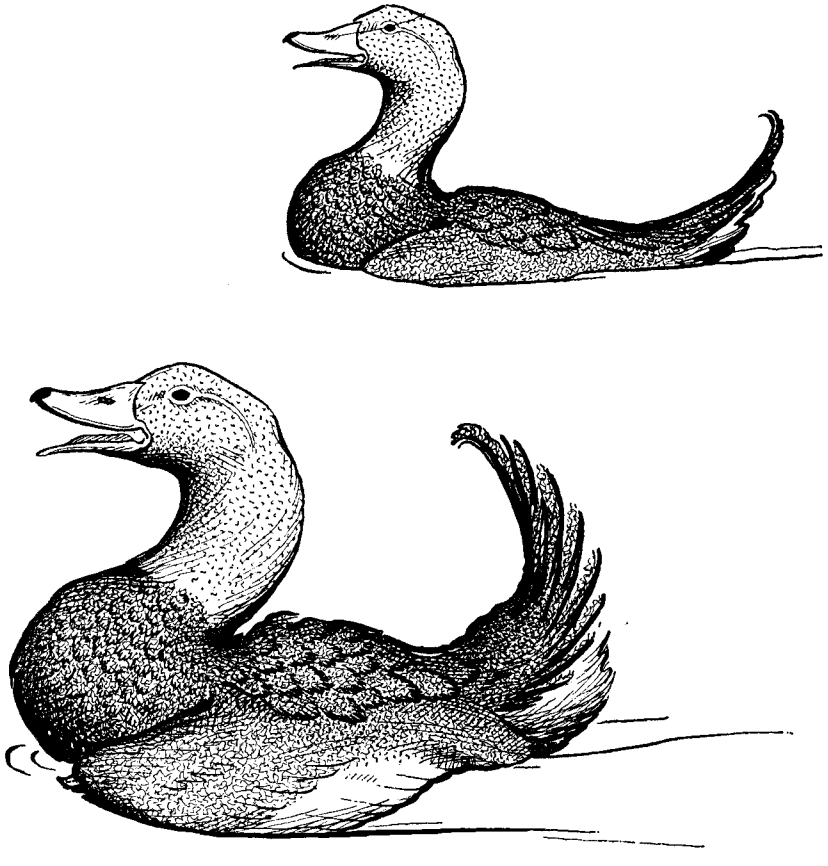

FIGURE 3. Short-high-and-broad Postures of the Flying Steamer Duck. a. Top, a weak form of the posture. b. Bottom, the extreme form.

escape drives are stronger than in the Rasping Grunts delivered from an unritualized posture. Rasping Grunts plus the Short-high-and-broad Posture are certainly rarer than Rasping Grunts alone. The extreme Short-high-and-broad Posture seems to enhance the threat valence of Rasping Grunts.

"Weaker" forms of the Short-high-and-broad Posture, with neck and tail less raised and wings less spread (see figure 3a), are also common during the same territorial disputes. Some of them, also accompanied by Rasping Grunts, are apparently produced by slightly weaker motivation than the more extreme postures—with attack still predominant. Others are less aggressive. This seems to be true of the declining postures with Ticking or Sibilant Grunts, and some even weaker and

silent postures which may continue after the Sibilant Grunts have ceased. They seem to be produced when the attack drive is relatively weaker than it is in the more extreme forms of the posture.

(9). *The Submerged Sneak.*

This pattern is almost as remarkable as the preceding one, but it is probably less ritualized. It appears to be another essentially masculine pattern, and almost confined to territorial disputes. Extreme forms of the Submerged Sneak are only shown by males chasing or advancing toward an opponent (another duck of the same or another species), sometimes continuing briefly after the advance has stopped.

A male usually begins the Submerged Sneak by swimming toward his opponent and, at the same time, gradually sinking lower and lower in the water, until only his head and bill, a small but broad "hump" of his back, and his curled tail feathers, are visible (see figure 4b). It is obvious that his neck must be stretched forward, and his head and bill are usually pointed diagonally upward. His wings are probably spread to some extent.

