SOME FUNCTIONS OF THE RECTRICES AND THEIR COVERTS IN THE LANDING OF PIGEONS

BY HARVEY I. FISHER

THE tails of birds are used in many ways; at least, observational data have led to several postulated functions. This study is concerned with two of these—the tail as a supporting surface for part of the body weight, and the tail as an air-brake. Observations under field conditions have indicated to many workers, including the present one (1946:625), that the tail is frequently of major importance as a supporting surface and a balancing mechanism in flight. Further, depression of the tail just before the impact of landing indicates its probable use as a braking air-foil to slow forward motion.

Unfortunately, there has been no definite experimental evidence to support these hypotheses of function; and this information is virtually impossible to obtain under field conditions. Therefore, resort was taken to the experimental conditions used in previous studies (Fisher, 1956a, 1956b, 1957, 1958). Function of the tail in landing forms the basis of this study because the effects of experimental procedures can be measured.

Acknowledgments

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Methods

Pigeons (*Columba livia*) were trained to fly through a cloth tunnel and to land on an apparatus capable of measuring the three vectors of force involved in landing.

The forces of landing were measured in groups of 100 landings made at weekly intervals. The control series (300 landings) was made first, and then successive series of 300 landings were made after each successive removal of feathers.

There were two patterns of removal of rectrices: 1) removal of the inner two rectrices on each side, followed by removal of the two next most medial ones, and finally elimination of all rectrices; and 2) removal of the two outermost rectrices on each side, followed by the two next outermost, and then all remaining tail feathers. As a last experimental act in each of the two procedures described, all tail coverts were taken off. In each instance the feathers were eliminated by clipping them next to the skin, using scissors. Replacement feathers were similarly eradicated in the few instances of their occurrence.

Thus, for each of the eight pigeons used (four for each of the two patterns of sequential removal of rectrices) there were 15 sets of data, obtained over a period of 15 weeks, as follows: 300 control landings, 300 landings with four tail feathers off, 300 with eight rectrices removed, 300 with all tail feathers gone, and, finally, 300 landings of each bird with all rectrices and tail coverts removed.

The numerical data obtained were analyzed in several ways: 1) change during the 100 landings on any one day (Figs. 1 and 2); 2) change between consecutive weeks of the same series, that is, change within any one group such as the control landings; and 3) change between the different experimental and control series (Tables 1 and 2). In these analyses, comparison was made on the basis of averages of successive sets of 20 landings, of the 100 landings each week, of the first 100 landings after each experimental procedure, and averages of the 300 landings in each series.

TABLE 1

AVERAGE FORWARD (BRAKING) FORCES OF LANDING BEFORE AND AFTER REMOVAL OF TAIL FEATHERS[1]

	Removal progressive from inner to outer				Removal progressive from outer to inner			
Series	No. 106	107	109	111	No. 108	110	112	114
controls	13.2[2]	12.1	11.4	11.9	9.8	9.3	10.1	9.9
4 rectrices off	13.5	12.0	12.6	12.8	9.5	7.5	9.6	9.8
8 rectrices off	10.6	10.1	10.7	11.8	7.5	8.1	9.0	8.3
all rectrices off	11.5	11.5	10.4	11.0	8.3	7.5	8.5	8.6
tail coverts off	11.9	11.2	11.0	11.8	6.6	—	7.7	7.8

[1] Each average is of a total of 300 landings made on three successive weeks following feather removal.
[2] Forces are in millimeters of deflection. For conversion to grams see Fisher (1956b:338).

TABLE 2

AVERAGE DOWNWARD FORCES OF LANDING BEFORE AND AFTER REMOVAL OF TAIL FEATHERS[1]

	Removal progressive from inner to outer				Removal progressive from outer to inner			
Series	No. 106	107	109	111	No. 108	110	112	114
controls	10.6	10.9	10.7	11.0	9.4	9.3	9.9	8.9
4 rectrices off	11.9	12.0	12.6	12.1	9.6	7.5	9.7	9.0
8 rectrices off	10.3	10.5	12.0	11.5	9.4	8.1	8.6	9.3
all rectrices off	10.8	10.9	12.7	11.7	10.3	7.6	9.5	10.2
tail coverts off	11.8	12.3	12.0	12.2	10.1[2]	—	9.8	9.9

[1] See footnotes to Table 1.
[2] Only 240 landings; bird refused to land more than 40 times on first day.

