JOURNAL OF THE EXPERIMENTAL ANALYSIS OF BEHAVIOR 1999, **72,** 407–423 NUMBER 3 (NOVEMBER)

SATIATION, CAPACITY, AND WITHIN-SESSION RESPONDING

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Responding may change substantially over the course of a session (McSweeney, Hinson, & Cannon, 1996). The role of satiation in this effect was investigated in three experiments. Experiment 1 showed that the capacity of pigeons to consume milo over a 1-hr period was relatively stable across three different methods of measurement. In Experiment 2, pigeons were divided into two groups that differed in their capacity based on one of those measures. Key pecking was then reinforced under a variable-interval 30-s schedule with hopper durations of 2 or 5 s. According to the satiation hypothesis, subjects with small capacities should satiate faster and therefore show greater decreases in food-reinforced responding than would subjects with larger capacities. The results confirmed this prediction and showed that the magnitudes of within-session decreases were better predicted by the amount an animal consumed relative to its capacity than by absolute amount alone. In Experiment 3, each pigeon was prefed 0, 5, 15, or 25 g of milo prior to each session. Consistent with the satiation hypothesis, increases in prefeeding produced lower overall response rates in the smaller capacity subjects than in the larger capacity subjects at each level of prefeeding. These experiments demonstrate the importance of a new variable in the control of behavior, and provide a recommended technique for its measurement.

Key words: arousal, crop capacity, satiation, within-session responding, key peck, pigeons

In a typical operant procedure, animals are trained to make a response such as a lever press, a key peck, or a chain pull to receive food. Experimenters often aggregate those responses over the session to serve as a dependent variable. However, overall session measures such as these can sometimes be misleading, masking phenomena that may occur within the course of individual sessions. One example recently reported in the literature is the within-session decrease or increase in response rates over the course of a session in both pigeons and rats under a wide variety of fixed and variable ratio and interval schedules (e.g., McSweeney, Roll, & Weatherly, 1994), autoshaping (McSweeney, Swindell, & Weatherly, 1996), and delayed matching-to-sample procedures (McSweeney, Weatherly, & Swindell, 1996).

These within-session changes in response rates may be due to the interaction of two opposing processes: the arousal of the animal and later, after repeated feedings, satiation (Killeen, 1995). Arousal is an energizer of the animal's behavior that is proportional to the rate of reinforcement and may become conditioned to the particular context in which it occurs. The rise of response rates early in a session may reflect the accumulation of arousal. As the session progresses, however, and the animal consumes more of the reinforcer, the animal may gradually become satiated, thereby lowering responses rates and producing the within-session decline in responding reported in the literature. In fact, within-session decreases in responding are often steeper under richer rather than leaner schedules of reinforcement, which is consistent with this explanation (McSweeney, 1992; McSweeney, Roll, & Cannon, 1994; McSweeney, Roll, & Weatherly, 1994).

Satiation has been defined in a number of ways. For example, Roll, McSweeney, Johnson, and Weatherly (1995) define satiation as "reinforcers losing their ability to increase, or maintain, behavior when too many have been consumed" (p. 324). A definition couched in terms of the phenomenon one wishes to explain, however, renders the concept circular and thus unhelpful as an explanation. Mor-

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This research was supported by NSF Grant IBN9408022 and NIMH Grant K05MH01293 to the second author. We thank Krista Rolands and Jennifer Cioni for their assistance in collecting and analyzing data.

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gan (1974) argued that to avoid circularity, the consummatory activities of the animal must be the criterion for satiation, for animals have been shown to learn responses while apparently satiated, and conversely, to respond appropriately after learning even when not deprived. According to Morgan (1974), satiation may be defined as "a state in which the animal will no longer engage in a particular consummatory response (eating) even in the presence of the appropriate incentive (food)" (p. 449).

If capacity is defined as the amount of food an animal will consume before no longer engaging in a consummatory response, the first question should be: How is capacity best measured and how reliable are such measures? In the first experiment three different methods of assessing capacity were evaluated: free feeding over a 1-hr period, periodic reinforcement over a 1-hr period, and continuous reinforcement of each response that occurred during a 1-hr period. One of these methods was then used in a second experiment as the basis for dividing pigeons into two groups, a large-capacity group (Group LC) that consumed the largest amount of food and a small-capacity group (Group SC) that consumed the smallest amount during a capacity pretest. The capacity measure was then used to predict the amount of within-session decreases in responding on a variable-interval schedule. Finally, a third experiment manipulated the amount of food consumed during a session by prefeeding pigeons in each group at the beginning of each session.

EXPERIMENT 1

In the first experiment three different methods of assessing pigeons' capacity to consume food were examined. In the first method subjects were placed in an apparatus for a 1-hr period and were given free access to a cup full of food on the floor of the chamber. In the second test, food was periodically delivered from a standard food hopper located behind an intelligence panel on a fixed-time schedule. In the third test pigeons were required to peck once to an illuminated key to produce reinforcement. The effects of these methods were then compared by measuring the difference between the weights of each subject before and after each session to estimate the capacity of each subject to consume food over the course of each test session.

METHOD

Subjects

Sixteen adult homing pigeons (*Columba livia*) were used in this experiment. Each had prior experience on interval and ratio schedules. The birds were individually housed in stainless steel cages with free access to water and grit under a 12:12 hr light/dark cycle beginning at 6:00 a.m. The birds were maintained at 80% of their free-feeding weights and were given additional food following an experimental session as needed to maintain their 80% weights. A subject's session was conducted only if its weight at the beginning of each session was within ±2% of its 80% weight. Because of this, subjects (especially those with small capacities) would sometimes require 1 or 2 days off before returning to their 80% weight.