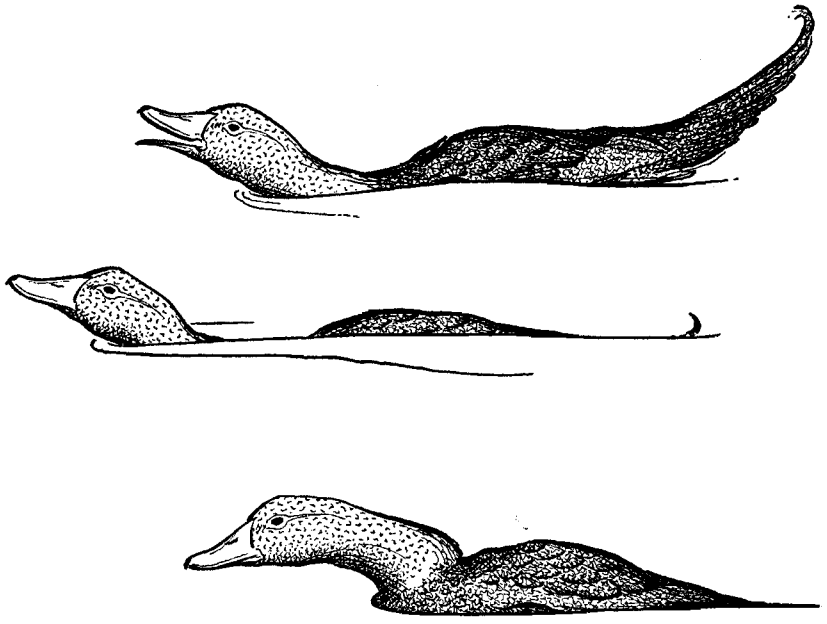

FIGURE 4. Aggressive patterns of the Flying Steamer Duck. a. Top, a posture which may be intermediate between the Submerged Sneak and the Short-high-and-broad Posture. b. Center, a typical Submerged Sneak. c. Bottom, an unritualized aggressive posture often assumed by the pursuing bird during chases.

The male may swim forward very rapidly in this posture, sinking still lower until he disappears completely in a very smooth forward dive. This often looks as if he were preparing to attack his opponent from underneath; but I never saw such an attack completed during my brief observations. The mere sight of a bird approaching in the Sneak is usually sufficient to cause any opponent to retreat very rapidly.

Some Submerged Sneaks are quite silent, and performed with the bill closed. Others seem to be accompanied by Gaping (see below). The majority are accompanied by Rasping Grunts. Less extreme forms of the Submerged Sneak are also common. The male just sinks slightly and stretches his neck forward. These performances are more often silent than the extreme Sneaks. Submerged Sneaks may be alternated with the Short-high-and-broad Posture; and I have seen a few postures which appeared to be partly intermediate between the two patterns (*e.g.* figure 4a).

All the Submerged Sneaks are very aggressive, produced when the attack drive is relatively very much stronger than escape. They also appear to be high intensity patterns; but here again the actual strength of the two drives involved would seem to vary considerably from time to time. The Sneaks with Rasping Grunts are probably produced by stronger motivation than those with Gaping movements, and these in turn are probably produced by stronger motivation than the silent Sneaks.

I have seen females briefly assume postures like the least extreme Submerged Sneaks of males (or like the unritualized pre-attack posture from which the masculine Submerged Sneak pattern was probably originally derived). These reactions occurred during the longest and most violent territorial hostilities, and were accompanied by Gaping and/or the usual female Grunts.

10. *Gaping.*

This pattern seems to be relatively rare, much less common than Grunting, or even the Short-high-and-broad Posture or the Sneak. It appears to be only slightly ritualized. It can be performed by both males and females. Simple Gaping seems to be particularly characteristic of brief non-territorial disputes, and can occur in several different contexts (like some forms of Grunting, to which it may be related).

