THE LANDING FORCES OF DOMESTIC PIGEONS

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THE force with which a bird lands on a perch may have considerable ecological and anatomical significance. This force, along with the body weight of the bird, may determine the type of perch used for roosting at night and the sequence of perches or landing areas used in approaching the nest, and it may even play an important role in habitat selection. For example, it is difficult to envision a Mallard or a Pintail Duck landing on even the larger branches of a tree, if one has ever observed the apparent force with which these ducks hit the water. Other ducks of similar body weight do land in trees. Large herons may be seen landing very lightly on the smaller twigs of trees and bushes and on soft mud; much lighter birds of similar pedal structure almost never utilize such landing places.

Such differences in landing may result from differences in habit, in structure, in behavior, or in the situation encountered. The force with which a bird lands is not solely a function of its weight; action of wings, of tail, and of legs modify this force, as does the pattern of landing.

For the student of functional anatomy, the landing force may be a means of studying the locomotor organs—wings, tail, and legs. In the literature we find no information relative to the forces with which any of these appendages move. Wind tunnel experiments to determine flight characteristics of airplanes are fairly successful because, compared to the avian wing, the wing of an airplane is very simple. It has been estimated that there are at least ten times as many variables in the wing of a bird. We cannot yet measure the force of the movement of the wing or the tail when these parts are in use, under natural or experimental conditions, although it is not difficult to imagine a large bird trained to fly with small transistors attached to various parts of its body to record a host of data.

Fisher (*in press*) has described an apparatus that makes possible the actual measurement of leg thrust when a bird takes off or lands. Knowing the force of the legs at the time of the take-off and the weight and speed of the bird, it is possible to calculate the force that must have been supplied by the wings during take-off. At the time of landing there are three major groups of variables—the parts of the wing, of the tail, and of the leg. If the force of landing of a bird is constant under certain controlled conditions, any change in one of these groups may be reflected in different forces being exerted by one or both of the other groups. Unfortunately, because the force of only the legs can be measured at the time of landing, variation in wing force may be reflected in unmeasured changes in tail action, and the reverse is true.

The purpose of the present experiments was to ascertain the "normal" or "usual" force with which domestic pigeons landed. The usual force of an individual bird was to be compared with the force after surgical removal or impairment of a structure in that bird. It was soon learned that determination of the usual landing force was a major problem in itself and one with many interesting aspects. This paper is thus restricted to a discussion of usual landing forces; some 4000 landings were measured.

MATERIALS AND METHODS

Domestic pigeons (*Columba livia*) were selected as the experimental birds for a number of reasons. There were on hand several pigeons that had been in captivity for one to three years and were used to handling. Young birds are easily raised in our sheltered, outdoor pens and provide a supply of birds of known age. The pigeon is large enough to make experimental surgery fairly easy, and yet it is small enough to have room to fly and otherwise live successfully in the outdoor cages.

Six pigeons were used in the present experiments: No. 54, male (3 years of age and originally a wild bird); No. 57, male (more than 3 years of age, raised in captivity); and Nos. 55, 101, 102, and 104, sex unknown (all approximately 1 year of age and raised in captivity). A major part of the work was done with No. 57 because he had been a pet of children, had been handled extensively, and was thought to be more easily trained. However, it was found later that all the birds readily adapted to the conditions of the experiments.

The apparatus used to measure the three vectors of landing force—down, back, and lateral—and the basic methods of its use have been described by Fisher (*in press*).

All experiments were conducted under exactly the same conditions. The same room was used, and it was thermostatically heated to 70° F. The flight tunnel was hung from the ceiling at an angle of 15 degrees from the horizontal landing platform. Both ends of the tunnel were wide open, but the birds, for some unknown reason, did not fly out the open end above the platform. The 12-foot length of the tunnel was determined after repeated field observations indicated that pigeons generally did not start their landing patterns farther than 12 feet from the perch. A single light suspended above the middle of the length of the tunnel provided the only illumination; the windows were at all times covered by dark shades. The thin walls of the tunnel permitted the light to pass through; the result was an excellent, soft light inside the tunnel and on the landing platform.

The landing platform was 15 inches in diameter, flat, and covered by hardware cloth with an eighth-inch mesh. The hardware cloth virtually eliminated slippage except on the most forceful landings. The flatness and rigidity of the platform must be noted, for it is likely that forces of landing would be quite different if a flexible, cylindrical perch (similar to a small branch of a tree) were used.

Before any experiments were started, the birds were kept in two small rooms, joined by a doorway, for several weeks. Between experiments they were returned to these rooms. By chance, the rooms were of such size and arrangement that the longest straight-line flight possible for a pigeon was about 10 feet. Food and water were placed on a shelf, and the birds flew freely to them and to perches in the room. However, in no way did conditions in these rooms simulate conditions in the room used for experimental flights. In the holding rooms the perches were mostly wooden bars and window ledges.

ACKNOWLEDGMENTS

The Research Board of the University of Illinois provided funds for the construction of the measuring device. Miss Doris Krull aided in running many of the test flights, as did my sons, Fred, George, and James, and my wife, Mildred. Because of the need for close observation of each landing, one of the above persons worked with me each time birds were flown. My sincere thanks go to all of them and to the Research Board.

THE EXPERIMENTS

The original reason for initiating this work was to measure the function of certain parts of the pigeon's locomotor apparatus. It was planned that 100 landings per bird would be measured each week for three weeks, giving 300 landings to use as a "normal average" or control for each bird. It soon became evident that the force of landing changed during each day's trials and from week to week. Therefore, it was necessary to run extensive series of landing experiments to determine the nature and degree of these changes.

The general pattern of the experiments was to record the forces when the bird was landed at least 100 times on one day of each week. After several weeks of this the bird was to be landed 100 times at daily intervals for a week and for two-day intervals for a week. These trials were to be followed by landings at one-week intervals and finally by trials two weeks apart.

At least two birds were to be landed each day. They would act as a kind of control for each other to insure that possible differences between birds and between different periods of trials of the same bird were truly differences and not the result of unknown changes in method of handling, in temperature, or in the machine. This procedure was not possible each day; it was followed on 18 of the 30 days.

Moving pictures were made of some 300 landings.

