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Food and Water Intake and Weight Regulation in the Pigeon

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ZEIGLER, H. P., H. L. GREEN AND J. SIEGEL. *Food and water intake and weight regulation in the pigeon.* PHYSIOL. BEHAV. 8 (1) 127-134, 1972.–The interaction of eating and drinking and the relation between intake and body weight was examined in pigeons maintained under laboratory conditions in order to obtain normative data on intake and weight regulation in this species. Under ad lib conditions food and water intake values are correlated, while deprivation of either nutrient leads to a reduction in the intake of the other. A linear relation between the log food intake and the log body weight was found under both ad lib and deprivation conditions. Following a period of food deprivation the pigeon shows both a short-term and a long-term compensatory increase in food intake whose magnitude is directly proportional to the degree of body weight loss produced by deprivation. The findings for the pigeon are similar in many respects to those reported for the rat and are discussed in relation to weight regulation and motivational mechanisms in hunger and thirst.

Pigeon Hunger Food and water intake Body weight Deprivation Weight regulation Eating and drinking

THE STUDIES reported below were designed to provide, for the pigeon, a body of normative data on food intake and weight regulation comparable to that which now exists for the rat. In addition to its comparative interest, the acquisition of such data is a first step in the study of regulatory processes in any species. Furthermore, it provides a baseline against which to evaluate the significance of changes in feeding behavior or weight regulation produced in neuro-behavioral studies of hunger and thirst [24].

In the first of the present studies the stability of daily intake and body weight values and the relation between food and water intake were examined in pigeons maintained in the laboratory under ad lib conditions. The second study explored the interaction of eating and drinking under conditions of food and water deprivation. A third group of experiments dealt with the regulation of body weight in pigeons during periods of deprivation and following recovery from deprivation.

GENERAL METHODS

Animals

A total of 70 White Carneaux pigeons of both sexes, obtained from a commercial supplier, were used in the three studies. Each of the experimental groups contained approximately equal numbers of each sex. However, because sex did not prove to be a significant variable in any of the studies, it is not specified in describing the makeup of specific experimental groups.

Housing and Maintenance

The birds were housed in individual cages and adapted to the laboratory for at least two months prior to their use in any study. During this period food and water were available ad lib. Ambient temperature was maintained between 70° and 80°F and a 12 hr light/dark cycle (7 a.m.-7 p.m.) was in effect.

Apparatus

A food magazine (capacity 500 g) designed to minimize spillage was used and birds were fed a grain mixture containing 50% kaffir, 40% vetch and 10% hemp. (An analysis of the nutrient values of each component of the diet is available from the senior author). Water was provided in 250 ml graduated glass drinking tubes.

EXPERIMENT 1: INTAKE AND BODY WEIGHT UNDER AD LIB CONDITIONS

Adult animals given unrestricted access to an adequate diet characteristically control their daily food and water intake so as to maintain a relatively stable body weight. In their attempts to clarify the mechanisms by which such regulation is achieved, a number of workers have systematically explored the relationship between food and water intake and body weight and have described these relationships with some precision. It is well established, for

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example, that under ad lib conditions food and water intake are highly correlated and that intake is a relatively constant fraction of body weight [2, 4, 6, 21].

Most of the data on the control of intake and the regulation of body weight come from studies of mammals. Because the alimentary apparatus and digestive system of birds differs in a number of respects from the typical mammalian patterns [9] data obtained from an avian species may be useful in assessing the generality of the mammalian findings. The present study was designed to provide normative data on food and water intake in pigeons maintained under ad lib conditions and to examine the relationship between intake and body weight.

METHOD

Animals and Procedures

A group of 12 pigeons was adapted to the laboratory and maintained under ad lib conditions for three months. During this time the drinking tube was refilled and grain was added to the food magazine at irregular intervals as needed. During the last four weeks of the adaptation period food and water intake and body weight were recorded on four successive days each week (Monday through Friday) between noon and 1 p.m. The drinking tube was refilled and the food magazine emptied and refilled with fresh grain.