One bird may swim after another in a mild chase, the pursuer swimming in an unritualized aggressive posture (see below) but opening and closing its bill repeatedly. This certainly looks as if the pursuing bird were uttering notes of some sort; but I am sure that some, at least, of these performances are nearly or absolutely silent. I have observed such

Gaping movements at distances of less than five feet, and heard absolutely no sound at all. Similarly, when two birds come close together, accidentally or after a brief chase, one of them may make a pecking or jabbing movement toward the other, briefly opening the bill quite silently during the movement.

These incidents, and the occasional association of Gaping with weak forms of the Submerged Sneak, would suggest that Gaping is another relatively very aggressive pattern. Gaping by itself alone is probably a lower intensity pattern than any of the Submerged Sneak performances.

11. *Possible cases of redirected attack.*

I have seen a few males, in aggressive situations, make repeated bill-dipping movements of such speed and force that they seemed to be literally "pounding" the water. The violence of these movements would suggest that they may have been cases of redirected attack behavior (see Bastock, Morris, and Moynihan, 1953), produced by relatively stronger attack motivation than any of the extraneous activities or displays listed above.

12. *Direct attack.*

The only other purely hostile patterns I observed were simple "pure" attack reactions, behavior patterns in which only the attack drive is externally visible. They were relatively uncommon. The examples I saw may have been no more than a fraction of the potential attack repertory of the species. They took the form of simple unritualized advances toward an opponent, swimming rapidly with neck stretched forward (see figure 4c), or violent steaming rushes. Most of the rushes were performed by territorial males chasing intruders, usually female, who fled immediately.

RELATIONS BETWEEN MATED MALES AND FEMALES

1. *Apparent direct hostility.*

I did not see very much hostility between the males and females of well-established pairs (it was probably too late in the season). Directly hostile reactions, *i.e.*, hostile patterns performed by one bird of a pair and directed toward its partner, apparently as a result of a definite hostile stimulus from the latter, were particularly rare.

There were only a few cases of False Drinking, Stretches, and simple Grunting, performed by one bird of a pair or by both birds more or less simultaneously, which appeared to fall into this category. They were performed by mated birds when there were no other ducks or potential

predators visible in the neighborhood (I myself being thoroughly concealed and having arrived on the scene before the birds).

2. *Timing and orientation of other purely hostile reactions between mated males and females.*

The most common hostile patterns between mates were not completely direct. They were obviously provoked by stimuli outside the pair—some definite activity by another animal.

This was certainly true of many Grunting performances. Whenever one bird of a pair began to Grunt as a response to outside stimuli, its partner would usually begin to Grunt also. The mates tended to face one another during such mutual performances. This general orientation was rough and rather variable; but certain movements of males during some of their most elaborate Grunting reactions were more rigid and interesting. It was noticeable that males often turned their heads directly toward their mates when beginning the Ticking Grunts; and the subsequent Sibilant Grunts were usually accompanied by a conspicuous reverse movement, which may be called Head-flagging. A male beginning the Sibilant Grunts and assuming the erect alert posture would simultaneously turn his head away from the female in a definite, stiff, and "ceremonious" manner (see figure 5).