Apparatus

The experiment was conducted in three Lehigh Valley experimental enclosures measuring 31 cm long by 36 cm wide by 36 cm high. A shielded houselight provided illumination for the chamber and was located on an intelligence panel 33 cm from the chamber floor. Three Plexiglas keys, 2.5 cm in diameter, were located horizontally 26 cm above the chamber floor and were spaced 8 cm apart. Only the center key was used in this experiment and could be illuminated with a white light projected onto it from the rear. Each response key required approximately 0.23 N force for activation. An illuminated Lehigh Valley food hopper delivered milo through an opening (6 cm by 5 cm) located 11.5 cm from the floor. Masking noise (73 dB) was provided by a speaker mounted behind the left side of the panel 5 cm from the floor and 6 cm from the wall. Additional noise was provided by a ventilation fan mounted on the outside of the chamber. Experimental events were scheduled and the data recorded by an IBM 386 PC clone.

Procedure

Because each subject had had prior experience in the chamber, training with the food hopper and shaping to peck the keys were not necessary. Each subject was tested for its capacity to consume milo grain over the course of 1-hr sessions by three different methods: a test in which responding was continuously reinforced (CRF test), a test in which milo was periodically delivered (fixed-time, or FT, test), and a test in which subjects were given free access to milo in a food cup located on the chamber floor (a free-feeding, or FF, test). Each test was conducted for three sessions in the order listed above. To estimate the amount eaten during each session, pigeons were weighed immediately prior to and following placement into the experimental chamber. This method has been a reliable measure previously used to estimate pigeons' consumption of food during a session (Bizo, Bogdanov, & Killeen, 1998). Excreta were not measured, as they typically constitute only a small fraction of weight change.

Continuous reinforcement test. During the CRF test, each response to an illuminated white center key darkened the key and produced 4-s access to an illuminated hopper containing milo. Immediately following reinforcement, the white center key was again illuminated for the next trial. Each session began with the illumination of the houselight, which terminated after 1 hr when the session was completed.

Fixed-time test. During the FT test, 4-s access to an illuminated hopper of mixed grain was presented every 15 s regardless of responding. Each session began with the illumination of the houselight and was terminated after 1 hr.

Free-feeding test. In this test, the capacity of each subject to consume milo was measured by placing individual subjects in an illuminated experimental chamber for 1 hr with free access to a food cup (10 cm by 6 cm by 5 cm) located on the chamber floor and filled with approximately 145 g of milo.

For all statistical analyses, the Type I error rate was set at .05 on a per decision basis based on Rodger's (1975) table of critical F values.

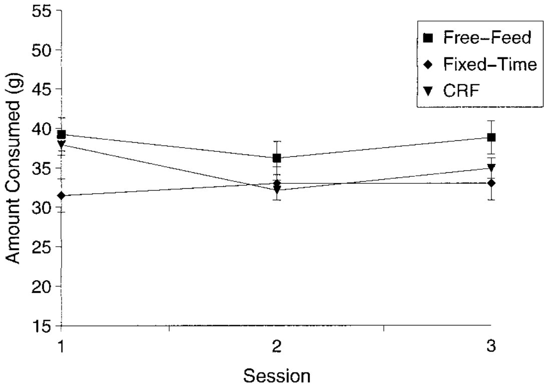

Fig. 1. Average capacity estimates for the CRF, FT, and FF methods in Experiment 1. Error bars represent the average standard deviation of the means.

RESULTS

Figure 1 shows the average amount of food consumed over the course of each 1-hr session during the FF, FT, and CRF tests, averaged over the three sessions for each test. Of the three tests, the FF test produced the highest overall estimate of capacity ($M = 38.13$ g) followed by the CRF test ($M = 35.0$ g) and the FT test ($M = 32.5$ g). An ANOVA conducted over these data with test and session as factors supported this conclusion. There was a main effect of test method, $F(2, 30) = 8.93$, a main effect of session, $F(2, 30) = 5.37$, and a Method × Session interaction, $F(4, 60) = 2.64$. Post hoc contrasts between each method indicated a significant difference between the FF and FT tests and the FF and CRF tests, Fs$(2, 30) = 8.88$ and 2.75, respectively, but no significant difference between the FT and CRF methods, $F(2, 30) = 1.75$. Separate analyses were then conducted for each method across the 3 days each was tested. Of the three methods, only the CRF method produced significant differences in estimated capacity across the 3 days, $F(2, 30) = 5.84$. There were no significant differences in the FF method, $F(2, 30) = 1.86$, or the FT method, $F(2, 30) = 1.14$.

There were substantial differences in measured capacity across the 16 subjects. Table 1 shows the amount of food consumed by each subject for the three methods used to assess capacity averaged over the three sessions. The amount consumed ranged from 17 to 43 g in the CRF test, 21 to 41 g in the FT test, and 20 to 49 g in the FF test. Overall averages of the three measures ranged from a low of 19.44 g (Bird 50) to 43.67 g (Bird 17) consumed over the course of each 1-hr session. There was no significant correlation between body weight and the capacities estimated from the FF, FT, and CRF methods, $r = -.12$, $-.17$, and $-.19$, respectively. Furthermore,

Table 1

Eighty percent weights and estimated food capacities for each subject from the CRF, fixed-time, and free-feeding tests.

Subject	80% weight	CRF	Fixed time	Free feeding	Overall average
3	327	37.33	39.33	47.00	41.22
5	276	38.00	40.67	49.33	42.67
14	272	33.00	28.33	41.67	34.33
17	252	43.67	40.00	47.33	43.67
24	283	31.33	31.33	41.67	34.78
25	357	43.33	34.00	36.67	38.00
27	341	42.00	37.00	49.33	42.78
28	270	40.33	32.67	38.00	37.00
50	307	17.33	20.67	20.33	19.44
54	367	43.00	27.00	37.00	35.67
55	287	31.67	32.67	31.00	31.78
56	313	37.33	37.33	43.00	39.22
57	231	36.67	41.00	42.00	39.89
58	277	23.00	23.67	23.33	23.33
59	257	29.67	25.67	32.33	29.22
95	391	32.67	29.33	30.00	30.67
M		35.02	32.54	38.13	35.23

there was little evidence that these measures were related to the amount of food required to maintain each subject's 80% weight during nonexperimental days. The correlations between the measures of capacity (FF, FT, and CRF methods) with maintenance intake assessed following the study produced correlations of $r = -.22$, $-.39$, and $-.11$, which were not significant. If anything, the negative relationships found in each of the three tests, although not significant, suggest that larger capacities or body weight may be associated with *smaller* amounts of food required to maintain 80% weight.