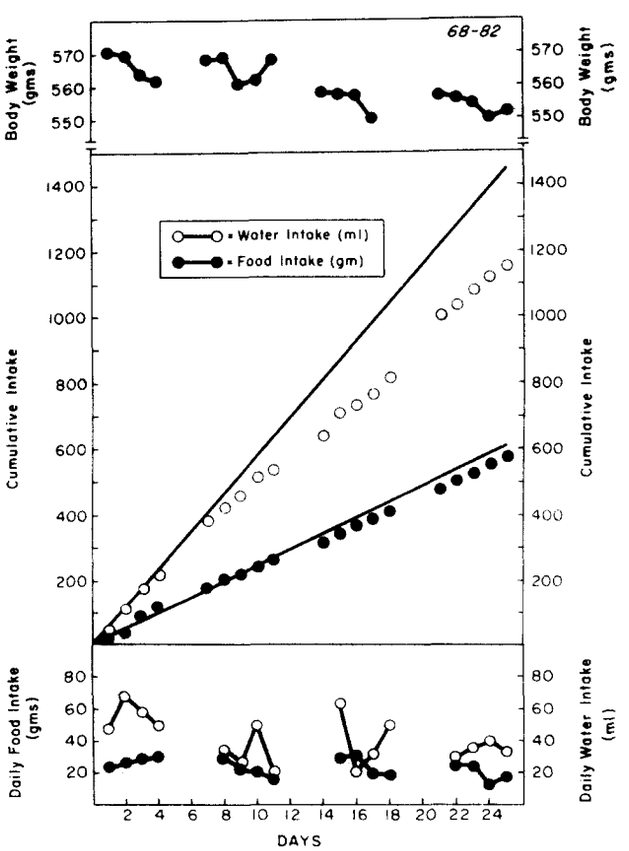

FIG. 1. Food and water intake and body weight in the pigeon. Data are for a single bird over four successive weeks with food and water available ad lib.

RESULTS

Intake and weight data for a single representative bird are presented in Fig. 1. In the bottom portion of the figure food and water intake are plotted for four successive 24 hr periods in each week (weekends omitted) over a four week period, while body weight is plotted in the top portion. A slight decline in both intake and weight is apparent in the last two weeks of the observation period. (The relatively high food intake values during the first week and at the start of the three succeeding weeks may reflect a response to the fresh grain in the bird's food magazine. Under ad lib conditions birds given a three grain mixture tend to sort out preferred types of grain [26] and show a burst of eating when the magazine is refilled.)

Daily intake fluctuates about a mean which is characteristic for a given bird but these variations may be considerable, particularly in the case of water. However, by contrast with the variability of daily intake, the rate of eating and drinking tends to remain relatively constant over extended periods of observation. This is evident in the middle portion of Fig. 1 where intake data are plotted cumulatively (weekends included). The solid diagonal lines represent extrapolations based upon the means of the first two days of food and water intake, respectively. While total food intake over the 25 day period (575 g) is very close to the predicted value (612 g) the greater variability of water intake is reflected in the difference between the predicted value (1459 ml) and the actual 25 day intake (1148 ml). Variability in body weight over the four week period never exceeded four percent despite variations in daily intake ranging from about 20 per cent for food (Mean 23.6; SD 5.1) to 30 per cent for water (Mean 41.3; SD 13.9). An estimate of individual differences in the variability of intake and body weight may be obtained from Table 1 which presents data for each of the 12 birds used in this study.

The correlation of food and water intake over four successive weeks was calculated for each of the birds, based upon daily intake values, and Spearman rank-order correlation coefficients are presented in Column 4 of Table 1. Although some of the correlations of individual birds are not significant, the coefficient of correlation calculated for the group as a whole is highly significant ($r=+0.84$; $df=10$; $p < 0.01$). The quantitative relationship between eating and drinking may be specified more precisely by examining the ratio of food intake to water intake (Column 5). Under ad lib conditions the average water intake of the pigeon is about 150 per cent of its average food intake (Mean ratio=1.64) and the ratios of individual birds are maintained fairly consistently from week to week.

The body weight of individual birds (Column 6) is quite stable, with individual variability rarely exceeding two or three per cent over the four week period. Columns 7 and 8 of Table 1 indicate the relation between mean daily intake and body weight in individual birds. For the group as a whole food intake averages about five per cent (Mean = 0.047) and water intake averages about eight per cent (Mean = 0.079) of body weight.