Similar Head-flagging also occurred in other situations. It occurred after copulations (see below); and I have seen it performed by a male

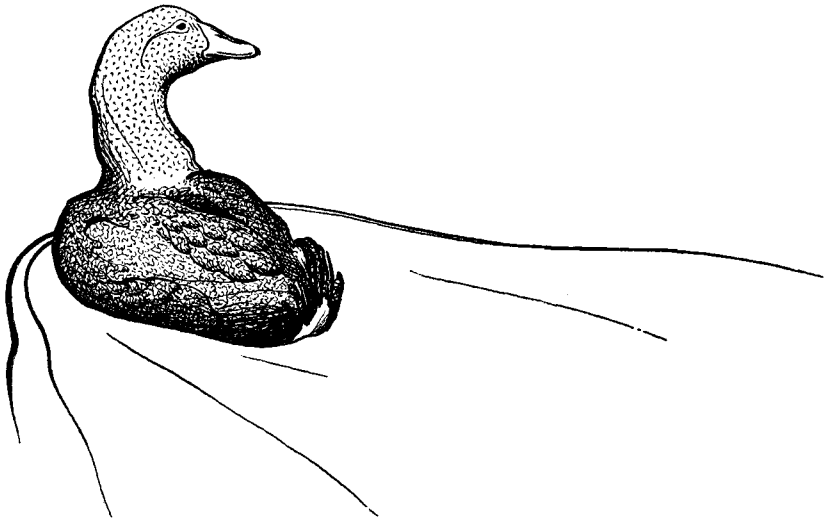

Figure 5. The Head-flagging of the Flying Steamer Duck.

swimming away from a potential predator in complete silence. The physical form of this Head-flagging is very reminiscent of certain appeasement ceremonies in other birds. It certainly seems to hide some of the stimuli revealed and emphasized by some of the threat displays, *e.g.* the brightly colored bill. It is probably one of the less aggressive hostile patterns; and the fact that it is almost always performed *vis-à-vis* the mate would suggest that it is produced by an activated sex drive in addition to the hostile motivation.

The evident tendency of mates to reorientate and synchronize the hostile behavior provoked by outside stimuli was most conspicuous during the most intense territorial disputes, when a male turned back to face his mate after chasing or threatening an opponent. Most of the patterns performed by the male in such circumstances have been mentioned earlier, *e.g.* all kinds of Grunting, the Short-high-and-broad Posture, with Head-flagging, head-shakes, etc. The female usually responded to this performance by joining the male with her own Grunting and related patterns. These patterns were sometimes alternated with other hostile displays, *e.g.* False Drinking movements by both male and female, Stretches by the female, and even traces of the Submerged Sneak by the male. This whole complex of mutual reactions, many of which must have been redirection activities, was very reminiscent of the so-called "Triumph Ceremonies" which have been described in many species of Anatidae (especially the Anserinae); and it is quite possible that most of these Triumph Ceremonies will eventually be found to be nothing more than similar cases of redirection.

3. *Copulation and associated behavior patterns.*

I observed only two complete copulations; but these were rather similar in form and may suggest the usual course of events in such circumstances. One of these copulations was preceded by a long sequence of introductory activities.

The male and female were swimming near one another when they began to dip their bills in the water. This appeared to be quite "relaxed" at first, quite like normal feeding; and there were long pauses between successive dips. The dipping gradually became more rapid, however; and both birds began to dip the whole head and neck under water. At the same time, they both tended to assume the erect alert posture between dips. This continued for a while, both the dips and the intervening alert postures becoming more extreme. Finally, the female was submerging the whole fore-part of her body during most of her dips. Then the male suddenly swam to the female, she immediately went flat and sank low in the water, and he mounted her without further pre-

liminaries. In the case of the other copulation I observed, the dipping was confined to the male. In both cases, there were also a few False Drinking movements before the copulations; but I think that these were probably provoked by outside stimuli. The actual copulations were brief, apparently successful, and much the same as those of other ducks.

The events after both copulations were almost identical. As soon as the male slid off the female, both birds assumed the alert posture, Head-flagged away from one another, and Grunted as they swam apart (I think that the male's Grunts were Sibilant, but I am not sure of this). Then both birds seemed to relax, and they began a long series of apparently genuine comfort movements.

