

FOOTEDNESS IN DOMESTIC PIGEONS

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IN studies of the landing forces of Domestic Pigeons (*Columba livia*) it was noted (Fisher, 1956*a*, 1956*b*) that the birds did not always land simultaneously on both feet. The apparatus used made it possible to determine which foot was of primary importance in landing.

In some landings both feet are uniformly extended forward and down to meet the platform; this is designated as landing on both feet. At other times and in other pigeons the right or left foot is extended farther forward and bears the main brunt of landing; the opposite leg and foot are moved laterally and apparently serve as a balancing brace at the time of contact with the perch. Any laterally directed push exerted by either leg is indicated as a lateral force on the recording drum of the machine. A right-footed landing is one in which the left leg and foot are the brace and the right foot touches down first to stop the bird. Left-footed landings are characterized by a balancing function of the right foot, while the left takes the force.

Correlation of slow-motion pictures, of observation at the moment of landing, and of the record of forces measured by the apparatus enabled me to establish "patterns of footedness" for each pigeon.

The general methods of handling the birds were as described earlier (1956*a*). In the present experiments the birds usually were landed at least 100 times in a 3-hour period at weekly intervals. Duration of experimentation with each bird can be found in Table 1. Birds nos. 54–104 were used in 1954–1955, the others (106–110) in 1956. Because many of these data were gathered from experiments designed for other purposes, only fragmentary information was available on several birds. On some dates, data on footedness were taken only part of the time. However, the data analyzed included 7259 landings by 11 different pigeons.

From the curves representing forces exerted by the feet it is possible to derive two kinds of information on footedness—footedness at the time of initial contact with the platform and footedness based on greatest lateral force exerted during landing. Both these analyses were made and the results did not greatly differ. The foot used as a brace on the initial contact with the platform was usually the one that exerted the greatest force later in the process of landing. For example, in Table 1 it may be noted that, on an initial contact basis, bird no. 102 landed 56 per cent of the time on the right, 37 per cent on the left, and 7 per cent on both; comparable data, on a greatest lateral force basis, are 50 per cent right, 34 per cent left, and 16 per cent both. Further, it appeared that initial choice was a better indication of innate behavior than was greatest force, which might depend on other variables, such

as imperfect balance after landing, for example. Therefore, all data in this paper were derived on the basis of the initial contact.

RESULTS

Data in Table 1 indicate that, if all the landings for each bird are considered, seven of 11 pigeons were right-footed most of the time, three were left-footed, and one (no. 108) showed no significant preference for either foot. (No. 57 is a special case to be discussed later; it is here considered to be right-footed.) In each instance the preference was significant (at least 3 to 1, except for pigeons 102 and 107); in no. 102, with only 244 observed landings, the difference may or may not be significant, but the difference between

TABLE 1
SUMMARY OF FOOTEDNESS IN ELEVEN PIGEONS

Pigeon number	Total landings	Duration of experiment (weeks)	Foot landed on (per cent)		
			Right	Left	Both
54	338	6	27.2	66.0*	6.8
55	218	6	63.8*	22.9	13.3
57 (first weeks)	477	7	70.2*	23.5	6.3
57 (last weeks)	496	8	13.3	82.5*	4.2
101	276	5	65.6*	24.6	9.8
102	244	7	56.1*	36.9	7.0
104	40	1	12.5	47.5*	40.0
106	61	1	91.8*	3.3	4.9
107	1312	16	35.1	52.6*	12.3
108	1443	16	44.4	43.2	12.4
109	1302	12	92.5*	2.6	4.9
110	1052	14	93.3*	5.2	1.4

* Indicates predominant use.

35 per cent and 53 per cent for pigeon 107, which was observed on more than 1300 landings, was significant.

It is of interest that three birds (nos. 106, 109, 110) were right-footed more than 90 per cent of the time. The other extreme is of course no. 108 which was nearly "ambidextrous."

Simultaneous and equal use of both feet usually occurred less than 15 per cent of the time (Table 1, Figs. 1 and 2); bird no. 104 showed 40 per cent of the landings on both feet, but this was seemingly a phenomenon associated with the small number of landings.