EXPERIMENT 2: INTERACTION OF EATING AND DRINKING UNDER FOOD OR WATER DEPRIVATION

In several species of mammals and birds food deprivation

TABLE 1

Interrelations Between Food and Water Intake and Body Weight
Under *Ad Libitum* Conditions in the Pigeon

Bird No.	Daily Food Intake (gm) Mean	S.D.	Daily Water Intake (ml) Mean	S.D.	Correlation of Water and Food r_{wf}	p	Ratio of Water to Food Mean	S.D.	Body Weight (gm) Mean	S.D.	Ratio of Food to Body Weight	Ratio of Water to Body Weight
68-79	20.8	6.4	38.4	6.9	-0.06	NS	1.84	0.65	503	4.2	.041	.075
68-80	19.9	6.6	33.5	8.2	+0.76	.01	1.68	0.30	533	4.7	.037	.061
68-82	23.6	5.1	41.3	13.9	+0.73	.01	1.75	0.29	560	7.4	.042	.073
68-83	25.3	4.8	49.0	12.4	+0.95	.01	1.93	0.05	616	10.2	.040	.079
68-84	20.0	9.2	19.6	6.2	+0.78	.01	0.98	0.20	506	4.7	.039	.039
68-85	38.0	8.5	75.0	12.4	+0.80	.01	1.97	0.30	530	7.3	.070	.14
68-86	35.8	6.9	87.6	41.0	+0.42	.10	2.44	1.10	542	5.6	.064	.14
68-87	32.4	7.2	41.5	5.0	+0.55	.10	1.28	0.27	595	11.9	.053	.069
68-88	20.5	7.9	25.8	7.3	+0.47	.10	1.25	0.24	494	6.4	.041	.052
68-89	25.4	7.2	32.8	12.7	+0.70	.01	1.29	0.27	517	11.4	.048	.064
68-90	24.5	6.6	43.9	12.6	+0.63	.01	1.79	0.32	523	9.9	.046	.083
68-91	33.2	6.7	42.6	10.8	+0.45	.10	1.28	0.12	583	11.6	.056	.073

produces a reduction in water intake while water deprivation leads to decreased food intake [3, 15, 23]. However, the relationship between eating and drinking under deprivation conditions is a species-dependent one [12]. It therefore seemed appropriate to explore this relationship in the pigeon by examining food consumption during total water deprivation and water intake during both total and partial food deprivation.

METHOD

Animals and Procedures

A total of 20 deprivationally naive birds were divided into two groups. Group WD (N=10) was deprived of water for four days during which time food intake and body weight were recorded daily. Group FD (N=10) was deprived of food for a three week period during which water intake and weight were recorded on five successive days each week. In addition, data on the effects of partial food deprivation upon water intake were available from a group of 10 birds (Group PFD) five of whom had been fed 50% and the other five 80% of their respective ad lib food rations over a 10 week period. (See Experiment 3).

RESULTS

A non-parametric analysis of variance of the data of group WD (Fig. 2) indicates that during total water deprivation there is a significant ($p < 0.01$) reduction in food consumption. Similarly, over three weeks of total food deprivation (Fig. 3) water intake is reduced significantly ($p < 0.01$) with the major part of the reduction occurring during the first week of deprivation.

The effects of partial food deprivation (PFD) upon water intake are more complex. Water consumption over the 10 weeks of PFD was extremely variable in both the 50% and 80% groups. A number of birds in each group showed no change, while others increased their weekly water intake and the over-all mean intake of the two groups did not differ significantly Examination of the daily intake data of individual birds clarified these findings by suggesting that the PFD condition constituted a cycle of deprivation and recovery periods for both food and water. Birds in the PFD groups were given their entire weekly food ration at the start of the week and this ration was consumed within two to three days, depending upon the bird and the ration size. For the remainder of the week the birds were, in effect, on total food deprivation, which might be expected to produce a consequent reduction in the water intake. At the start of each week, therefore, water

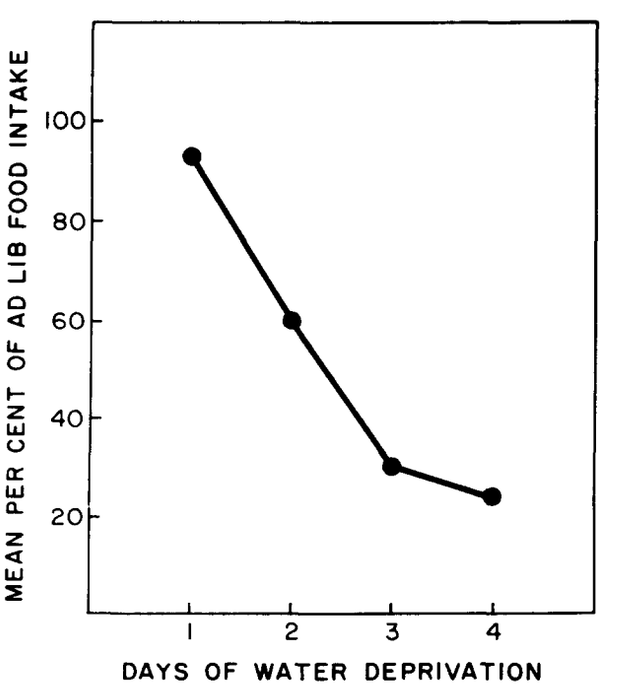

FIG. 2. The effect of total water deprivation upon food intake.