In order to estimate the degree to which each method produced similar estimates of capacity, a Pearson *r* correlation was conducted to compare the three measures. Of the three measures, the FF test provided the highest overall correlation with the other two measures, with correlations of .85 to FT and .84 to the CRF tests. The FT measure, which produced the lowest estimated capacity, also produced the lowest correlation relative to the CRF method. Figure 2 shows a scatter plot

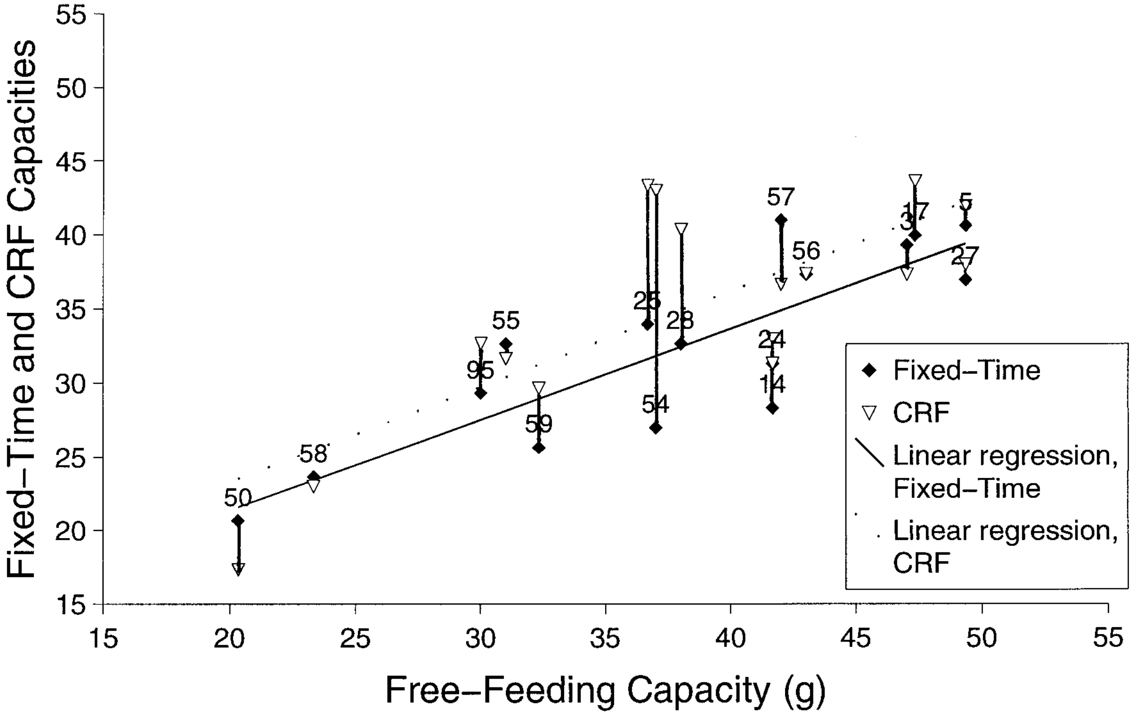

Fig. 2. Estimated capacities for the CRF, FT, and FF methods in Experiment 1. The *x* axis represents the amount consumed during the FF test, and the *y* axis represents the amounts for both the FT and CRF test methods for each subject. Each subject's data are connected by vertical lines. Best fitting lines are shown for the separate regressions.

of the estimated capacities of each subject from FF, FT, and CRF methods. Each of the three methods tended to produce a relatively consistent estimation of capacity within each subject and different estimates of capacity across subjects. In fact, measures of capacity of subjects whose capacities were the smallest remained that way in each of the three tests, whereas those whose capacities were largest remained the largest no matter which method was used.

Discussion

Although there were some differences among the three measures, they did tend to produce similar estimates of capacity. Of the three, the FF method produced the highest estimate of capacity followed by the CRF and FT measures. One possible explanation for these differences may be that each method provides slightly different amounts of total access time to the reinforcer. For example, the FF method provides continuous access to food because the food cup is available throughout the session. In contrast, the CRF method requires a single peck to gain access and hence, would tend to restrict access time, whereas the FT condition restricts this time further by allowing access only after each interval has expired.

Interestingly, body size (ad lib weight) was not significantly correlated with measured capacity. This suggests that differences between each bird's capacity were not due simply to systematic differences in body weights. In this study we used a variety of pigeon strains such as light, dark, and black checker, silver bar, and recessive red. Perhaps the use of a uniform strain would yield stronger correlations between body weight and speed of satiation, which have been reported elsewhere (Palya & Walter, 1997).

Because the results of all three techniques are highly correlated, we recommend use of the FF technique because (a) it is easy to administer, (b) it is most highly predictive of the other measures, and (c) it does not restrict access and, hence, yields the largest average capacity.

The average variability from one test session to the next is reflected in an average *SD* of 4.15 g for the FF technique, yielding a standard error of the estimate of $\sigma\sqrt{(n-1}$, in the present case 1.03 g (*SD*s and *SE*s in the FT and CRF were 2.48 and 0.62 g and 4.29 and 1.07 g, respectively). Thus, one to three measurements should yield an estimate of the capacity adequate for most researchers.

EXPERIMENT 2

Bizo et al. (1998) reported that the magnitude of within-session decreases in responding were correlated with pigeons' capacities. Using the FF method, Experiment 2 divided subjects into two groups, a large-capacity group (Group LC) and a small-capacity group (Group SC), on the basis of the amount of food required to satiate the animal over the course of an hour. Responding was then measured during sessions of variable-interval (VI) reinforcement. According to the satiation hypothesis, pigeons in Group SC should become satiated faster and show the largest within-session decreases in responding relative to pigeons in Group LC, who should become satiated at a slower rate. In contrast, if the capacity tests do not measure the propensity to become satiated, or if satiation does not contribute to within-session decreases in responding, then this categorization of the subjects should not predict any of the variance in within-session responding. In other words, if capacity is a factor in satiation, then this experiment moves us from correlational accounts to predictions based on these capacities.