The records of landings made on any one day were arranged in groups of 20 successive landings for statistical analysis. The heights of the curves recording down and back forces were measured to the nearest tenth of a millimeter, using vernier calipers. Lateral forces were unimportant in the present study except as they were used to note whether a bird landed properly and whether the record should be used. Statistical analysis was made of these measurements; the millimeters were not converted to grams, as is possible using the calibration of the machine (Fisher, *in press*). Conversion would have meant dropping fractional measurements, including possible errors in converting, and in general the obscuring of minor changes or differences.

Forces in grams are given in Figure 2 to present some concept of the forces involved in landing.

The machine is approximately twice as sensitive for down forces as for back forces. Therefore, a curve height of 13 millimeters for the down force equals about 2300 grams; the same height on the curve for the back force equals about 1100 grams. For simplicity, since millimeters were not converted to grams, total force is computed by multiplying the millimeters of down force by two and adding the millimeters of back force. Since all forces given are averages, there may be slight discrepancies in this calculation; these errors never amounted to more than 0.3

millimeters. Similarly, ranges given for total force are relatively meaningless because the extremes may be composites of records of different trials.

The data for total, down, and back forces of each day's trials were arranged as in Table 1. In this format it was relatively easy to make comparisons between successive groups of landings on one day (P values in right column) or between any group of these trials and the comparable group of another date.

TABLE 1

RECORDS OF ONE DAY'S LANDINGS BY PIGEON NUMBER 104

March 27, 1955. Weight: at start, 300 gms.; at end, 285						
Trials	*Mean in Millimeters*	*Range*	*Standard Deviation*	*Coefficient of Variation*	*Comments*	
	Total Force—no significant decrease from trials 1 to 100					
1–20	22.1±0.86	16.1–29.4	3.84	17.4		
21–40	21.5±0.51	16.6–25.9	2.30	10.7	↓	P >.10
41–60	22.0±0.75	16.6–25.9	3.36	15.3	↑	P >.10
61–80	21.4±0.70	15.0–27.6	3.15	14.7	↓	P >.10
81–100	21.1±0.64	16.9–25.9	2.85	13.5	↓	P >.10
101–120	18.7±0.80	13.8–28.2	3.57	19.1	↓	P <.05
	Down Force—no significant decrease from trials 1 to 100					
1–20	6.8±0.32	4.2–9.4	1.41	20.7		
21–40	6.6±0.18	5.1–7.9	0.82	12.3	↓	P >.10
41–60	6.8±0.27	4.4–9.1	1.23	18.1	↑	P >.10
61–80	6.4±0.24	4.7–9.2	1.08	16.8	↓	P >.10
81–100	6.3±0.18	4.9–7.7	0.82	13.0	↓	P >.10
101–120	5.7±0.31	4.1–9.1	1.38	24.3	↓	P <.10
	Back Force—no significant decrease from trials 1 to 100					
1–20	8.5±0.29	6.3–10.8	1.29	15.1		
21–40	8.2±0.24	6.4–10.7	1.07	13.1	↓	P >.10
41–60	8.3±0.32	5.7–10.9	1.42	17.1	↑	P >.10
61–80	8.6±0.30	5.6–10.7	1.37	15.9	↑	P >.10
81–100	8.5±0.32	6.3–11.6	1.45	17.1	↓	P >.10
101–120	7.2±0.30	5.6–10.0	1.35	18.8	↓	P <.01

The experiments represented in this study include records of 2660 landings by pigeon No. 57 and 1320 records of other pigeons. The great amount of time involved in the flights and in the statistical calculations made it necessary to concentrate on one bird and to use the others to provide additional checks on the conclusions reached.

TRAINING AND HANDLING OF THE PIGEONS

It was anticipated that training the pigeons to land on the platform might be difficult. Training proved to be simple. The first time a bird was flown down the tunnel it was placed on the palm of the launcher's right hand. The person jiggled the hand to encourage the bird to fly off. If the bird did not land on the platform, and usually it did not, it was left to walk about in the tunnel for a few moments. Frequently it would eventually hop on to the solid landing platform at the end of the tunnel. If the bird did not fly off the launcher's hand and land near the platform after several such "free-flight" trials, another method was used. The pigeon was grasped from below with its breast resting in the palm of the hand. The legs were extended posteriorly between the thumb and forefinger (to reduce struggling) and the bird's wings held against its sides. The bird was then tossed, headfirst, down the tunnel with just enough force to carry it to the platform. The bird usually flapped several times to make a halfway normal landing. If it landed on the platform, it was permitted to remain there and become acquainted with the surroundings before being flown again. After 10 to 40 such trials the birds would take off from my hand, without being thrown, and fly down to the platform. Apparently the important feature was for the birds to find out that there was a stable perch at the far end of the tunnel. Firm supports were purposely omitted from the floor of the cloth tunnel; when a pigeon landed on the floor of the tunnel it bounced about and had difficulty in balancing and walking. As soon as a pigeon climbed onto the platform from the tunnel or actually landed on the platform a few times, it seemed to be about as well trained to land there as it ever would be (Figure 8).

Thereafter, the procedure was to put the pigeon's feet on the horizontally held palm of the right hand, induce it take off by itself, fly through the tunnel, and land on the platform.

During these first flights the birds usually flew out into the room from the platform. They were caught in an insect net. After the first 20 to 40 trials each day the pigeons usually waited on the platform until I picked them up, always in the left hand, and carried them back to the upper end of the tunnel for other trials. When a pigeon failed to wait, it frequently flew to a perch in the room. On succeeding failures to wait to be picked from the platform, the bird usually chose the same perch. After the bird became used to this perch (3 to 10 times) I could walk up and grasp the bird with the left hand. These details of handling are presented to indicate that the pigeons were not frightened by the experiments or the handling; on only one or two occasions did a bird become excited and fly wildly about the room. At these times the bird was left alone in the room for 10 or 15 minutes or until it was quiet.

The hours required for a daily set of landings varied with the success we had in getting the bird started and with the number of landings we wanted on that particular day. On good days 100 landings could be recorded in about 2 hours, but sometimes it was 4 hours. On one occasion (January 8) 320 trials were made to obtain 220 successful landings. This required more than seven hours of more or less continuous work. Brief stops of perhaps 5 or 10 minutes were made each hour during this time, as indeed they were each day. Only on January 8 was fatigue made apparent by the behavior of any bird. It was assumed on later dates that fatigue in wings or legs would result in a bird landing with more force, as happened on this date.