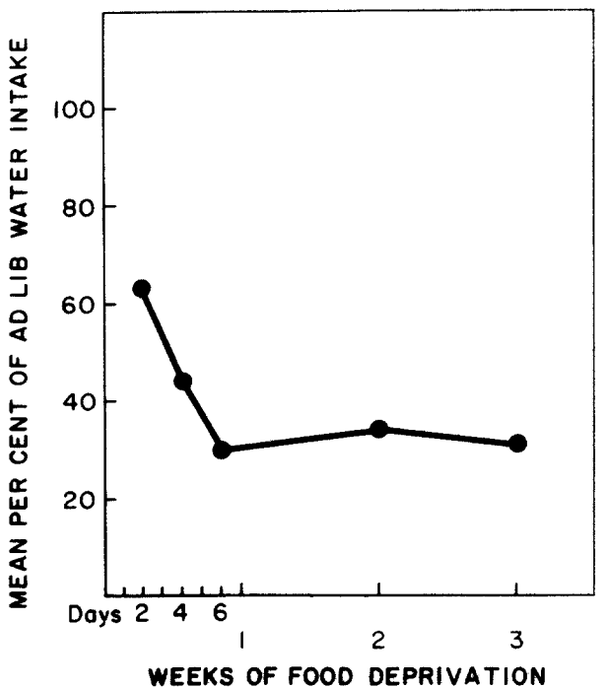

FIG. 3. The effect of total food deprivation upon water intake. Data for the first week of deprivation are plotted in two-day blocks.

consumption should reflect not only the presence of the partial food ration but also a compensatory response to the preceding period of water deprivation.

To test this hypothesis the PFD data were reanalysed so as to make possible a comparison of water intake during the first three days of the week with that during the last four days. Fig. 4 illustrates the results of such an analysis. Because there is very little variation in the week-to-week data, the results for the two groups have been summed across the 10 weeks of partial food deprivation. Data on the effects of three weeks of total food deprivation obtained from Group FD, are included for purposes of comparison.

In the period immediately following the introduction of the partial food ration (Days 1-3) mean water consumption in the 50% and 80% groups is at or above its ad lib value and drops to below that value during the remainder of the week (Days 4-7). By contrast, water intake under total deprivation is distributed evenly throughout the week.

Under the present conditions, therefore, the data of Days 4-7 provide the best estimate of the effects of partial food deprivation upon subsequent water intake. Statistical analysis indicates that while the water intake of the 80% group does not differ significantly from its ad lib value the difference in water intake between the 80% and 50% groups is significant ($t = 2.4$; $df = 9$; $p < 0.05$), as is that between the o% and 50% groups ($t = 2.3$; $df = 9$; $p < 0.05$).

EXPERIMENT 3: REGULATION OF BODY WEIGHT

Under ad lib conditions a linear relationship between log intake of food and water and log lean body weight has been found in a number of mammalian species [2]. During total deprivation of food or water, log body weight declines linearly with time [6] and animals maintained under partial food or water deprivation lose weight until they reach a final (asymptotic) body weight which is a linear function of the log ration size [5, 6]. The present experiment was designed to provide data on body weight regulation in the pigeon under ad lib conditions, during total and partial food deprivation, and during recovery from various levels of body weight loss.