Method

Subjects

Eight adult homing pigeons (*Columba livia*) were selected from the available population of 20 birds in the laboratory based on their capacities (see procedure section below). Each had had prior histories on interval and ratio schedules. The birds were individually housed in stainless steel cages with free access to water and grit under a 12:12 hr light/dark cycle beginning at 6:00 a.m. The birds were maintained at 85% of their free-feeding weights and were given additional food following each experimental session as needed to maintain their 85% weights. Experimental sessions were conducted 6 days per week but only if a subject's body weight was within ±5 g of its 85% weight. Because of this constraint, subjects would occasionally require a day or two to return to their criterion weights.

This was especially the case for subjects in the small-capacity large-hopper-duration condition (see below).

Apparatus

This experiment was conducted using a single Lehigh Valley experimental enclosure (31 cm by 36 cm by 36 cm). The locations and dimensions of the keys, the houselight, and the hopper that delivered milo were identical to those used in Experiment 1. An illuminated Lehigh Valley food hopper delivered milo grain through an opening (5.8 cm by 5 cm) located 11.5 cm from the floor. A platform stabilimeter located on the floor of the chamber raised the floor 8 cm but was inoperative in this experiment.

Procedure

Prior to the beginning of the experiment, the capacity of each subject was measured in a free-feeding test identical to the FF test used in Experiment 1: Subjects were given access to a food cup for a 1-hr period, with their weights measured before and after the 1-hr session to determine their capacities. Capacity tests were conducted with the pigeons at 80% weights for consistency with typical deprivation levels for pigeons. During the experiment, the pigeons' weights were maintained at 85% in an effort to minimize interruptions to restore a subject's weight. Table 2 shows the 85% weights and capacities of subjects in the available subject population prior to the experiment. (Note that some birds had been subjects in Experiment 1, as indicated by their subject numbers.) Two groups of 4 subjects were selected from the tails of this pool such that half of the subjects had the largest capacities (Group LC), eating 46, 48, 48, and 48 g over the course an hour, or had the smallest capacities (Group SC), eating 16, 19, 19, and 23 g during that hour.

Experiment 1 found little evidence relating body weight to capacity. Similarly, the correlations based on the data in Table 2 between body size (ad lib weight) and measured capacity were again insignificant ($r = -.06$). More important, there was no significant difference between the 85% body weights for the two groups, $t(6) = 0.17$. Hence, any differences in responding between the groups cannot be due to any systematic difference in body weights.

Table 2

Eighty-five percent weights and preexperimental food capacities of subjects available for Experiment 2.

Bird	85% weight (g)	Capacity (g)
67[a]	330	16
91[a]	411	19
94[a]	415	19
95[a]	415	23
57	287	22
59	283	23
3	357	33
1	254	34
4	326	36
16	362	36
14	327	38
55	307	40
28	252	43
25	272	43
56	367	45
9	365	46
11[a]	369	46
2[a]	413	48
10[a]	345	48
15[a]	425	48

[a] Subjects selected for Experiment 2.

Following the capacity measure, subjects were allowed to recover to their 85% body weights before the experiment began. During the experiment, subjects in Group SC and Group LC were trained under a VI 30-s schedule constructed using a constant-probability algorithm. To minimize any warm-up effect each 1-hr session began with a single peck to a white stimulus on the center key. A single peck to the center key terminated the keylight, produced reinforcement, and after 1 s began the experimental session. Thereafter food was delivered according to the VI 30-s schedule with the houselight illuminated throughout the session. For half of the subjects in each group, the duration of food hopper presentations was 2 s for the first 20 sessions followed by 20 sessions under a 5-s hopper duration. For the remaining half of the subjects these durations were reversed. Subjects' weights were again measured before and after each experimental session to estimate the amount consumed during a session.

RESULTS

Within-session declines in responding were apparent in both Group LC and Group SC over the course of the 1-hr sessions. Figure 3 shows the average number of responses per

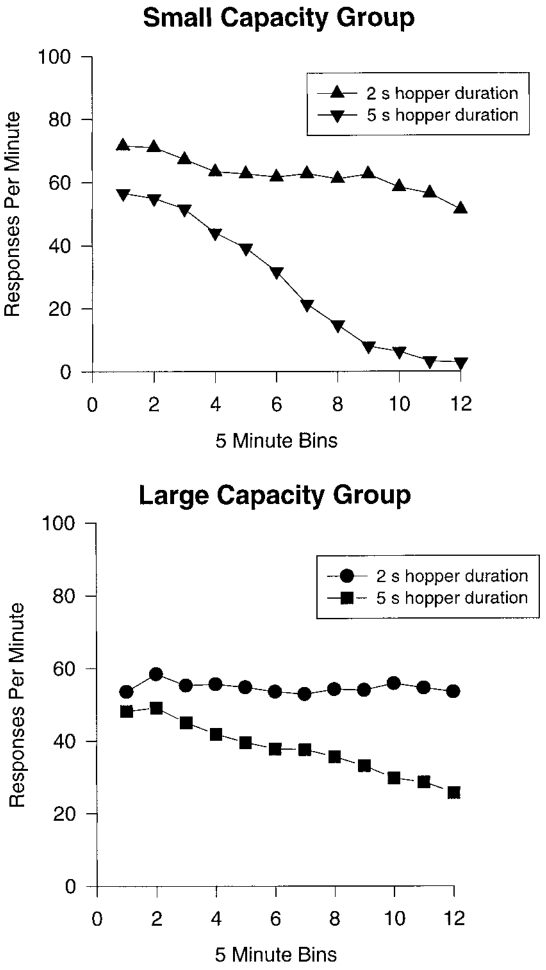

Fig. 3. Mean response rates over the course of each 1-hr session for Group SC (upper panel) and Group LC (lower panel) with the 2-s and 5-s hopper duration conditions, averaged over individual subjects.