As will be discussed later, all birds used in this study maintained their body weights and were otherwise healthy, as far as could be determined.

THE PATTERN OF A NORMAL LANDING

Observation in the field and under experimental conditions indicated that a fairly definite procedure was followed in landing. Slow motion moving pictures were made and studied to determine the sequence of events. There are exceptions to the description given below, but it is characteristic of perhaps 80 per cent of all landings by uncaged pigeons. The same features were observed in the tunnel.

Flapping flight, with the body held horizontally, is maintained to within about ten feet of the perch. The feet are pulled up against the abdomen with the toes flexed. Approximately eight to ten feet from the perch the pigeon begins to take measures to reduce its speed—the body is tilted backward; the wings continue their beat; and the tail is spread and slightly depressed. The change in the inclination of the body and tail presents a broader braking surface to the direction of flight. Wing beats, with the changed inclination of the body, now act as forces to decrease the speed and to increase the lift.

As the pigeon approaches to within a foot or so of the platform, the long axis of the body reaches a vertical position and the long axis of the tail is also vertical; maximum breaking action is now being accomplished by the surfaces of the body and tail (Figure 1). With the body vertical, the wing beats now serve primarily as brakes to reduce forward motion. The last wing beat comes as the bird moves over the near edge of the platform. The bird is usually one to four inches above the platform (Figure 1).

Just before the feet touch the platform, the toes are uncurled and the legs are extended forward. The body tilts forward and the platform is touched. Moving pictures of the positions of the legs indicate that only in approximately 25 per cent of the landings are the two feet and legs extended uniformly. One foot is usually extended forward only; the other moves forward and laterally, apparently to act as a brace in balancing the final let-down. If the bird is not balanced by wing action prior to landing, it balances in the above-described manner. The bird may skid if forward motion has not been braked sufficiently, or the pigeon may hop or take two or three fast steps; it may even tilt backwards to provide an air brake, even though its feet are on the platform.

The person who started and stopped the recording device watched each experimental landing through a slit in the side of the tunnel. That person was not visible to the landing bird. From my position at the upper end of the tunnel, I too watched each landing. All abnormal landings could thus be eliminated from the records. It was sometimes difficult to judge the "normality" of a landing, and such selection of records might be termed selection of data. However, for the data to be comparable from trial to trial we used only those records in which the landings were as described. If the bird landed sideways, was obviously off balance, skidded abnormally, hopped when landing, or if its wings or tail touched any part of the tunnel or platform, the record was not included in the results reported here.

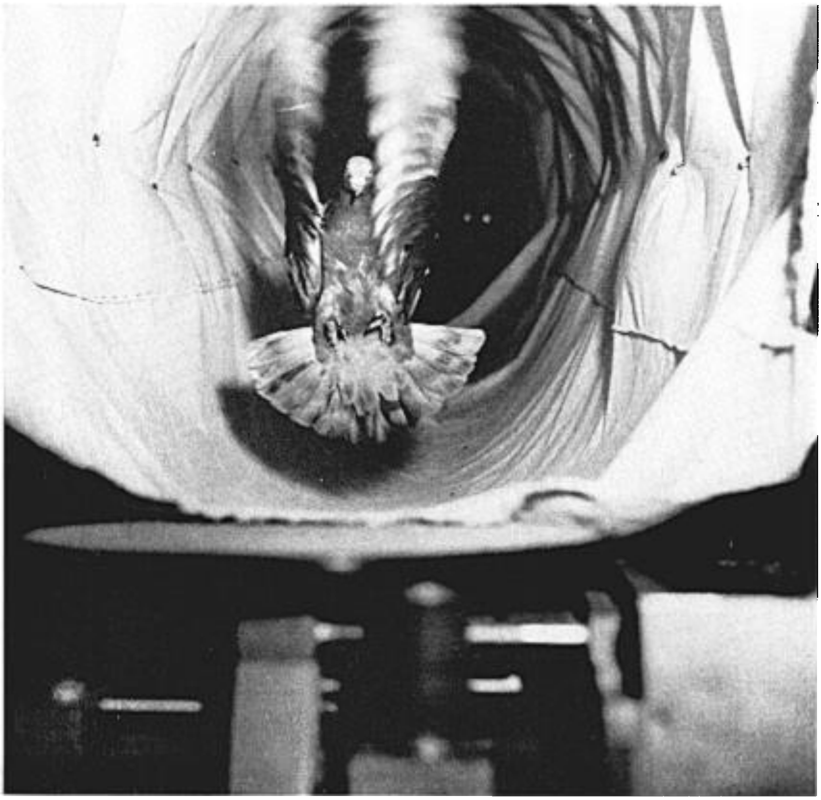

FIGURE 1. Domestic pigeon a moment before landing. Note the vertical position of the body, the widespread tail, and the toes which are being extended. The wings have just completed the last down beat.

THE RESULTS OF THE EXPERIMENTS

Changes in forces during a day's trials.—Figure 2 portrays the results of one day's landings by one bird. This particular day was chosen because it was fairly typical of most days and of most birds and because 200 successful landings were made in a continuous series. That the curves are representative may be checked by looking at each day's curves shown on Figures 3, 4, and 5.

Figure 2 shows that there is a decrease each day in total, back, and down forces. On this occasion the decrease was about 29 per cent of total, 28 per cent of down, and about 33 per cent of back force. As may be observed, the major decrease occurred during the first 80 trials. Another characteristic of the daily trials is a significant