METHOD

Animals and Procedures

Three new groups of animals were used in these experiments. Group FWD (N=10) was deprived of both food and water for four successive days and body weight was recorded daily. Group PFD (N=10) provided data on the effects of partial food deprivation upon body weight. Baseline weight and intake values were recorded under ad lib conditions for a four week adaptation period. Five of the birds were then given 50% and five 80% of their mean ad lib food ration for a period of 10 successive weeks. The ration was given once a week and water intake and body weight values were recorded five times each week. Group RFD (N=18) was used to study the relation between body weight loss and food consumption during recovery from food deprivation. Baseline weight and food intake data

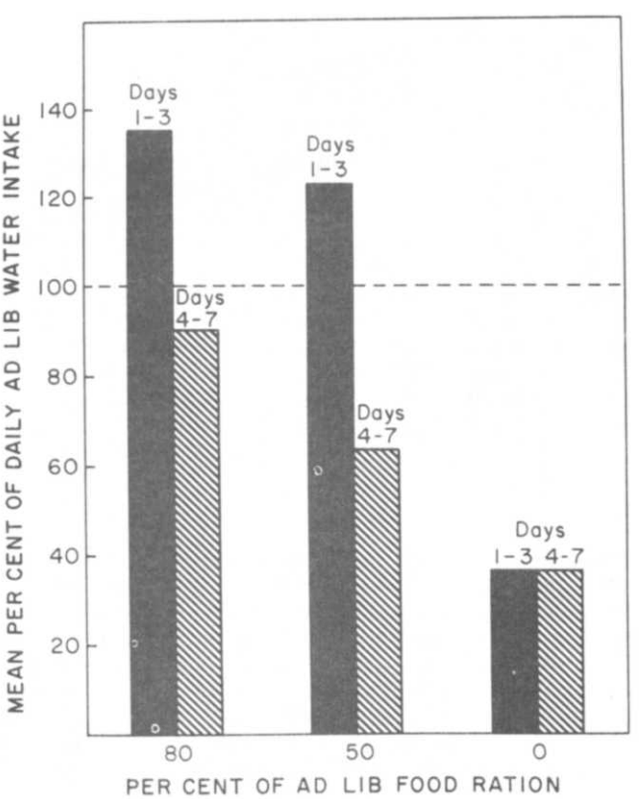

FIG. 4. Partial food deprivation and water intake. The relation between food ration size and water intake.

were recorded for several weeks of adaptation and the birds were then assigned to three equal subgroups (N=6). Animals in each subgroup were deprived of food until they reached, respectively, 95%, 85% and 75% of their ad lib body weights. They were then given unlimited access to food, and intake and weight values were recorded daily until the birds regained their ad lib body weights. Water was available throughout the entire experiment. In addition to these new groups, data on body weight regulation under total food deprivation and during recovery from such deprivation was available from the 10 animals in Group FD (Experiment 2). At the end of the deprivation period they were given unlimited access to food and intake and body weight data were recorded for five days each week until birds had recovered to their ad lib body weight values.

RESULTS

1. *The Relation between ad lib Food Intake and Body Weight*

As a starting point for the analysis of body weight regulation in the pigeon the relation between log food intake and log body weight was examined using ad lib data obtained from birds in Groups PFD and RFD (total N=28) during their adaptation periods. The body weights of these birds ranged from 490 - 714 g. The log mean body weight for each bird was plotted against its log mean food intake and the linearity of the resulting function was tested by calculating the Pearson product-moment correlation. The coefficient of correlation between the two variables is significant at beyond the 1% level (r=+0.75; df=26).

2. *Body Weight Regulation During Combined Food and Water Deprivation*

Fig. 5 compares the reduction in body weight produced by combined food and water deprivation with that produced by water deprivation alone. (Group WD, Experiment 2). A Friedman two-way analysis of variance indicates that the reduction is significant at beyond the 1% level in both groups and a non-parametric trend test (10) indicates that both functions are linear ($p \leqslant 0.01$).

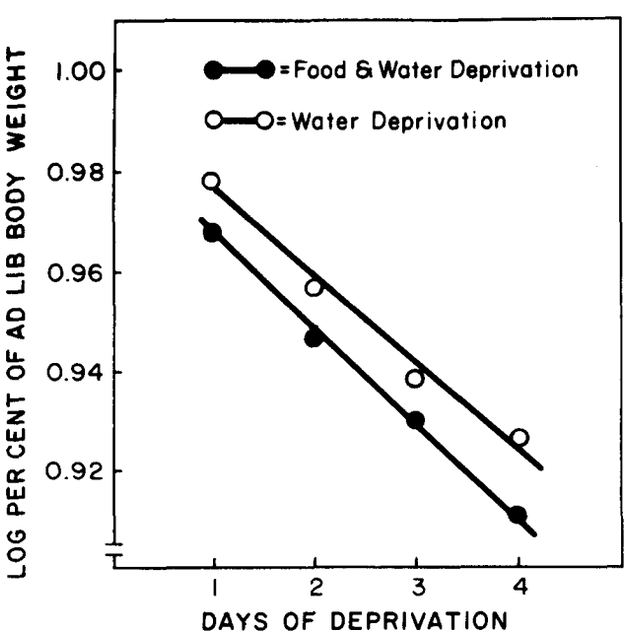

FIG. 5. Total deprivation and body weight loss in the pigeon. A comparison of the effect of combined food and water deprivation with that produced by water deprivation alone.