COMPARATIVE AND TAXONOMIC IMPLICATIONS

The relationships of the Steamer Ducks have long remained rather obscure. The most important recent classification of the family Anatidae (Delacour and Mayr, 1945) includes them as aberrant members of the tribe Tadornini, the sheld-ducks and sheld-geese. It may be interesting, therefore, to compare the behavior patterns of the Flying Steamer Duck with the known patterns of other Anatidae, to see if this assignment can be confirmed.

It must be admitted, however, that most of the purely hostile patterns are not very revealing. The voices of the male and female during Grunting are certainly reminiscent of the sheld-geese of the genus *Chloephaga* (personal observation; Delacour, 1955); but the other hostile patterns are more enigmatic. Most of them, *e.g.*, False Drinking and the extraneous comfort movements, are very widespread throughout the whole family (McKinney, 1953), while the remainder, *e.g.*, the highly ritualized Short-high-and-broad Posture and the Submerged Sneak, are quite different from the known patterns of the Tadornini whose behavior has been studied (personal observation; Lorenz, 1953: 90–91; Delacour, 1955; McKinney, oral communication). The ritualized Short-high-and-broad Posture is strikingly similar to such display patterns as the "Bubbling Posture" (the most common display) of the Ruddy Duck, *Oxyura jamaicensis* (H. Hays, oral communication), and the "Head-up-tail-up" of the dabbling ducks (Lorenz, 1951–1953); but some details of its physical form, its motivation, and the accompanying sounds, are different enough to suggest that the homology, if any, is remote (although all these patterns may have been derived from similar unritualized combinations of intention movements). The Submerged Sneak is very reminiscent of certain patterns of the Common Goldeneye, *Bucephala clangula*, and the White-winged Scoter, *Melanitta deglandi* (F. McKinney, oral communication); but such little-ritualized patterns may easily

develop quite independently by parallel evolution in many unrelated species. Such patterns as the Short-high-and-broad Posture and the Submerged Sneak would really seem to emphasize the isolated position of the Steamer Ducks.

The primarily sexual patterns may be more useful or reliable in revealing phylogenetic relationships. They are usually among the most "stable", the most conservative in evolution, of the displays of the Anatidae. Some of the elaborate hostile displays and partly-hostile "courtship" patterns of undoubtedly closely related species (*e. g.* the Mandarin Duck and the American Wood or Carolina Duck, *Aix galericulata* and *A. sponsa*) may be widely divergent; but the pre-copulatory displays are often diagnostic or characteristic of large groups of species, sub-families or tribes, retaining essentially the same form in all the species of a major group (see Lorenz, 1951–53). This would suggest that the pre-copulatory dipping of the Flying Steamer Duck may be particularly significant. Similar dipping is found in both the typical sheld-ducks and sheld-geese, and the species of the sub-family Anserinae (see Lorenz, 1951–1953; Heinroth, 1911), but not in most of the other ducks whose behavior has been studied.

This would tend to support the conclusion that the Steamer Ducks are most closely related to the Tadornini; but the other distinctive behavior patterns (or distinctive combination of patterns) of the Steamer Ducks, and their general morphology, would suggest that they should be placed in a separate tribe, the Tachyerini, by themselves (as already proposed by von Boetticher, 1952). It is unfortunate that such a tribe would contain so few species; but the Steamer Ducks seem to be quite as different from the typical sheld-ducks and sheld-geese as many other species of ducks which are now put in separate tribes.

SUMMARY

The Flying Steamer Duck (*Tachyeres patachonicus*) has a considerable variety of hostile and sexual behavior patterns.

Among the hostile patterns of one or both sexes are "pure" attack and escape reactions, extraneous comfort movements, and several displays: False Drinking, Stretches, Grunting, an elaborate and conspicuous Short-high-and-broad Posture, Submerged Sneaks, and Gaping. The majority of these displays are threat.

Most of the hostility between mates is more or less redirected, provoked by "outside" stimuli. This redirection may take the form of a complex mutual performance, a sort of "Triumph Ceremony". It is possible that the Triumph Ceremonies of other Anatidae will eventually be found to be essentially similar.