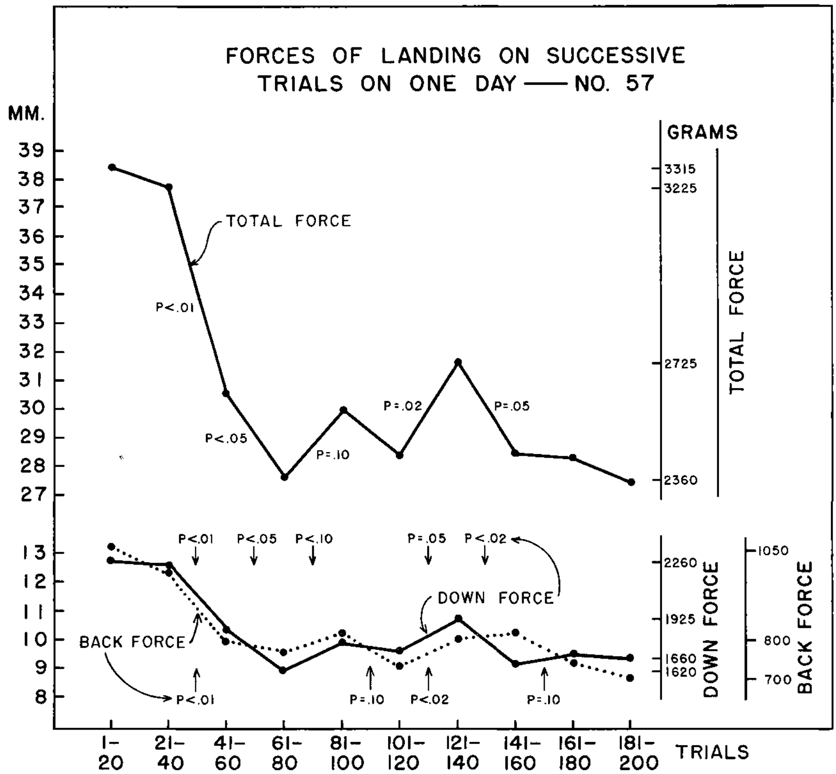

FIGURE 2.

increase following the described decrease. In Figure 2 the increase in force is shown between trials 80 and 140. Observations of Figures 3 to 5 will show that many of the daily trials show this increase.

The curves for down and back forces (Figure 2) aid in interpreting the changes in total force. The curve for down force rather closely approximates the one for total force. Back force declined sharply up to trial 60, held steady until trial 100 and then declined more or less gradually. Thus it appears that for this bird on this day the down force was more variable between successive sets of 20 trials but that it did not in general decrease as much as back force.

The magnitudes of the forces of pigeon No. 57 on this day were as follows: total force, 3315—2360 grams; down force, 2260—1620; and back force, 1050—700 grams. This same bird showed a maximum range of force over the period of the experiments, as follows: total, 4000—1850 grams; down, 2850—1400; and back force, 1150—450 grams.

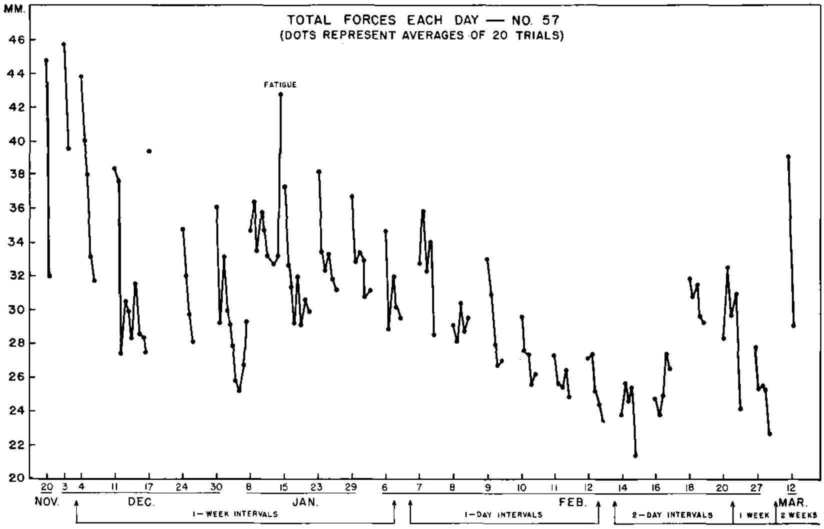

FIGURE 3.

The number of statistically significant changes that occurred between successive groups of 20 trials made on various dates by all birds is summarized in Table 2 (Omitted from this table are the data on No. 57 from February 6 to 12 when this pigeon was undergoing intensive work). *P* values higher than 0.05 were interpreted as indicating no change. About 50 per cent of the time all forces remained constant between sets 1 and 2 (trials 1–20 versus 21–40) on any one day; total force decreased 50 per cent of the time, back

TABLE 2

SUMMARY OF NUMBER OF SIGNIFICANT CHANGES BETWEEN AVERAGES OF SUCCESSIVE GROUPS OF 20 TRIALS

	Total Forces			*Down Forces*			*Back Forces*			
Between Groups	*Same*	*Up*	*Down*	*Same*	*Up*	*Down*	*Same*	*Up*	*Down*	*Number of sets of 20*
1 and 2	9	2	11	11	4	7	11	1	10	22
2 and 3	12	2	6	13	2	5	13	1	6	20
3 and 4	12	2	6	15	2	3	17	0	3	20
4 and 5	13	1	5	10	2	7	14	0	5	19
5 and 6	5	0	1	5	0	1	4	1	1	6
6 and 7	3	1	0	1	2	1	3	0	1	4
7 and 8	3	0	1	3	0	1	4	0	0	4
8 and 9	3	0	0	3	0	0	3	0	0	3
9 and 10	1	0	2	1	2	0	3	0	0	3
10 and 11	0	0	2	1	0	1	2	0	0	2

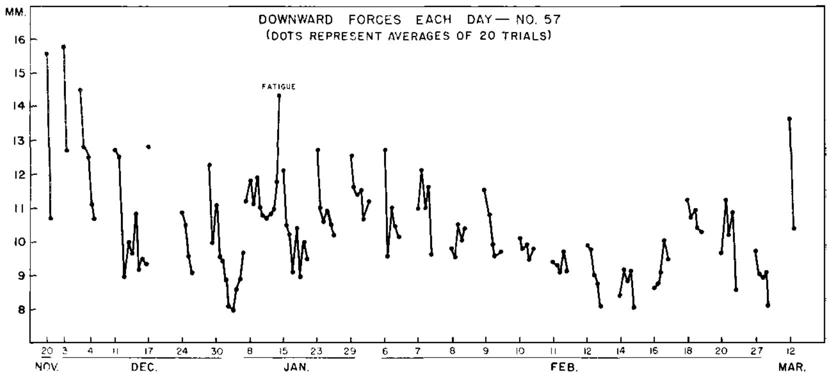

FIGURE 4.