minute for Group LC and Group SC with the 2-s and 5-s hopper durations over the course of an experimental session. The data are collapsed into 5-min bins averaged over the course of the 1-hr session and over the last five sessions of training. Response rates for the pigeons in both Group LC and Group SC decreased when the hopper duration increased from 2 s to 5 s. Also, response rates tended to decline over the course of each session, demonstrating the within-session effect. The greatest decrease occurred for pigeons in Group SC, whose response rates approached zero toward the end of each session under the longer (5-s) hopper duration. Overall, response rates were higher with the 2-s hopper duration than with the 5-s duration. An ANOVA conducted on these data with Group × Hopper Duration × Bin as factors confirmed these observations. Although there was no significant main effect of group, $F(1, 6) = 0.12$, there was a significant main effect of both hopper duration, $F(1, 6) = 33.01$, and bin, $F(11, 66) = 26.87$. There were also significant Group × Bin and Duration × Bin interactions, $F(11, 66) = 7.52$ and 9.09, respectively, but no significant Group × Duration, $F(1, 6) = 3.85$, or Group × Duration × Bin interactions, $F(11, 66) = 3.85$.

Figures 4 and 5 show the data for individual birds in Group SC and Group LC, respectively. Three of the 4 birds in Group SC produced a characteristic within-session decrease in response rates when the hopper duration was 2 s, and all 4 birds showed evidence of a decrease under the longer 5-s hopper duration. Similarly, 3 of the 4 subjects in Group LC showed within-session decreases with the long hopper duration (5 s). The response rate of the 4th (Bird 10) was lower when the hopper duration was 5 s than when it was 2 s, but there was no differential change over the course of the session. In contrast, none of the birds in Group LC (except perhaps Bird 15) appear to show evidence of a within-session decrease in responding under the 2-s hopper condition.

In order to assess the relative degree to which capacity and hopper duration affected within-session decreases in response rates, a difference score was calculated by subtracting the median response rate of the first three 5-min bins of the session from the median response rate from the last three 5-min bins, averaged over the last five sessions for each group. These difference scores indicate the change in response rate from the beginning to the end of a session, with positive and negative values indicating a net increase and decrease in response rates, respectively. Overall, larger average within-session differences in response rates were found for Group SC ($M = -14.4$ and -52.2 responses per minute in the 2- and 5-s hopper conditions, respectively) than in Group LC ($M = -1.8$ and -19.8 responses per minute), main effect of group, $F(1, 6) = 12.64$. In both groups, longer hopper durations produced greater within-ses-

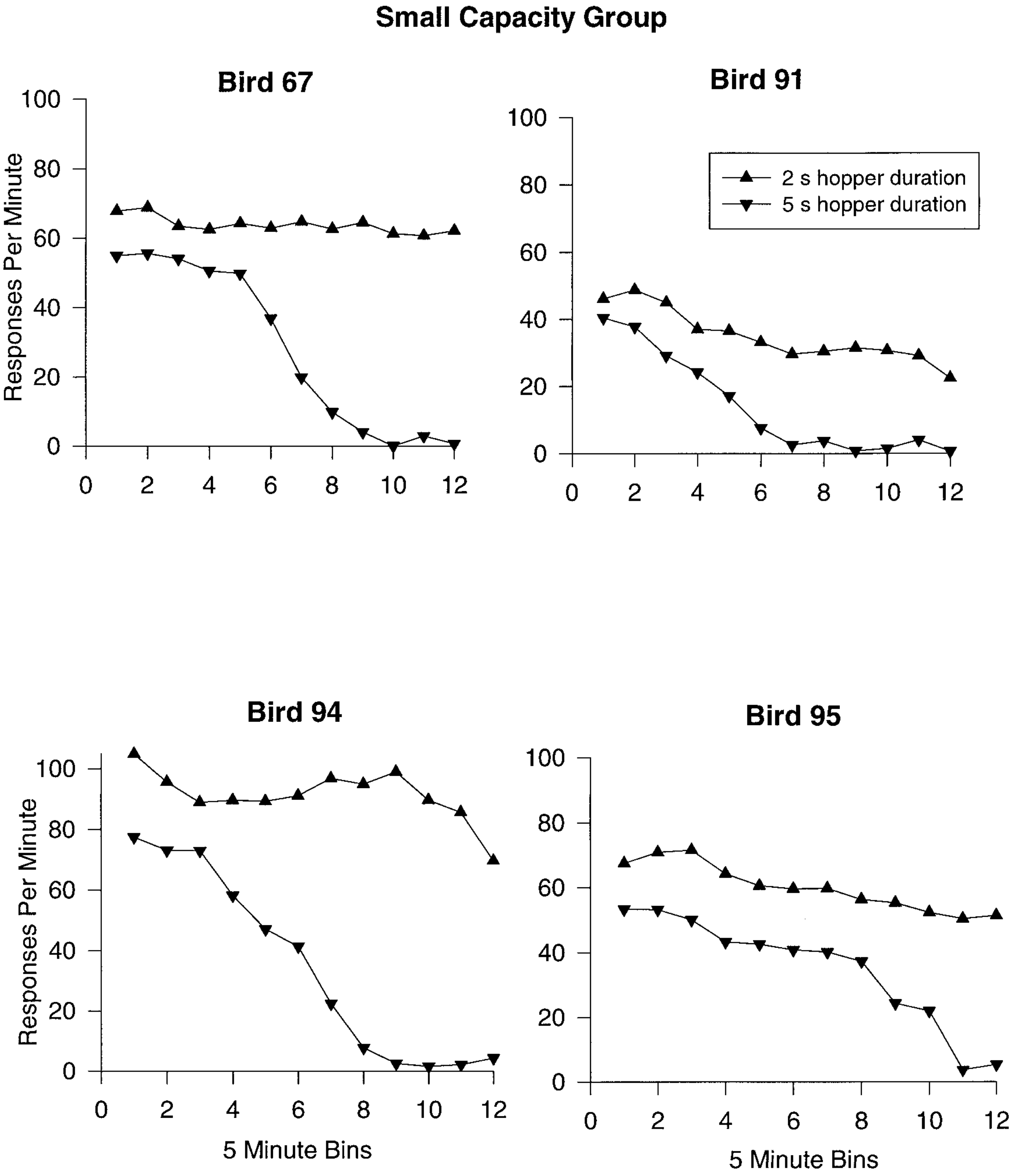

Fig. 4. Mean within-session response rates for each subject in Group SC with the 2- versus 5-s hopper durations averaged over the last five sessions of training.