Figure 1 illustrates the day-to-day variation in footedness as exhibited by

pigeon no. 107. Such working graphs were constructed for each bird. Figure 1 represents a situation similar to that found in pigeons 54, 55, 101, 102, and 108. Several interesting facts are evident, and they are generally true for all the pigeons just listed. On the first day's trials the birds showed less preference than was usual in later trials. The only pattern visible was that for several weeks (April 19–May 1, for example) a bird would be left-footed, then be right-footed for one to three or four weeks, and finally again be left-footed or right-footed, as the case might be. Footedness in these pigeons might thus be considered partly as a pattern set up each day by some event during

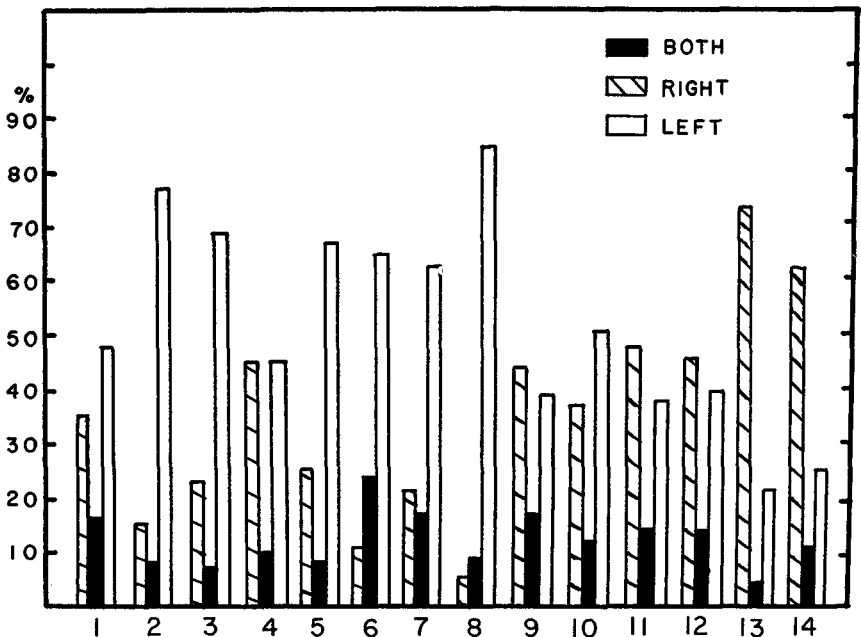


FIG. 1. Choice of foot during 14 successive, weekly sets of 100 experimental landings by pigeon number 107.

the first trials of that day or perhaps by something in the latter landings of the previous period of experimentation. However, it is evident in Figure 1 that no. 107 was essentially left-footed for the first eight weeks and then *gradually* became predominantly right-footed.

In an attempt to discover the causes of change in footedness, the data for each bird were set up in successive groups of 20 landings on each date. Information in Tables 2 and 3 is selected from the much more extensive working tables for these birds. Study of these working tables revealed that the pigeons demonstrated less preference for either foot during the early trials

on any one day than was generally the case for subsequent trials on that day. Note the data in Table 1 on pigeon no. 104. Further, in Table 2 compare landings 1 to 20 with the average of any other set of 20. Bird no. 108 (Table 3) did not show this pattern, but remember that, considering all dates and trials, it was the one bird that showed more or less uniform use of either foot. It is of passing interest that the landings from 40 to 80 in no. 108 were significantly right-footed, based on the averages of all trials, not just those shown in the table.

Rapid, perhaps day-to-day, changes from left to right or vice versa might be foreshadowed by changes in choice evident the preceding day of trials.