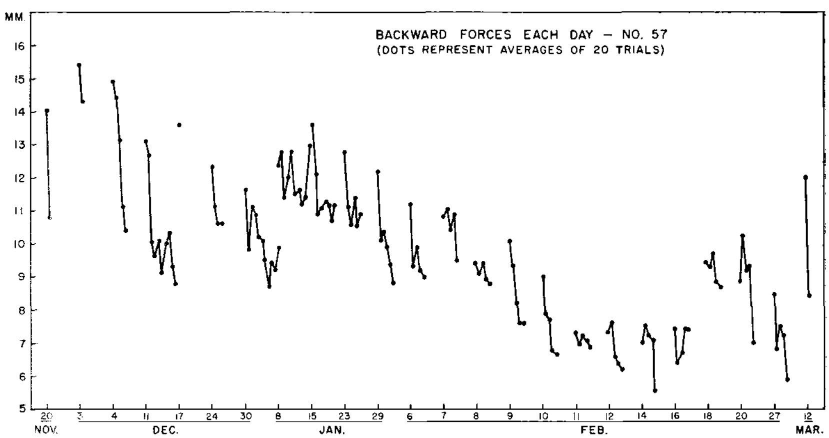

FIGURE 5.

force nearly 50 per cent and down force 30 per cent of the time. It seems then that back force tends to drop between sets 1 and 2 more frequently than does down force. None of the forces dropped as frequently between trial sets 2 and 3. About two-thirds of the time all forces remained the same, but again back force dropped more frequently. Between sets 3 and 4 and between 4 and 5 total forces dropped about as frequently as between sets 2 and 3. However, down forces tended to decrease more frequently than back forces, but both were more constant than in earlier trials. After the one hundredth trial (set 5) all forces remained approximately constant until fatigue set in at about the one hundred and sixtieth trial. Although the number of sets beyond 5 are few, it is important that about only once in ten trials did down or back force decrease and only on four of twenty-five sets did down force increase significantly after the one hundredth trial.

One matter of significance is obscured, or at least not fully discussed, by this consideration of only those changes between successive sets of 20 trials. Minor, statistically insignificant changes may occur between successive groups of trials. If two of these minor changes were in the same direction, the sum of the two differences might be significant. For example, if minor decreases occurred between sets

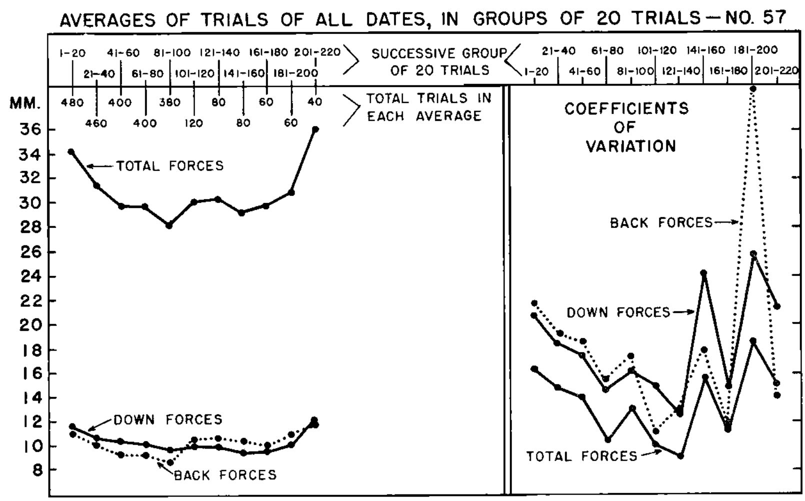

FIGURE 6.

1 and 2 and between 2 and 3, they would not be listed as decreases, but as no change. However, the difference between set 1 and set 3 might be a significant decrease. These possibilities were calculated and studied, but in no instance did they alter the pattern of changes described above.

Figure 6 was prepared to indicate the general trends, by use of simple averages, in the daily pattern of one bird. Compare Figures 2 and 6. The curves are nearly identical for the first 100 trials; all forces drop during the first 60 or 80 trials, but the upsurge in forces in Figure 2 starts 20 trials sooner than in Figure 6. Also note that down forces gradually decline as far as trial 160. Back forces decline more rapidly than do down forces during the first 100 trials of each date; between trials 100 and 120 (Figure 6) back forces increase sharply before leveling off as far as trial 180 (in Figure 2 this increase is between trials 120 and 140).

After trial 160 the number of trials in each average is small, but a definite upward trend is apparent in all forces. These increased forces perhaps arise from fatigue. During some of these trials the bird was observed to stumble occasionally while walking, to have a high respiratory rate, to be listless, and to fail to preen after each flight as was its custom. After an hour's rest and an opportunity to feed and drink the pigeon was again alert and preened.

One other feature of Figure 6 must be discussed. The average coefficients of variation for each group of 20 trials on all dates are plotted. It may be seen that the coefficients decrease sharply as far as trial 80 each day, increase between trials 80 and 100, and reach their lowest values between trials 120 and 140. The pattern of change in the coefficients follows fairly well the pattern of change in the forces of the first 140 trials. We may conclude, therefore, that the average forces vary directly with these coefficients. For example, not only does the bird land with decreasing force during the first 80 trials, it lands with increasing uniformity (decreasing coefficients of variation) during these trials. Even though average forces of landing remain fairly constant from trials 80 or 100 to 160 or 180, there is an increasing lack of uniformity or increasing deviation from the average. This increase in variation may well be one of the first signs of fatigue in these birds.

TABLE 3

CHANGE FROM START TO TRIAL 100 ON EACH DAY, BIRD NUMBER 57

	Total Force in per cent	*Down Force in per cent*	*Back Force in per cent*
December 4	down 27.6<.01*	down 26.2<.01	down 30.2<.01
December 11	down 21.9<.01	down 21.3<.01	down 22.9<.01
December 30	down 19.1<.01	down 22.7<.01	down 12.1<.02
January 8	down 0	down 1.8>.10	up 3.2>.10
January 15	down 14.2<.01	down 14.1=.01	down 14.4<.01
January 23	down 16.5<.01	down 17.3<.01	down 13.3=.02
January 29	down 16.1<.01	down 14.4<.01	down 22.9<.01
February 6	down 14.5<.01	down 19.7<.01	down 19.6<.01
February 7	down 12.8<.01	down 12.7<.02	down 11.9<.05
February 8	down 1.7>.10	up 6.1>.10	down 6.4>.10
February 9	down 18.2<.01	down 15.7<.01	down 24.8<.01
February 10	down 11.5<.01	down 3.0>.10	down 25.5<.01
February 11	down 8.8<.10	down 3.2>.10	down 5.5>.10
February 12	down 13.7<.01	down 18.2<.01	down 15.1=.01
February 14	down 9.7<.05	down 4.8>.10	down 21.4<.01
February 16	up 7.3>.10	up 10.5<.10	0
February 18	down 7.9>.10	down 8.0>.10	down 7.4>.10
February 20	down 15.2<.05	down 11.3<.10	down 21.3<.01
February 27	down 18.6<.01	down 16.5<.02	down 30.6<.01

* Second column of figures under each heading is of *P* values.