sion decreases, main effect of hopper duration, *F*(1, 6) = 15.23. There was no main effect of session, *F*(4, 24) = 1.74, and no significant Group × Hopper Duration, *F*(1, 6) = 2.00, Group × Session, *F*(4, 24) = 1.49, Duration × Session, *F*(4, 24) = 0.73, or Group × Duration × Session interactions, *F*(4, 24) = 0.68.

If the amount an animal eats relative to its capacity has an effect on the magnitude of any decreases in within-session response rates, then the more the animal consumes

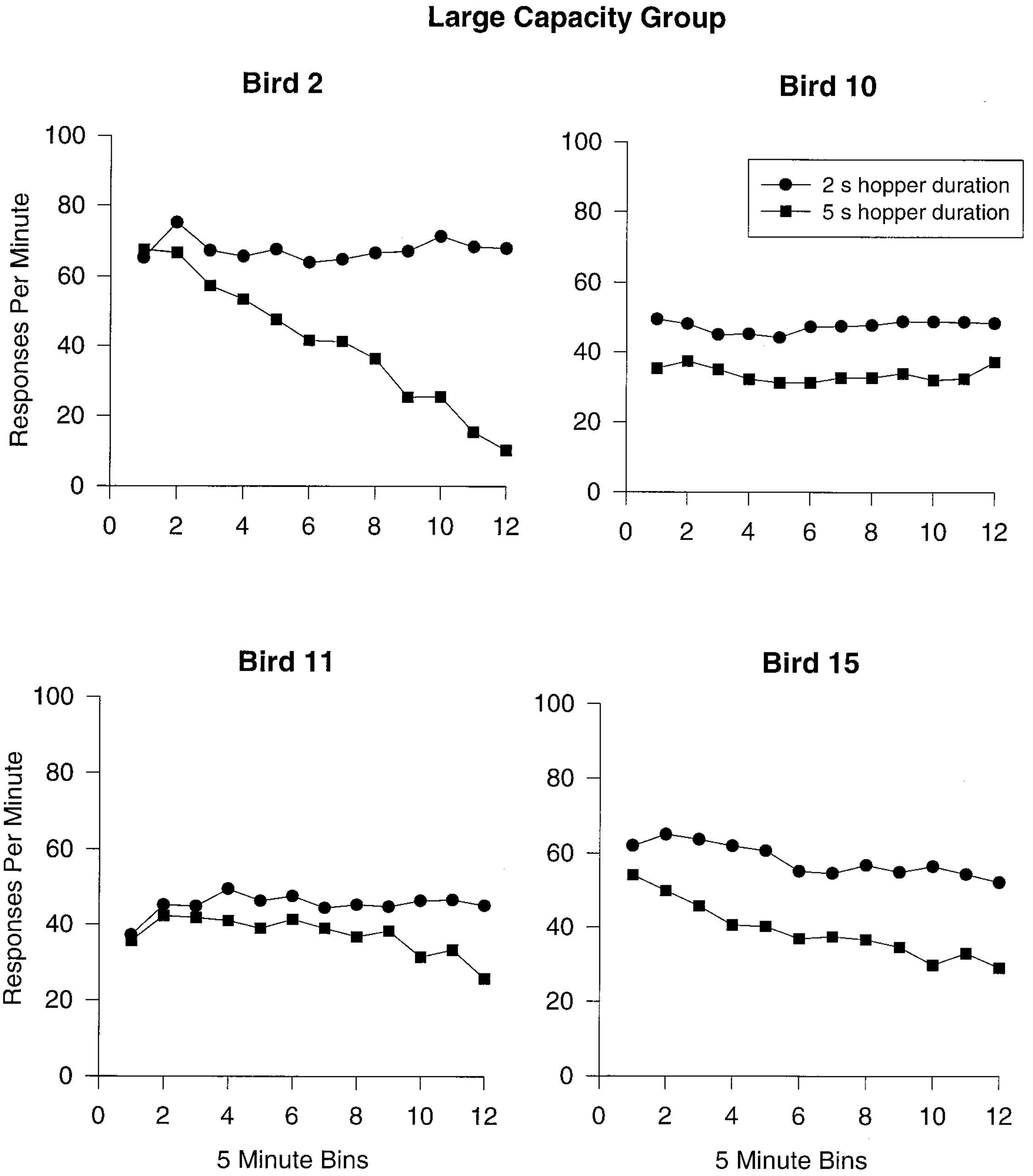

Fig. 5. Mean within-session response rates for each subject in Group LC with the 2- versus 5-s hopper durations averaged over the last five sessions of training.

relative to its capacity, the greater any decreases in response rates should be over the course of a session. Figure 6 is a scatter plot showing each subject's average relative change in response rates (difference scores) as a function of the average percentage of each subject's capacity consumed during sessions in the 2- and 5-s hopper conditions. The changes in difference scores are orderly. Hopper durations of 2 s resulted in difference scores near zero for pigeons in both groups, whereas hopper durations of 5 s pro-

