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POST-FLIGHT TAIL-WAGGING IN THE MALLARD

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Abstract.—Tail-wagging is a display in the Mallard (*Anas platyrhynchos*) hypothesized to have evolved from a maintenance activity elicited by water on the tail. Birds taking off from or landing upon water show high occurrences (≥84%) of tail-wagging in the post-flight sequences of activities. In a simple field experiment eliciting takeoff from and landing on land were found a statistically indistinguishable incidence (83%) of post-flight tail-wagging. The maintenance activity therefore is not specifically related to water on the tail and may function instead to reset feathers disrupted by flight or any other strenuous activity. As such its incorporation at the end of courtship display sequences is readily explained, although its occurrence at the beginning of such sequences remains puzzling.

MOVIMIENTO DE LA COLA POST-VUELO EN *ANAS PLATYRHYNCHOS*

Sinopsis.—Se ha propuesto como hipótesis que el movimiento de la cola por parte de *Anas platyrhynchos* ha evolucionado como una actividad de mantenimiento estimulada por agua sobre ésta. Las aves que despegan de o aterrizan en agua muestran una alta frecuencia (≥84%) de movimiento de la cola en la secuencia de actividades post-vuelo. En un experimento en donde se estimuló el despegue y aterrizaje sobre suelo, encontramos una incidencia similar (83%) al patrón de conducta observado sobre agua. Por lo tanto, esta actividad de mantenimiento no está especificamente relacionada a agua sobre la cola y la conducta muy bien puede tener como función el rearreglo de las plumas que son desarregladas por el vuelo o cualquier otra actividad. Como tal, la incorporación de este patrón de conducta al final de una secuencia de cortejo, queda de por sí solo explicado. Sin embargo, queda sin explicación este comportamiento al principio de una secuencia de cortejo.

We present data rejecting the hypothesis that post-flight tail-wagging in the Mallard (*Anas platyrhynchos*) is elicited by water on the tail or functions to shake water from the tail. Tail-wagging is a typical avian maintenance activity, being of uncertain significance and also widely used as a signal in communicative contexts. Analysis of non-signal uses of such acts is therefore an important foundation for understanding the evolution of communicative signals.

The Mallard's tail-wagging (Schwanzschütteln of German papers) has long been known to occur during courtship display (Lorenz 1958; Weidmann 1956:216, 244), in "conflict" or "frustration" situations (Weidmann 1956) and as one of many maintenance activities (McKinney 1965). Tail-wagging during courtship commonly precedes one or a series of highly ritualized displays and then follows that series as well, thus acting as a sort of punctuation (Hailman and Dzelzkalns 1974). Writing of the Anatidae in general, McKinney (1965:139) noted that "Tail-wagging normally follows every activity which involves, or could involve, wetting of the tail" and he hypothesized that "The primary function is apparently the removal of water from the tail."

METHODS

Our data on post-flight tail-wagging stem from annual fieldwork by the ethology course on the urban population of Mallards at the University of Wisconsin's Arboretum (e.g., Derrickson 1986, Hailman 1978, Hailman and Dzelzkalns 1974, Stillwell and Hailman 1978). We initially recorded post-flight action patterns in sequence after birds landed on the pond after having arrived from some distance away from the pond on which they landed (takeoff locality unknown). From these data we discovered that one or more tail-wags occurred with high probability, although there was no fixed order of post-flight acts. As landing on water wets the tail, we next began charting post-flight acts when birds flew from the pond to nearby land, and again found high instances of post-flight tail-wagging. As it could be that the tail enters the water during takeoff, we developed a simple technique of walking rapidly toward birds on land, causing them to takeoff and then land 3–20 m away on land, so that the tail could not possibly be wetted.

Proportions of post-flight sequences in which one or more tail-wagging acts occurred were tested for significant departure from 50:50 random association using a two-tailed binomial test written as shareware for the Apple Macintosh by W. R. Engels. Pairwise comparisons between proportions in different takeoff and landing contexts were tested by Fisher's Exact Test (also Engels shareware).

RESULTS

Table 1 summarizes the proportion of landings where post-flight acts included one or more tail-wags. Each proportion in Table 1 (except the 2/2 instances of taking off and landing on water, where the sample size was too small) differed significantly from a 50:50 expectation (e.g., taking off from and landing on land: $P = 0.022$, two-tailed). All 10 possible pairwise comparisons were then made between proportions and there were no significant differences between any pair of proportions (all P's > 0.2, two-tailed). We therefore conclude that post-flight tail-wagging occurs regardless of whether or not the tail becomes wet in takeoff and landing.

DISCUSSION

McKinney (1965:139–140) partially anticipated this kind of result when noting that "At times the movement is given as a direct response to water on the tail but more often it is linked in sequence with another activity and occurs even when the tail is not wet." Our data provide quantitative support for the occurrence of tail-wagging when the tail is not wetted, but the data are not consistent with the "linkage in sequence" interpretation. Decades ago it was widely believed by ethologists that action patterns were commonly linked in invariant sequences; little supporting evidence for such linkage has been subsequently reported except in specific sequences of certain displays. Furthermore, our data show that

TABLE 1. Proportion of post-flight sequences in which one or more tail-wags occurred (sequences with one or more wags/total sequences).

Takeoff place	Landing place	
	Water	Land
Unknown	25/27	—
Water	2/2	11/11
Land	42/50	10/12

there is no fixed sequence of post-flight activities; tail-wagging may occur as the first or any other act(s) in sequence. Yet another fact that makes the "linkage" interpretation untenable is the occasional occurrence of post-flight sequences in which tail-wagging does not occur, regardless of whether or not the tail is wetted (Table 1). Finally, bill-lowering, which occurs with about the same frequency as tail-wagging when birds land on water (so may be called bill-dipping in this context), does not occur when birds land on land. Thus, other post-flight acts can occur regularly when landing on water without having to occur when landing on land.

The fact that the Mallard's post-flight tail-wagging is not associated with wetting the tail does not rule out shaking of water from the tail as the ultimate evolutionary origin of the signal. In his classical paper on the evolution of signals Tinbergen (1952) pointed out that a derived behavioral pattern could be "emancipated" from its original context. It is difficult to test the notion that tail-wagging is so emancipated from wetting of the tail, but perhaps data from other *Anas* species would shed light on this possibility.

Our quantitative data on post-flight acts, combined with McKinney's (1965) qualitative notes on other contexts of tail-wagging when the tail could not have been wetted, suggest that this action pattern may simply reset the tail feathers in proper alignment after disruption. This hypothesis is testable, as it predicts that activities other than takeoff and landing that disrupt the tail feathers will induce tail-wagging. If feather-disruption is the stimulus for tail-wagging as a maintenance activity, its evolutionary incorporation at the end of display sequences (Hailman and Dzelzkalns 1974) makes good sense. However, an explanation for the evolutionary incorporation of tail-wagging to begin a display sequence remains elusive.

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