Table 3 shows changes in forces by percentages. The data lend further support to the view that all forces decrease significantly during each day's landings.

During the one-week period (February 6 to 12) of intensive work to which bird No. 57 was subjected, there was less evidence of a uniform decrease in all forces in the course of each day's trials (Table 3). Total force followed the usual pattern of decrease fairly well, but there was a lesser actual decrease because the total forces were relatively low to begin with and because the bird was approaching a minimal, terminal, total force each day. On three of these six days, down force was not significantly less on the one hundredth trial than

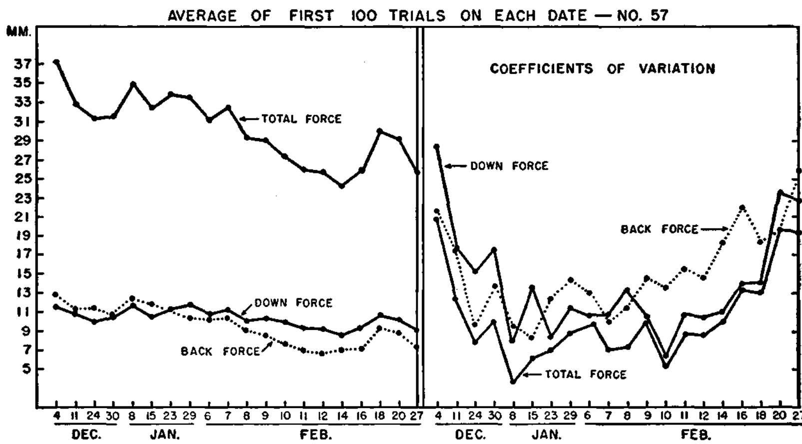

FIGURE 7.

on the first. On two of the six days, back force did not show a significant decrease from beginning to end.

Changes in forces from day to day.—The dates on which pigeon No. 57 was flown are indicated in Figure 7. The records of the landings of this individual on March 12, after an interval of two weeks, are not included in Figure 7 because only 40 trials were possible on this date.

It is apparent from Figure 7 and from Figures 3, 4, and 5 that the shapes of the curves for changes in forces over a long period of time are very similar to the curves for the changes in forces each day. At least this is true for the period of weekly landings. All forces decreased significantly the first week, and total and down forces decreased the second week. Beginning with the third week and ending with the fourth all forces increased somewhat. Although there were changes in all forces between January 8 and February 6, these average figures show that forces used in landing on February 6 were essentially of the same magnitude as those of December 24 and 30. In other words, the bird was landing just as hard on February 6, after approximately 1800 landings, as it had on December 24 after only about 500 landings. (In Figure 7 we are using only the first 100 landings per date; see Figure 8 for total number on each date.)

It was concluded that the bird had reached a low level of forces which would not be further depressed by weekly periods of training. A series of daily landings was started on February 7. Total force and back force decreased throughout the period of daily trials. After a sharp decrease on February 8, down force declined very gradually in this period and for two days thereafter (Figures 3, 4, 5, and 7). The diverging curves for down and back forces are very evident during this time. Daily trials were halted on February 12 not because the forces had reached a plateau, although the similarity of forces of February 11 and 12 might indicate this, but because of the lack of time.

On February 14, 48 hours after the last daily trial period, total and down forces were still decreasing, but back force was starting to increase. All forces increased significantly between February 14 and 16 and 16 and 18. Statistical analysis showed that all forces on February 20 were the same as on February 18. We may conclude that the usual tendency at this time was for all forces to increase when the bird was flown at 48-hour intervals.

With a lapse of one week, forces decreased significantly on February 27. This will be more fully discussed later.

During the weekly trials the pattern of the coefficients of variation (Figure 7) shows the same characteristics as the coefficients for the trials during one day. Increasing uniformity of landing force (decreasing coefficients) within each average figure accompanies decreasing forces. However, it is perhaps significant that the relatively low (for this experimental work) coefficients attained by January 8, after approximately 1200 landings, were more or less maintained until February 7. The early part of the period for daily trials produced a sharp decrease in the coefficients of variation for down force. In other words, the bird was landing more uniformly as far as down force was concerned. Coefficients of down force increased with landings at 48-hour intervals and continued to rise until they were nearly as high as for the first trials of the experiment. Coefficients of back force started to increase with the beginning of daily trials and continued to increase until the end of the experiments.

The use of the average of 100 trials (Figure 7) shows major variations and the central tendencies, but it was possible that the averages were not accurate representations of the entire curve for each date. Average forces produced from data in such curves as shown in Figure 2 may be misleading. The averages may be unduly affected by any abnormally high or low part of the curve. In an attempt to check the accuracy of the representation by Figure 7, curves were prepared for all forces during the first 20 trials on each date and for trials 80 to 100 on each date. All these curves were similar to those in Figure 7, indicating that the first trials and the final trials of each day possessed the same characteristic changes over the period of experiment.

In general, then, we may say there is evidence for the following conclusions: 1) all forces decreased abruptly for three or four weeks after initiation of weekly periods of flights; 2) all forces increased slightly in the fourth to seventh weeks; 3) thereafter, all forces decreased gradually, but only slightly, until February 6, the end of the weekly trials; 4) back force started to decrease, after the slight increase, as early as January 8, and its decrease during weekly trials was far more evident than the decrease in down force; 5) when daily trials were started, all forces decreased more rapidly than when trials were at weekly intervals; 6) during daily trials back force again dropped more uniformly and more rapidly; 7) low forces attained with daily flights continued for at least two days after the period of these flights ended; 8) when the 48-hour interval was used, all forces increased sharply; 9) with any further lengthening of the interval between periods of trials the forces became greater, although for some reason the forces after a week's time decreased; and 10) coefficients of variation indicate increased uniformity of landing force as forces decreased, and decreased uniformity accompanied increased forces of landing.