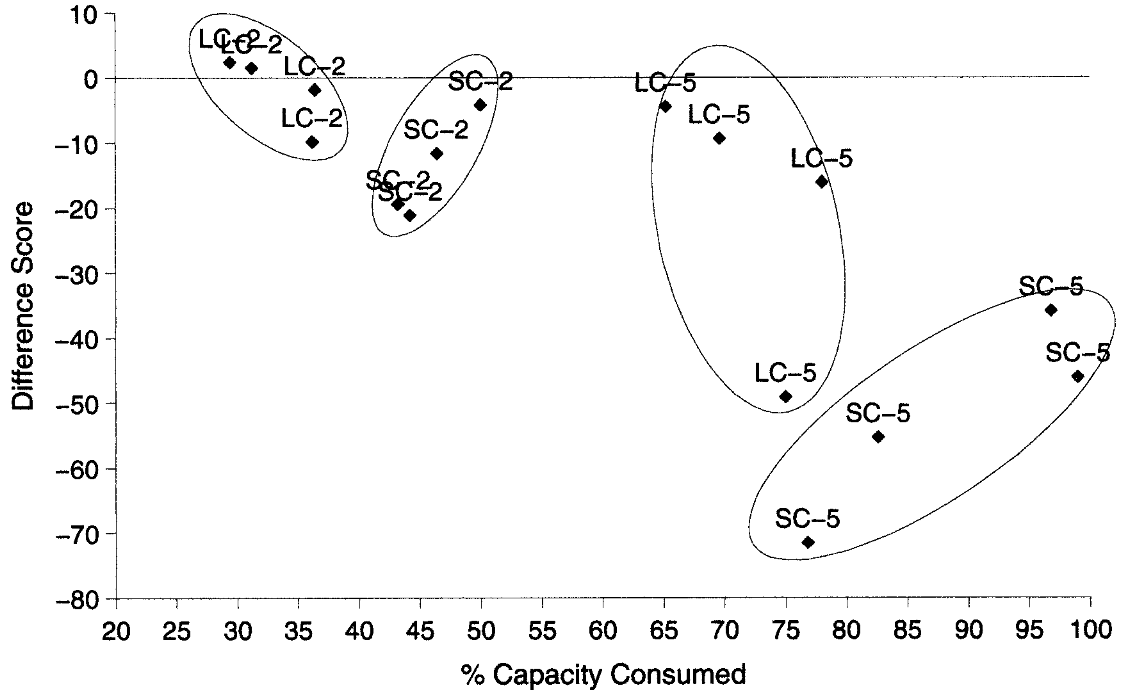

Fig. 6. Median within-session decreases in response rates (relative difference scores) with the 2-s and 5-s hopper durations relative to the average percentage of capacity consumed (amount consumed divided by capacity) for each subject in Groups SC and LC. The numbers indicate the hopper duration.

duced substantial within-session decreases for pigeons in Group SC and moderate decreases for those in Group LC.

DISCUSSION

According to the satiation hypothesis, within-session decreases in responding are the consequence of pigeons' becoming satiated over the course of the session. In this experiment, within-session decreases in responding of two groups of subjects differing in one measure of satiation, their food-intake capacity, were compared during sessions containing short (2-s) and long (5-s) hopper durations. If satiation produces these within-session decreases, then pigeons with limited capacities should show greater within-session decreases than those with larger capacities, which is in fact what occurred. Within-session decreases in responding (difference scores) were greater for the pigeons in Group SC than for those in Group LC. This was especially apparent for Group SC during the 5-s hopper durations, when responding approached zero near the end of each session (see Figure 3). Moreover, these differences correlated with changes in the amount each animal ate relative to its capacity (see Figure 6). As pigeons consumed more food and approached their individual capacities, greater within-session decreases were observed, which is again consistent with the predictions of the satiation hypothesis.

There are a number of ways in which the amount an animal consumes may affect the magnitude of any change in within-session response rates. For example, one possibility is that both groups of pigeons could consume equivalent *amounts* of milo over the course of the session. However, this amount relative to each subject's capacity (e.g., as percentage of capacity) would be different for each subject. Because the capacities of Group SC were smaller, this amount would represent a value greater than that of Group LC and should therefore produce larger within-session decreases in response rates. In fact, the average percentage of the capacity consumed by birds in Group LC was smaller than that of Group SC (see Figure 6). However, inspection of the average *amount* of food eaten by each group indicated that Group LC consumed significantly more grain during each session than

Group SC under both the 2-s [$M = 15.8$ vs. 8.8 g, respectively, $t(6) = 6.73$] and the 5-s hopper conditions [$M = 34.2$ vs. 17.1 g, respectively, $t(6) = 7.45$]. Thus in terms of the amount eaten, Group LC consumed significantly more grain than Group SC but showed the smallest within-session decreases. Hence, the amount of food consumed by itself is not predictive of the within-session decreases shown in this experiment. However, the amount consumed relative to an animal's capacity *is* a good predictor of the magnitude of within-session changes in responding. Birds in Group SC, which consumed 77.2% and 45.9% of their capacities, on average, in the 5-s and 2-s hopper conditions, showed the largest relative declines in responding compared to Group LC, which consumed 73.0% and 35.3%, respectively, of their capacities under the same hopper conditions. Therefore, it appears that the amount consumed relative to an animal's capacity is the important factor predicting these within-session decreases and not the rate of reinforcement (it was the same for both groups) or the amount of food per se. It is the amount relative to an individual's capacity that is the controlling factor and is exactly what the satiation hypothesis predicts to be important.

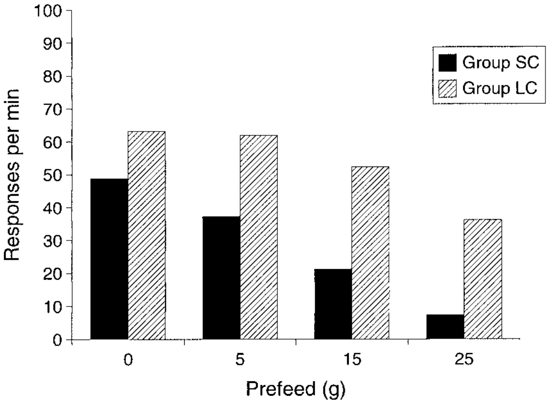

Fig. 7. Average response rates for Groups SC and LC over the last five sessions of each prefeeding condition.