3. *Body Weight Regulation During Total or Partial Food Deprivation*

Fig. 6 compares the reduction in body weight produced by three different levels of food deprivation. The three groups of birds were maintained under, respectively, 80%, 50% or 0% of their ad lib food ration. (The 0% data were obtained from Group FD, Experiment 2).

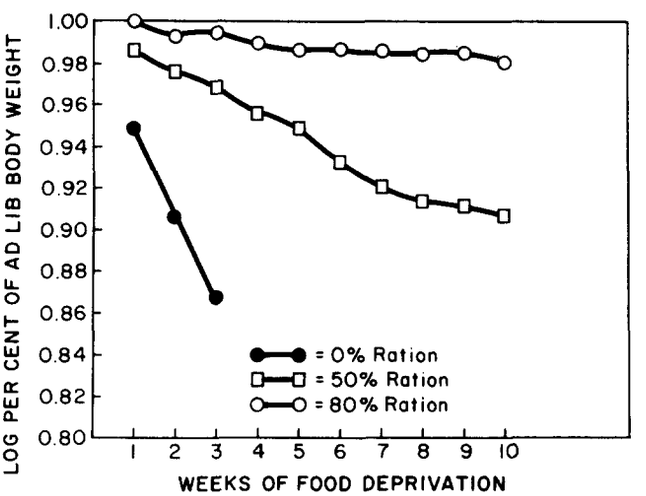

FIG. 6. Partial food deprivation and body weight loss. The relation between food ration size and the rate of weight loss during deprivation.

A non-parametric analysis of variance indicates that the reduction in body weight is significant at all three levels of deprivation ($p < 0.01$ for the 0% and 50% conditions; $p < 0.05$ for the 80% condition). Under total food deprivation (0% group) log body weight appears to decline linearly with time, while under partial deprivation the rate of decline is proportional to the size of the food ration. In the 80% group birds were showing both gains and losses in weight during the last four weeks suggesting that body weight was approaching a stable, asymptotic value. Two of the birds in the 50% group continued to lose weight throughout the 10 weeks of deprivation, although the rate of decline decreases markedly during the last few weeks. (At the end of three weeks of total deprivation, birds in the 0% group had dropped to about 70% of their ad lib weight and deprivation was discontinued to prevent inanition).

The relation between log food intake and log final body weight under partial deprivation was examined using the intake and weight data of the 10th week of deprivation. A significant Pearson product-moment correlation coefficient (r+0.78; df=8; $p < 0.01$) was obtained indicating that the function is a linear one.

4. *Food Intake and Body Weight Regulation During Recovery from Food Deprivation*

The relation between food intake and body weight during recovery from three weeks of food deprivation (Group FD) is plotted in Fig. 7. During the first weeks intake levels are well above normal, declining gradually as body weight approaches it ad lib value. (The persistence of high intake values beyond that point reflects the fact that many of the birds are still growing and have yet to reach their final ad lib weights.) Examination of the quantitative relation between food intake and body weight gain provides some additional information on the regulation of body weight during recovery from deprivation. At the start of the recovery period, the mean body weight of the group is 70% of its ad lib weight. During the first week of recovery the birds made a 16% increase in mean body weight, while eating 165% of their normal mean food intake. In the second week of recovery, with approximately the same food intake (170%) they increased their weight only 7% and an even smaller weight gain takes place in the third week. Such data suggest that equivalent amounts of food do not produce equal gains in body weight during recovery, but that as birds approach their ad lib weight increasing amounts of food are required to produce a net unit gain in body weight.

As a test of this hypothesis the relation between food intake and body weight gain was examined in individual birds over the first three weeks of recovery. For each of the three weeks, the ratio of intake to gain for each bird was plotted against its body weight at the start of the week. The resulting function is linear on a log plot and the correlation between the two variables is significant (Pearson product-moment r=-0.68; df=28; $p < 0.01$).