Failure to Land Successfully

Failure to land successfully on the platform was frequent in the first training flights of each bird. This was expected, for the bird had to learn that there was a solid platform at the other end of the tunnel. What was not expected was that the number of such failures did not decrease with experience during each day's trials or during the three months of the experiments.

The curve in Figure 8 indicates that during each day's trials there was an increase in the percentage of failures until about the 100th or 120th trial. Between the 100th and 200th trials the percentage of failures decreased. The total number of trials in each group of 20 above 200 is too small to justify conclusions.

I am unable to explain the shape of the curve for successive sets of 20 trials up to 200 trials. The increasing number of failures up to the end of 100 trials might have been explicable on the basis of fatigue except for the decrease in failures after 100 trials. It does not seem likely that the bird must each day land 100 times *before* it begins to learn to land successfully.

There is no evidence to indicate any pattern in the percentage of failures on successive trial days during the three-month period (Figure 8). The lowest percentage was 6.5 on December 11; the highest was 48.3 on December 3. The average of failures on the first 12 trial days was about 24 per cent; on the last 11 trial days it was 31

	TOTAL TRIALS	PERCENT FAILURES
NOV. 20	40	15.0
DEC. 3	60	48.3
4	120	23.3
11	200	6.5
17	40	30.0
24	80	8.8
30	280	22.9
JAN. 8	320	29.7
15	220	25.0
23	180	26.1
29	180	33.9
FEB. 6	120	17.5
7	160	39.4
8	140	27.9
9	140	27.9
10	160	36.9
11	160	41.2
12	140	29.3
14	140	34.3
16	140	23.6
18	160	40.6
20	140	27.1
27	120	12.5

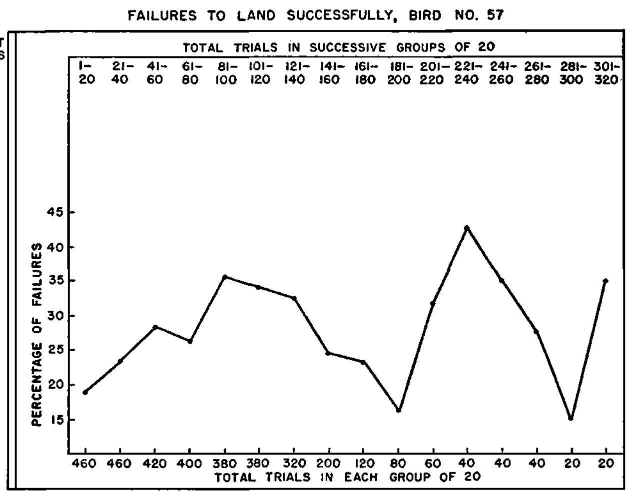

FIGURE 8.

per cent. The average percentage of failure for the landings of the daily trials during the week of February 6 to 12 was about 34; no decrease was noted.

One can only conclude that the bird did not improve in this part of its ability to land successfully under the experimental conditions imposed. It must be noted, however, that there are included, as failures, patterns of landing which are perhaps successful as far as the pigeon is concerned. Among these patterns are those in which the pigeon hopped one or more times on landing, turned sidewise just before touching the platform, landed with one foot off the platform, or landed on the extreme edge of the platform as if it were a twig perch. It is possible, but I think improbable, that inclusion of these obscured a pattern.

CHANGES IN MANNER OF LANDING

When the pigeons are first being trained, the initial records (Figure 9, December 4 and February 9) on each day are quite different from the later ones of the same date. Records of the same bird, after approximately 1500 more landings (Figure 9, February 9) are not like those of December 4. Not only are the forces less in each instance, the forces are applied more gradually and over a longer period of time. Once the bird has landed 30 to 40 times on the platform, no records of normal landings are as abrupt as that of trial Number

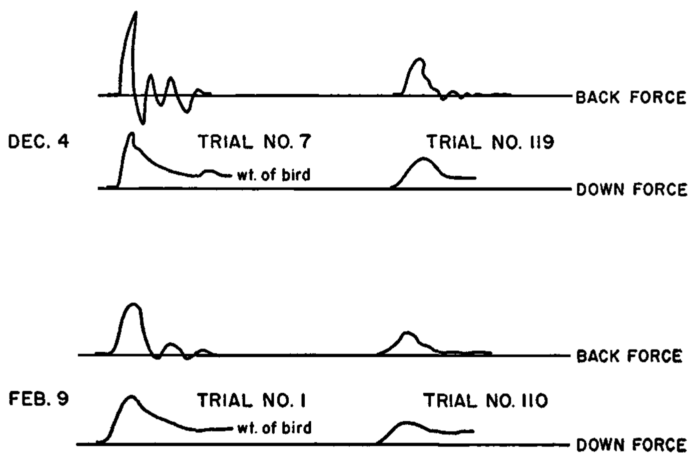

FIGURE 9. Characteristic curves of forces of landing of one bird to show changes during each day and changes during a period of training.

7 on December 4. Initial forces on any date are always more abrupt and applied for a briefer period of time than are later forces of the same date.

One may conclude that the bird has changed some details in its pattern of landing and is setting down without the extreme stresses of earlier landings. Even though actual forces may be as great in some later trials, a more gradual and "careful" landing is made. Fatigue in the muscles might be partly responsible for the change during any one day's landings, but there is something more here; the bird is not fatigued at the time of the initial trials on later days, trial Number 1 of February 9, for example, when the forces are not so abrupt.

BODY WEIGHT AND LANDING FORCE

Although the pigeons used in the experiment and the data are too few for definite conclusions, some facts are indicative. In Table 4 are data on body weight and landing forces of six different pigeons. For all practical purposes pigeons Numbers 54, 55, 101, 102, and 104 weighed the same. Yet, total landing forces varied from 21.1 to 36.2 millimeters, a range equal to about 43 per cent of the maximum. Down and back forces seemed to be equally variable in these birds of similar body weights; down force varied from 6.4 to 12.2, and back force from 8.2 to 12.2. Pigeon Number 57, which weighed nearly 100 grams more than the other pigeons, landed somewhat more lightly than Number 102 (particularly as regards down force) and only insignificantly more forcefully than Numbers 54 and 55, except for back force which was considerably higher in the heavier bird. Note, however, that Number 102 had a back force just as great as that for Number 57.