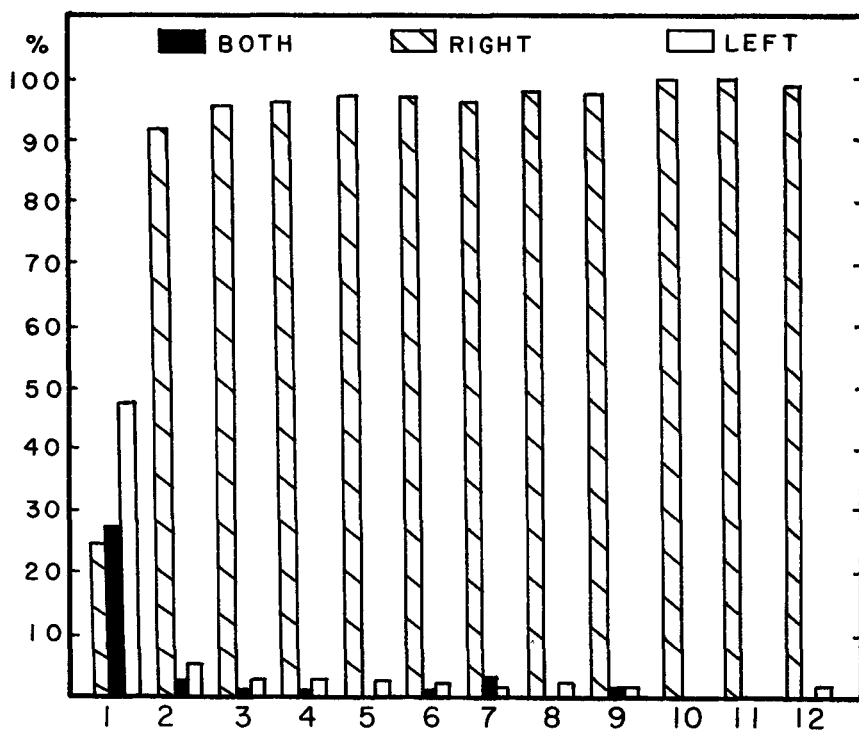


FIG. 2. Choice of foot during 12 successive weekly sets of 100 experimental landings by pigeon number 109.

This did not seem to be true, however. There was no tendency, for example, for a right-footed bird to be more left-footed in the later trials of the day preceding its change to the left-footed condition.

Figure 2 illustrates successive experiments with a bird that was unquestionably right-footed. Birds 109 and 110 were extremes of this type.

Pigeon no. 57 represented a particularly interesting example of an apparent

TABLE 2
FOOTEDNESS IN PIGEON NO. 107 ON SELECTED DATES

Date	Foot	Trials				
		1-20	21-40	41-60	61-80	81-100
April 19	right		6	6	9	8
	both	lost	0	4	4	5
	left		14	10	7	7
April 24		1	5	4	3	
		2	3	0	2	none
		17	12	16	15	
May 22		9	4	7	4	1
		2	3	1	2	0
		9	13	12	14	19
May 29		3	2	4	1	1
		7	4	4	4	5
		10	14	12	15	14
June 19		10	7	10	8	10
		5	1	6	2	4
		5	12	4	10	6
June 26		7	10	9	7	3
		4	2	2	3	1
		9	8	9	10	16
July 3		17	4	6	8	13
		1	4	4	5	1
		2	12	10	7	6
July 24		10	13	18	15	18
		1	1	0	1	0
		9	6	2	4	2
All 14 days of trials—percent	right	41.9	34.6	36.2	29.7	33.9
	both	16.2	11.6	10.8	13.3	9.4
	left	41.9	53.8	53.1	57.0	56.7

change in footedness. This bird was one of six used in extensive experiments in 1954-1955 (Fisher, 1956a). Some time after the culmination of the initial experiments, all the birds exhibited typical symptoms of Vitamin B deficiency and their condition was later diagnosed as such. The pigeons had been held indoors for nearly a year, and fed a diet of cracked corn, cracked wheat, and sorghum grain. However, for three months prior to the appearance of the symptoms the diet was primarily cracked wheat which was stored in a heated building; the vitamins were largely lost under these conditions.