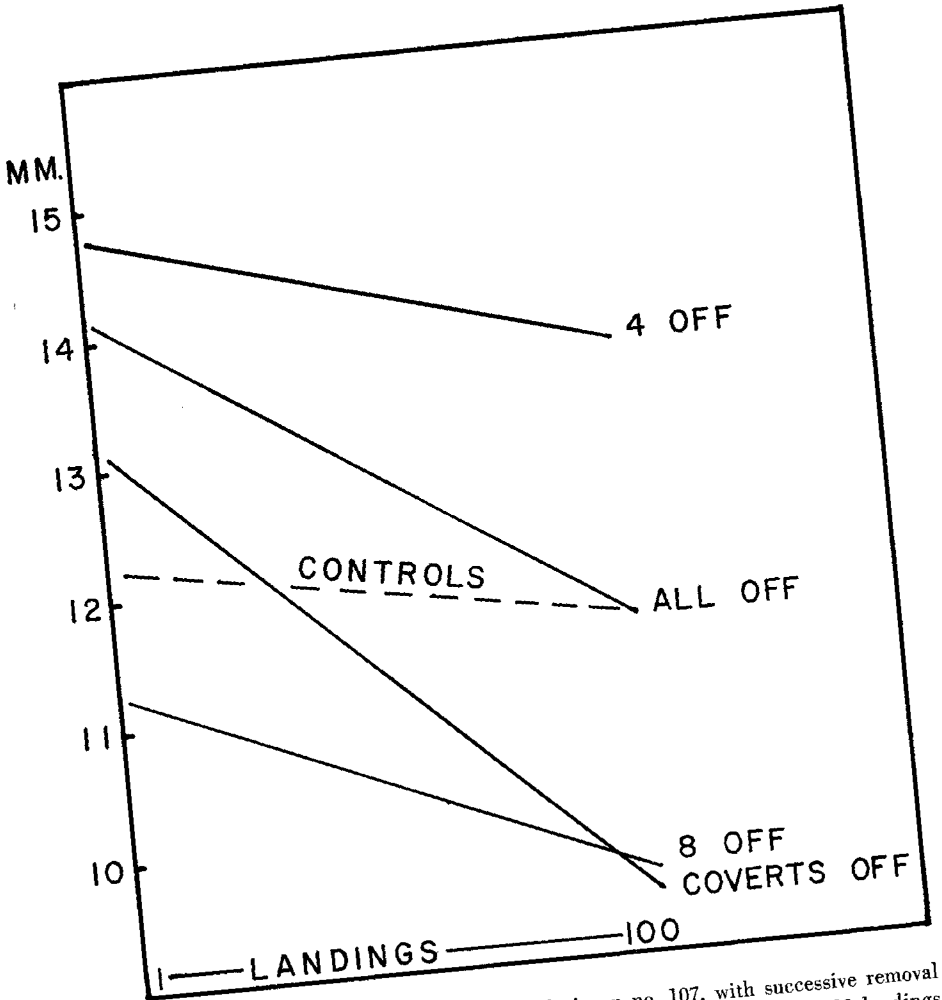

FIG. 1. Changes in braking force of landing of pigeon no. 107, with successive removal of tail feathers. Each line represents the averages of the first 20 and the last 20 landings on the first day of each series.