The recovery data of Group FD (Fig. 7) illustrate the pigeon's long-term adjustment of its food intake during recovery from a prolonged period of total food deprivation. That the pigeon is also capable of a more rapid compensatory adjustment in food intake following deprivation is evident from the data of Group RFD. Table 2 indicates the relation between body weight loss, food intake on day 1 of recovery, and the number of recovery days required to regain the original, ad lib body weight. On the first day of recovery intake is significantly greater than its ad lib value for all three groups and the relationship between the level of deprivation (body weight loss), and subsequent food consumption is significant (F=7.80; df=2/15; $p < 0.01$). The number of days required for recovery increases with increasing body weight loss and this increase is also significant (F=9.67; df=2/15; $p < 0.01$).

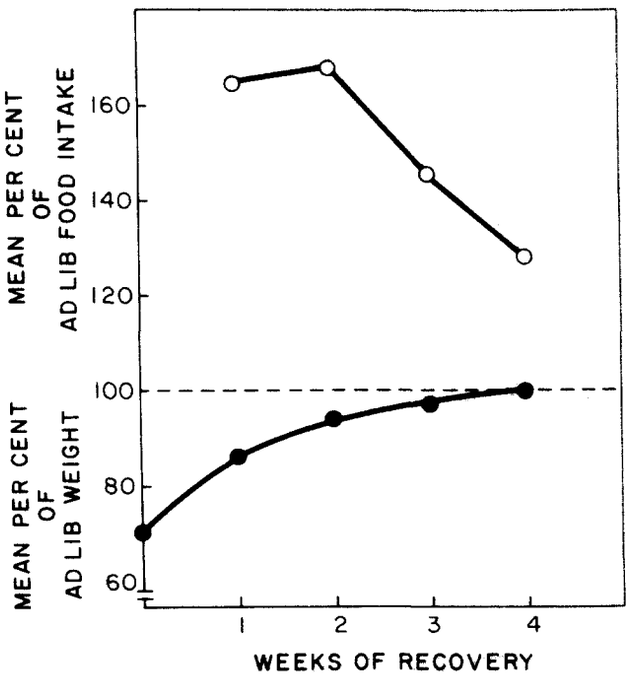

FIG. 7. Food intake and body weight during recovery from three weeks of total food deprivation.

DISCUSSION

The studies reported in this paper were designed to provide data on food and water intake and weight regulation in the pigeon, a species whose digestive system [9] and feeding behavior patterns [25] differ in many respects from those of such typical laboratory mammals as the rat. Despite these structural, physiological and behavioral differences, the functions relating food and water intake to each other and to body weight in the pigeon are strikingly similar to those previously reported in studies of intake and weight regulation in the rat.

1. *The Relation Between Eating and Drinking*

Experiments 1 and 2 confirm for the pigeon the existence of a complex interaction between eating and drinking such as has been previously demonstrated for a number of mammalian and some other avian species. This

TABLE 2

Food Intake During the First 24 Hours of Recovery from Food Deprivation in the Pigeon

	Days of Food Deprivation		Days to Recover Original weight		*Ad libitum*		Food Intake Day 1 Recovery		
Weight Loss	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	% Increase
5%	3	0	5	1.4	27		36.1	4.2	133
15%	7.8	1.2	10	2.7	26.5		43.0	4.5	165
25%	18.8	3.8	15.3	2.0	27.1		60.1	8.3	222

interaction may be manifested in a variety of ways, both under ad lib conditions and during food or water deprivation. Under ad lib conditions eating and drinking in the rat are closely associated in time [11], food and water intake values are highly correlated and the ratio of food intake to water intake is fairly constant [21]. A close association between eating and drinking has been reported for the quail [22] and McFarland has shown that in the Barbary dove, a species closely related to the pigeon, food and water intake vary in phase with each other under ad lib conditions [16]. The data of Experiment 1 indicate that under comparable conditions food and water intake in the pigeon also tend to be highly correlated and that there is a fairly constant ratio of water intake to food intake in individual birds.

The interdependance of eating and drinking in the pigeon are even more striking during periods of food or water deprivation. Total deprivation of water is followed by a drastic reduction in food intake, comparable in its magnitude to that reported for the rat [3] and the Barbary dove [15, 17] and in all three species the bulk of the reduction occurs within the first few days of deprivation. Conversely, food deprivation produces a reduction in water intake which is proportional to the size of the available water ration, reaching a limiting value under conditions of total deprivation. Comparable data have been reported for the rat and the dog [4, 21]. (By contrast with the abrupt reduction in food intake during total water deprivation, is more gradual and its time course may reflect the gradual removal of food from the crop.) McFarland [17] has shown that the reduction in food intake during water deprivation is an important means of water conservation in the Barbary dove, while Collier has suggested that another function of the reduction in food intake is to produce a loss in body weight in order to conserve the ratio of water intake to body weight [5, 6].