TABLE 4

BODY WEIGHT AND LANDING FORCE

Pigeon number	*Average weight in grams*	*Average forces of first 300 landings in millimeters*		
		Total	*Down*	*Back*
54	328	29.6	10.0	9.6
55	317	29.4	9.9	8.6
57	407	33.4	10.7	11.7
101	320	23.7	7.7	8.4
102	329	36.3	12.2	12.2
104	293	21.1*	6.4*	8.2*

* Only 120 landings.

We may conclude that differences in body weight of different pigeons have little to do with differences between the landing forces of these same pigeons. Individual differences in forces seem to result from differences in manner of landing, in approach, and in wing action. Pigeon Number 102 came in to the platform high and fast and virtually plopped into a landing. Numbers 101 and 104, however, came in easily and nearly hovered before touching the landing place.

It should be explained that body weight for any pigeon on any date is an average. Birds were weighed before and after the experimental landings; the average of these two was the weight used. Of passing interest only was the loss of weight, largely through voiding of excrement, that occurred during each day's trials. On days when 250 or more landings were made, birds lost from 15 to 24 grams (4.5

to 5.5 per cent of body weight). When only 140 to 180 landings had to be made to get the desired number of records, birds lost an average of 9 grams (5 to 18) or 1.6 to 4.0 per cent of body weight.

Changes in weight of an individual pigeon do seem to affect its landing forces. Data on three birds reveal that sudden changes in body weight are frequently accompanied by changes in forces. Since Figures 3, 4, and 5 show forces in No. 57, this bird will be used to demonstrate the effect of changes in weight. Between October 20, when the bird was first brought in for experimentation, and December 3, its weight rose from 375 to 420 grams. This increase was accompanied by an unexpected increase in all forces (Figures 3, 4, 5). Body weight increased from 437 grams on December 11 to an all-time high of 477 grams on December 17; on all the force curves the dot representing force on December 17 is above the expected position. On February 6, Number 57 was 30 grams lighter than on February 7 and 20 grams lighter than on January 29; total and back forces were less on February 6, but down force did not seem to be affected.

The intensive work of 100 landings each day for a week did not cause loss of weight (419 versus 412 grams). Nevertheless, on February 14 the weight of Number 57 was down to 391 grams and to 370 grams on February 16. These low weights no doubt played a part in producing the low forces of these dates. They may furnish part of the explanation for continued decreases in forces even after the end of the period of daily trials. Observation in the two rooms where the pigeons were kept showed that this large male (Number 57), which had been dominant, was now continually pecked, wing-flogged, and chased by two other males. Street lights kept the room semi-lighted at night and the bird had no opportunity to rest or feed. Apparently the fact that we had had this bird out of the room for three to six hours on each of seven successive days for trial landings had destroyed his dominance. Fatigue may have been another factor.

Number 57 was placed in a separate room on February 16. On February 18 his weight was up 61 grams to 431 grams. This sudden increase made the bird noticeably clumsy in landing on February 18 and 20, and all forces, except possibly down force, showed unexpectedly great increases.

On February 27 his weight was down to 400 grams and forces were generally lower than was expected.

DISCUSSION AND SUMMARY

It has been demonstrated that pigeons weighing 300 to 400 grams landed on a flat platform with total forces varying from 1200 to 4000 grams. This total force was composed of a downward vector of 900 to 2800 grams and a backward or braking vector of about 300 to 1200 grams. These figures apply only to landings for which the bird approached at an angle of 15 degrees above the horizontal.

All forces decreased with repeated landings. During each day's trials (100 to 220 landings) forces frequently decreased by as much as 30 per cent. If a day's forces of landing by a single pigeon be plotted, the resulting curve is sigmoid in nature. All forces decreased over a period of three months of training. If the characteristic changes of this period be plotted, the curve is also a sigmoid.

Weekly periods of training at first resulted in sharply decreased forces, but these forces only gradually went slightly lower when weekly training was continued. When further training was at daily intervals all forces declined most abruptly, and this training may have carried over into the period when landings were made at 48-hour intervals. Using 48-hour intervals, all forces began to increase and continued to do so for the remainder of the experiment.

It is noticeable in all the curves depicting forces that back force is more affected by the interval of training than is down force. Changes in back force are greater and more rapid. In these experiments back force is really braking force to halt the forward momentum of the bird. This reduction of speed involves wing angles and beats and the inclination of the body and tail, among other things—a complex series of integrated activities. Down force, on the other hand, is apparently a simpler matter; the bird is nearly in a stall over the platform, is within a few inches of the platform, and just drops down.

Not only do the pigeons land more lightly after various periods of training, but the forces are more gradually and constantly applied. The curves on recordings of these later forces have broad, plateau-like peaks rather than the sharp peaks of the initial trials.

Body weight is not the major factor causing variation between the forces used by different pigeons. This variation is apparently a behavioral matter involving differences in patterns of landing. Changes in body weight of a single bird may affect its forces of landing on different days.

It is suggested that during these periods of training the birds have learned how to land under the experimental conditions, but each uses his innate pattern of landing. This learning occurred during each day's trials, as evidenced by the sigmoid, learning curve of forces and by the increased uniformity of forces which is demonstrated by decreased coefficients of variation.

With this daily learning during the entire experimental period, it is remarkable that there was so little retention. At weekly intervals the initial forces were always much greater than the final forces of the preceding week; no major improvement was noted after the first three or four weeks, when the weekly interval was retained. When daily trials were started all forces decreased and the forces of landing were more uniform, apparently because the birds could retain a greater portion of what had been learned on the preceding day. These pigeons could not retain as much, or as well, over a 48-hour interval; forces increased and were less uniform than on the 24-hour interval. Intervals of two weeks may be long enough for pigeons to forget anything they may have learned about easing their force of landing. Only two such long intervals were used, but they do indicate this conclusion.

Our data indicated that the birds never demonstrated any continued improvement in finding the platform and in landing on it successfully. But, we have trained some pigeons for three weeks and then not used them at all for six weeks. After this interval they landed just as hard as they had when first flown, but they did find the platform immediately and did not require any retraining. They also waited to be picked up from the platform, as they had six weeks earlier. Thus, the evidence is not at all conclusive as regards retention of learning to find the fixed platform.

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