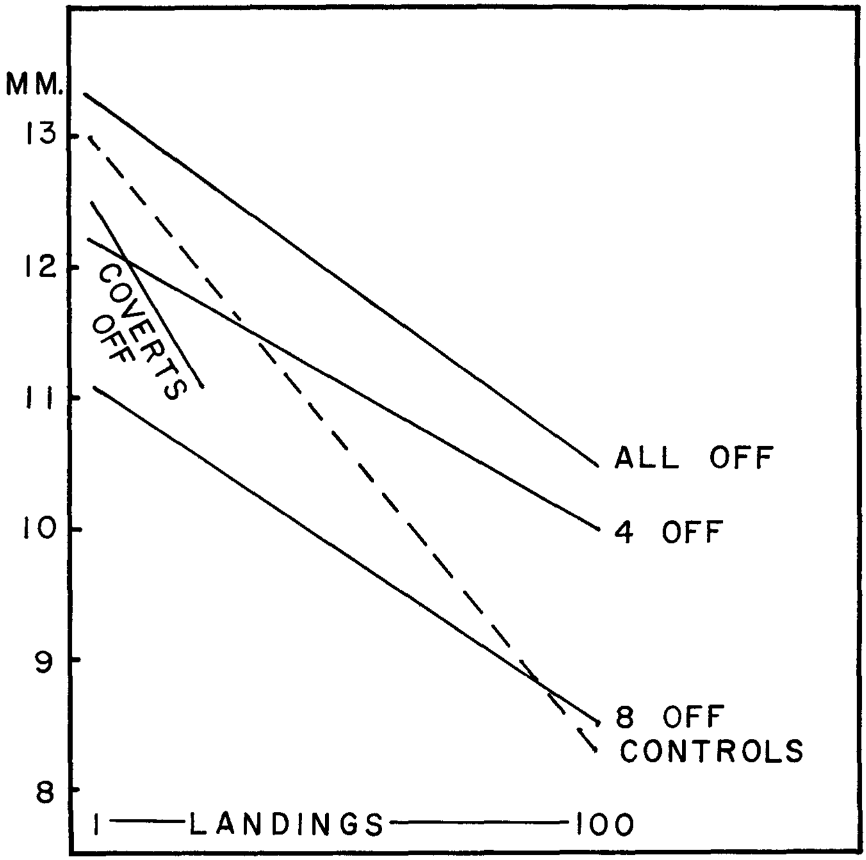

FIG. 2. Changes in downward force of landing of pigeon no. 108, with successive removal of tail feathers. Each line represents the averages of the first 20 and the last 20 landings on the first day of each series.

Results and Discussion

In most instances the various pigeons demonstrated the "learning to land" phenomenon postulated by Fisher (1956a). As before, this learning was observed within the 100 trials of each day (Figs. 1 and 2) and between consecutive weeks of each control and each experimental series.

In the analysis of successive trials it must be remembered, then, that a progressive decrease in forces would be expected. This decrease could be anticipated between the various experimental series. Thus, even in those instances where forces did not change, the very lack of change may be significant.

When feathers are removed from the center of an air-foil such as the tail, the surface area is not only decreased, it is broken into two foils. Each foil has turbulence along either edge and across its end; the increased turbulence reduces the effectiveness of the foil. Removal of feathers from either side of the tail reduces the area of the foil but probably does not materially affect the turbulence.

Under normal conditions the coverts probably do not directly affect either area or turbulence, but after removal of the rectrices the projecting coverts form an air-foil and affect both supporting area and amount of turbulence.

Successive removal of rectrices from medial to lateral.—Taking off the four central rectrices caused a major increase in both the braking and downward vectors, but the effect was greatest on the braking force (Tables 1 and 2, Figs. 1 and 2). Nevertheless, both forces decreased during the 300 trials, as the pigeons learned to land with their new tail-foil. Removal of four additional central rectrices did not interrupt this learning, and forces continued to decrease. However, when all the rectrices were taken away a new situation was presented, and the forces either increased or decreased only insignificantly. With expected learning, decreases should have occurred.