Copulations are preceded by bill-dipping and followed by hostile or partly-hostile Head-flagging and Grunting.

The Grunting and pre-copulatory dipping patterns are very reminiscent of sheld-ducks and sheld-geese; but the other displays are peculiar enough to suggest that the relationship between the Steamer Ducks and the typical Tadornini is fairly remote. It may be better to put the Steamer Ducks in a separate tribe of their own, the Tachyerini.

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APPENDIX: SOME BEHAVIOR PATTERNS OF THE MAGELLANIC FLIGHTLESS STEAMER DUCK

While watching the Flying Steamer Ducks (*T. patachonicus*) near Porvenir, I caught a few brief glimpses of certain hostile reactions of the local Magellanic Flightless Steamer Ducks (*T. pteneres*). These observations were so very incomplete that I can do little more than list the patterns seen.

The escape reactions, slight tail-raising, and most of the possibly extraneous comfort movements of the Flightless birds were apparently identical with those of Flying Steamer Ducks.

The Flightless birds performed many single bill-dipping movements, as a reaction to the appearance of a potential predator; but I never saw them do anything like the second phase of False Drinking. They seemed to perform lateral head-shakes instead; (many of these shakes came right after dipping). The head-shakes of the Flightless birds were much more common than those of the Flying birds in the same area and circumstances.

The *pteneres* females performed extreme Stretch movements, accompanied by a very faint single Grunt-like noise.

Both the male and female *pteneres* uttered more complex Grunting as well.

The females did some Grunting like that of *patachonicus* females; and they also uttered some distinctive louder Grunts (probably the "bull-frog" sounds mentioned by earlier observers), which I only noted when they were frightened by a potential predator.

The *pteneres* males had a variety of Grunts, including two sounds which appeared to be homologous with Rasping Grunts and Sibilant Grunts. Some of the latter were accompanied by a definite alert posture (see figure 2b).

I also saw a few traces of what may have been a very low intensity Short-high-and-broad Posture.

These were all the patterns I had time to notice; but they do indicate that the hostile repertory of *pteneres* must be very similar to that of *patachonicus*.

LITERATURE CITED

BASTOCK, M., D. MORRRIS AND M. MOYNIHAN. 1953. Some comments on conflict and thwarting in animals. Behaviour **6**: 66–84.

BOETTICHER, H. VON. 1952. Ganse- und Entenvögel aus aller Welt. Geest und Portig, Leipzig.

DELACOUR, J. 1955. The waterfowl of the world. Vol. 1. Country Life, Ltd. London.

DELACOUR, J., AND E. MAYR. 1945. The family Anatidae. Wilson Bull. **57**: 3–55.

HEINROTH, O. 1911. Beiträge zur Biologie, namentlich Ethologie und Psychologie der Anatiden. Verh. V Int. Ornith. Kongr. Berlin. 1910: 589–702.

LORENZ, K. 1951–1953. Comparative studies of the behaviour of the Anatinae. Avicult. Mag. **57**: 151–182; **58**: 8–17, 61–72, 86–94, 172–184; **59**: 24–34, 80–91.

MOYNIHAN, M. 1955a. Remarks on the original sources of displays. Auk, **72**: 240–246.

MOYNIHAN, M. 1955b. Types of hostile display. Auk **72**: 247–259.

MURPHY, R. C. 1936. Oceanic birds of South America. Vol. 2. American Museum of Natural History, New York.

TINBERGEN, N. 1952. Derived activities; their causation, biological significance, origin, and emancipation during evolution. Quart. Rev. Biol. **27**: 1–32.

WEIDMANN, U. 1956. Verhaltensstudien an der Stockente (*Anas platyrhynchos* L.). Zeits. f. Tierpsych. **13**: 208–271.

Canal Zone Biological Area, Drawer C., Balboa, Canal Zone.