2. *Intake and Body Weight Regulation*

Under ad lib conditions, in a controlled and familiar environment, daily food and water intake in the pigeon vary within a range of values which is characteristic for a given bird. These short-term variations may be considerable but over a more extended period the rate of eating and drinking is maintained at a fairly constant value. Similar findings have been reported for a number of mammalian species [13] and have led some investigators to postulate the existence of long-term compensatory mechanisms controlling intake over extended periods. Whatever the nature of these long term control mechanisms, their regulatory function is reflected in the fact that while daily variations in the pigeon's food and water intake values may be on the order of 20 - 30 per cent, daily variations in its body weight rarely exceed two or three per cent.

The data on food consumption during recovery from food deprivation provides another measure of the regulation of body weight by the control of food intake. Intake levels during recovery are significantly above normal, declining gradually as body weight approaches its ad lib value. Our findings thus indicate that following a period of food deprivation the pigeon regulates its body weight by controlling food intake so as to compensate over an extended period of time, for the food lost during the deprivation period. Comparable findings have recently been reported for the rat [14]. Thus both species can apparently detect the extent of body weight loss and respond to it by means of long-term adjustments in their food intake.

In addition to this long-term adjustment the pigeon also shows a more immediate compensatory response which is evident on the very first day of recovery and which reflects the extent of body weight loss produced during deprivation. In the 24 hour period immediately following deprivation, food intake is significantly greater than normal, even for a minimal (five per cent) body weight loss. Moreover, the extent to which food consumption in this 24 hour period is elevated above normal is directly proportional to the level of body weight loss. Similar findings have been reported in a previous study of deprivation effects in the pigeon, utilizing a one hour test period [18]. In a somewhat comparable study of the rat, utilizing a 24 hour test period, Levitsky [14] found that although both a 7% and a 15% body weight loss produced a significant increase in food intake the level of deprivation had no significant effect on the rat's subsequent food consumption. Similar findings have been reported for more extensive periods of deprivation in the rat [7, 19]. This difference in the deprivation-intake functions of the rat and the pigeon may be attributable to the greater storage capacity provided by the pigeon's crop. A similar explanation has been advanced to account for the differences in deprivation-intake functions of several species of fish whose digestive systems differ in an analogous manner [20].

3. *Quantitative Relationships Between Food Intake and Body Weight*

There is in the pigeon, as in many mammalian species [2] a linear relation between the log intake of food and the log body weight. This relation holds not only under conditions of ad lib intake but also under food deprivation. Thus during a period of total food deprivation log body weight declines linearly over time while under partial food deprivation the reduction in body weight is proportional to the size of the food ration and there is a linear relation between log food intake and log asymptotic body weight. (It should be noted that interpretation of the data on partial food deprivation is complicated by the fact that it was obtained under conditions in which several days of free access to food alternated with several days of food deprivation. Fábry [8] has reviewed a number of studies indicating that both morphological and metabolic changes may occur in animals trained to ingest their entire daily food ration within a restricted (e.g., 2 hr) time period. While the experimental conditions for Group PFD certainly do not constitute such a severe stuff and starve regimen, their data may be confounded by an interaction between the amount of deprivation and the nature of the intake pattern.) Finally, the linear relation between log intake and log body weight is also present during recovery from food deprivation since log body weight gain during recovery is a linear function of log food intake. This finding may be accounted for by assuming that as recovery proceeds the proportion of the pigeon's daily food intake needed merely to maintain its current body weight increases with each increase in weight. Thus as the bird approaches its ad lib weight a decreasing proportion of its food intake is available for conversion into new body weight.

In a series of papers on weight regulation, Collier has advanced the hypothesis that body weight loss is "an active process involved in the defense of certain physiological parameters." ([6], p. 594). This hypothesis is based upon

studies which indicate that nutrients such as food or water are consumed in some fixed proportion to each other and that for any given nutrient a constant ratio is maintained between the amount of that nutrient consumed and the animal's body weight. Although our experiments on the pigeon were not designed to provide quantitative tests of this hypothesis they are certainly compatible, in many respects, with Collier's formulation.

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