TABLE 3
FOOTEDNESS IN PIGEON NO. 108 ON SELECTED DATES

Date	Foot	Trials				
		1-20	21-40	41-60	61-80	81-100
April 19	right	10	8	3	2	
	both	2	2	6	0	none
	left	8	10	11	9	
April 24		6	5	3	2	4
		2	4	6	6	2
		12	11	11	12	14
May 1		11	17	17	18	14
		0	0	3	1	1
		9	3	0	1	5
July 3		2	1	4	2	1
		2	2	2	0	1
		16	17	14	18	18
July 10		4	2	4	2	0
		6	2	4	5	3
		10	16	12	13	12
July 24		10	16	19	20	18
		3	3	1	0	1
		7	1	0	0	1
All 14 days of trials—percent	right	43.2	41.4	49.4	47.8	43.0
	both	10.4	13.9	12.8	12.0	12.1
	left	46.4	44.6	37.7	40.2	44.9

Treatment of the birds with concentrated vitamins apparently resulted in complete recovery.

No. 57 which had been a right-footed bird prior to the deficiency (Table 4) became decidedly left-footed and remained so until its death from other causes some six months later. It is significant that the change took place within a two-week period. At autopsy there was observed a macroscopic lesion of the central portion of the central lateral part of the right cerebral hemisphere. Whether the damage was induced by the deficiency and whether the lesion caused the change in footedness could not be determined; the evidence was circumstantial.

This pigeon showed the typical less-defined choice of foot in the initial 20 to 40 trials each day. As a right-footed bird the initial trials each day were about 54 per cent right and 39 per cent left; by the end of the first 100 landings each day it landed 90 per cent on the right foot and 5 per cent on the

TABLE 4
FOOTEDNESS IN PIGEON NO. 57, IN PERCENTAGES

Date	Foot	Trials					Average
		1-20	21-40	41-60	61-80	81-100	
Dec. 3-30	right	54.3	59.2	88.8	82.5	89.5	70.2
	both	7.1	9.2	2.5	5.0	5.3	6.3
	left	38.6	31.7	8.8	12.5	5.3	23.5
Jan. 8-Feb. 9	right	25.4	8.3	9.2	8.1	9.9	13.3
	both	3.0	4.2	7.3	1.6	4.2	4.2
	left	71.6	87.5	83.5	90.3	85.9	82.5

left. As a left-footed bird, it averaged 72 per cent left and 25 per cent right in the first 20 trials each day, and by the finish of the day's trials it averaged 86 per cent left and 10 per cent right.

It should be noted here that the birds were worked in pairs in so far as was possible; that is, nos. 54 and 55, 101 and 102, 107 and 108, and 109 and 110 were flown and landed on the same days. The fact that the two birds in a pair did not always show the same preference indicated the probability that external factors were not the deciding factors on any one day. Further evidence for this probability is in Tables 2 and 3. Compare, for example, the percentage for the two birds on July 3.

SUMMARY

Observations and mechanical recordings were made of 7259 experimental landings by 11 domestic pigeons. During the five to 16 weeks of experimentation with each bird it was noted that seven pigeons used the right foot predominantly, three the left foot, and one bird showed no particular preference for either. Three birds used the right foot more than 90 per cent of the time. No individual showed such a significant choice of the left foot; no. 57 used the left foot 83 per cent of the time but only under abnormal conditions. One might say, therefore, that the right-footed condition was usual and that the left-footed pigeons were not as strongly left-footed as the right-footed birds were right-footed.

To my knowledge, predominant use of right or left limbs has not been demonstrated previously in any animal except man.

The pattern in pigeons does not, however, seem to be of the same kind as in human beings. In pigeons, although they may show an average preference for one foot over a long period of time, choice of foot seems in part to be a matter of daily preference. In general, there was less choice shown on the first

day a pigeon was landed and on the first 20 to 40 landings each day. Analysis of records preceding day-to-day changes in footedness did not reveal any gradual change in choice of foot. There may, however, be a gradual change over a period of several weeks.

It may be that there was a determining stimulus in the way the birds were handled, but all birds were treated in exactly the same manner and pairs of birds landed on the same days exhibited different patterns. If there was an external stimulus provided by the experimental situation, it did not affect all pigeons in the same way.

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SAW-WHET OWL (*Aegolius acadicus*)
with meadow vole (*Microtus*). Photographed on the Weber River, Weber
County, Utah, in April, 1948, by R. J. Erwin and Richard D. Porter.