In these birds, removal of the coverts increased the initial forces of landing or at least prevented anticipated decreases (Tables 1 and 2), but, as exemplified by pigeon no. 107 (Fig. 1), the birds learned to land very lightly by the end of the first 100 trials after the coverts were clipped.

It was apparent in these four pigeons that the downward vector was affected more than the braking vector.

Successive removal of rectrices from lateral to medial.—This sequence of removal did not disrupt the previously established patterns of forces as much as removal from medial to lateral. This was expected.

Braking forces decreased at approximately the same rate as in previous experiments, except for the series of birds with four lateral rectrices off and with all rectrices off. These latter decreases were less.

Downward vectors of force exhibited no significant changes on the basis of averages (Table 2) and this indicated a loss of effectiveness in supporting the body weight. It may be observed in Fig. 2 that the typical bird showed decreased downward forces during the first 100 trials after each removal. Nevertheless, all final trials had these forces as great or greater than the forces during the control landings.

Another phenomenon associated with removal of all rectrices and with removal of coverts was observed in three of the eight pigeons. Pigeon no. 106 was very hesitant to fly and land after covert-removal; many unsuccessful attempts were made. Pigeon no. 108 refused to fly and land more than 60 times immediately after covert removal; this same pigeon was "difficult" after all the rectrices were taken off. No. 110 never would perform properly after the coverts were eliminated. These three birds were well trained, and there had been no "reluctance" in prior landings. It is my feeling that these pigeons may not have performed because the tail was so ineffective.

In six pigeons Fisher (1956a: 95, Fig. 6) noted, during the first 100 trials, that downward force was greater in terms of millimeters of deflection than forward (braking) force and that the latter was more variable. In the four pigeons of this study in which removal of rectrices started medially, braking force exceeded down force in the first 600 landings and the two forces were approximately the same at the end of all experiments. In the four pigeons from which removal of lateral rectrices was first, the two forces were nearly equal initially, but downward force was much greater by the time the entire tail and coverts were removed, but only because braking forces decreased. The comparisons of the controls of this and the previous study indicate individual variation, of course, but the differences between the control series of 1956 and the present experimental ones are significant in their support of several opinions expressed above concerning the disruption, by the experimental procedure, of the decreases in forces that might be expected to result from learning. For example, only in the braking forces of pigeons subjected to removal of rectrices from lateral to medial is there consistency with the postulated pattern of decrease with learning.

Summary

Evidence is presented to show that the tail, in domestic pigeons, is used both as a mechanism for slowing forward motion (braking) just prior to landing and as part of the surface to support the weight of the bird.

Obviously the removal of rectrices, medially or laterally, reduces the supporting area; this would be expected to increase the downward vectors of force at the time of landing. However, the pigeon can compensate in some manner to hold these forces down to the control level. Removal of medial rectrices, because it forms two air-foils, with attendant increases in turbulence, where only one existed before, causes a greater increase in the downward vec-

tors. When the rectrices are removed in sequence from outermost to innermost, removal finally of the coverts causes no great increase; when the removal starts medially, taking off the coverts as a last procedure results in significant increases in downward vectors. In the latter instance the coverts form an important part of the functioning air-foil, replacing in part the absent medial rectrices.

The braking functions of the tail were less disturbed by removal of rectrices, probably because it is easier for the bird to compensate by varying its landing speed, its rate of wing-beat, and its angle of inclination at the moment of landing. Progressive removal from lateral to medial results in a pattern of braking forces not different from the patterns of decrease exhibited by control birds over comparable lengths of time. In other words, there is nearly complete compensation by the pigeons.

When medial rectrices are taken off first, the bird cannot compensate so completely for the effects of added turbulence and the decreased surface of the resulting double air-foil. In some pigeons little compensation, as indicated by little if any decrease in braking forces during the experiments, occurs. This breakup of the expected pattern of decrease reveals the use of the tail as an air-brake.

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DEPARTMENT OF ZOOLOGY, SOUTHERN ILLINOIS UNIVERSITY, CARBONDALE, ILLINOIS, FEBRUARY 16, 1958