EXPERIMENT 3

Another method of varying satiation in pigeons is to feed them before the beginning of each session. In the third experiment, pigeons in Group SC and Group LC were provided with either 0, 5, 15, or 25 g of food in the apparatus prior to the beginning of each experimental session. According to the satiation hypothesis, pigeons that are prefed larger amounts of food should become satiated faster than those given smaller amounts. Furthermore, prefeeding should have a systematically greater impact on responding in small-capacity than in large-capacity subjects as the amount of food given during prefeeding increases.

METHOD

Subjects and Apparatus

The subjects from Experiment 2 were used in this experiment. Feeding and housing conditions were the same as for Experiment 2. Experimental sessions were conducted only if a subject's body weight was within ±5 g of its 85% weight. Thus subjects occasionally required 1 or 2 days off before returning to their 85% weights—in particular, subjects under the largest prefeeding conditions and subjects with small capacities.

The apparatus was the same as that used in Experiment 2.

Procedure

Subjects from Group SC and and Group LC were prefed either 0, 5, 15, or 25 g during the first 15 min of each session. The order of prefeeding was counterbalanced in a quasi-random order within each group. Each subject was exposed to each level of prefeeding for 10 sessions. During this time, a food cup was placed in the chamber, which was illuminated with the houselight only. After the 15-min prefeeding period was completed, the food container was removed and the session began with the illumination of the houselight and a white center key. A single peck to the center key produced reinforcement and initiated a 1-hr session, similar to Experiment 2, in which reinforcement was delivered on a VI 30-s schedule. However, in this experiment the hopper duration was fixed at 3 s for both groups.

Subjects were weighed before prefeeding and after each session to estimate the amount consumed over the course of each session. Thus, this amount reflected both the food earned during the session and any food given the animal during the prefeeding phase.

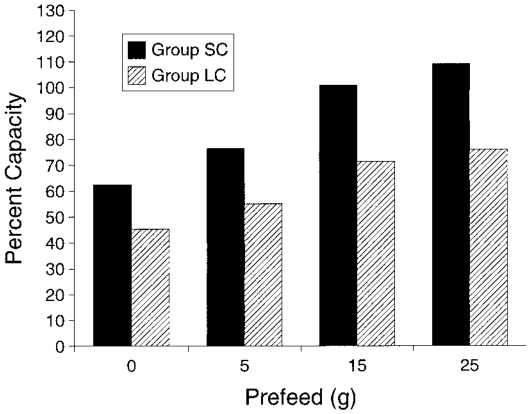

Fig. 8. Average percentage of capacity consumed in Groups SC and LC during each prefeeding condition.

RESULTS

Figure 7 shows the average response rates during each session for Group LC and Group SC at each level of prefeeding. As the amount of food given to the animals in each group prior to the session increased, the average response rate decreased. For each prefeeding amount, average overall response rates were lower for Group SC than for Group LC. An ANOVA with group, prefeed amount, and within-session responding (5-min bins) as factors indicated a main effect of prefeeding, $F(3, 18) = 20.77$, and main effect of bin, $F(11, 66) = 29.62$. However, the overall difference in response rates between Group SC and Group LC did not reach significance, $F(1, 6) = 3.70$. There was no significant Group × Prefeed, $F(3, 18) = 1.18$, Group × Bin, $F(11, 66) = 1.07$, or Prefeed × Bin interaction, $F(33, 198) = 0.40$. However, the interaction between Group × Prefeed × Bin was significant, $F(33, 198) = 1.76$.

Figure 8 shows the average percentage of the capacity of food consumed by the pigeons in each group for the four levels of prefeeding. These data represent the average over the last five sessions. As prefeeding level increased, the percentage of the capacity consumed by the pigeons in Group SC and Group LC increased accordingly. The average overall percentage capacity consumed by Group SC was significantly greater than that of Group LC at each level of prefeeding. Thus, subjects in Group SC were closer to their capacities than were those in Group LC. An ANOVA confirmed these observations regarding consumption. There was a main effect of group, $F(1, 6) = 7.01$, and a main effect of prefeeding, $F(3, 18) = 28.36$, but no significant Group × Prefeeding interaction, $F(3, 18) = 1.15$.

Figure 9 shows the response rate versus percentage capacity consumed for individual subjects in Group SC and Group LC when prefed 0, 5, 15, and 25 g. Overall response rates were lower and the percentage of each subject's capacity consumed was higher in Group SC relative to Group LC at each level of prefeeding. As the amount of food prefed prior to each session increased, the amount of responding in each group decreased systematically. This was especially true for Group SC whose responding by 25 g (over 100% capacity consumed) was nearing zero over the course of each session.

The motivation to work for food (hunger) decreases as subjects become repleted. Killeen (1995) suggested that the decrease might be a linear function (his Equation 5) or exponential function (his Equation 6) of depletion. The exponential form provides a much better account of the present data than does the linear form, which deviates systematically from the data (even when embedded in his hyperbolic compensation for approach to ceilings). However, an even better account of these data are provided by a logarithmic equation:

$$B = B_0 - k \log(t + 1), \qquad (1)$$

where B is response rate, B_0 is the rate at the very start of the session (the intercept of the satiation curves), k is the rate of decrease in motivation, and t is the number of minutes into the session and thus the nominal amount of food repleted. Here both B_0 and k are treated as free parameters. This equation accounted for an average of 95% of the variance in the group data, and is shown as the curves in Figure 10. (The exponential function accounted for 90% of the variance in the data.)

Although Equation 1 provides a good representation of average performance, and of many of the individual within-session functions, some animals (in particular, the small-capacity animals in the large prefeed condition) abruptly ceased responding part-way through the session when they became satiated. Within-session responding for individual

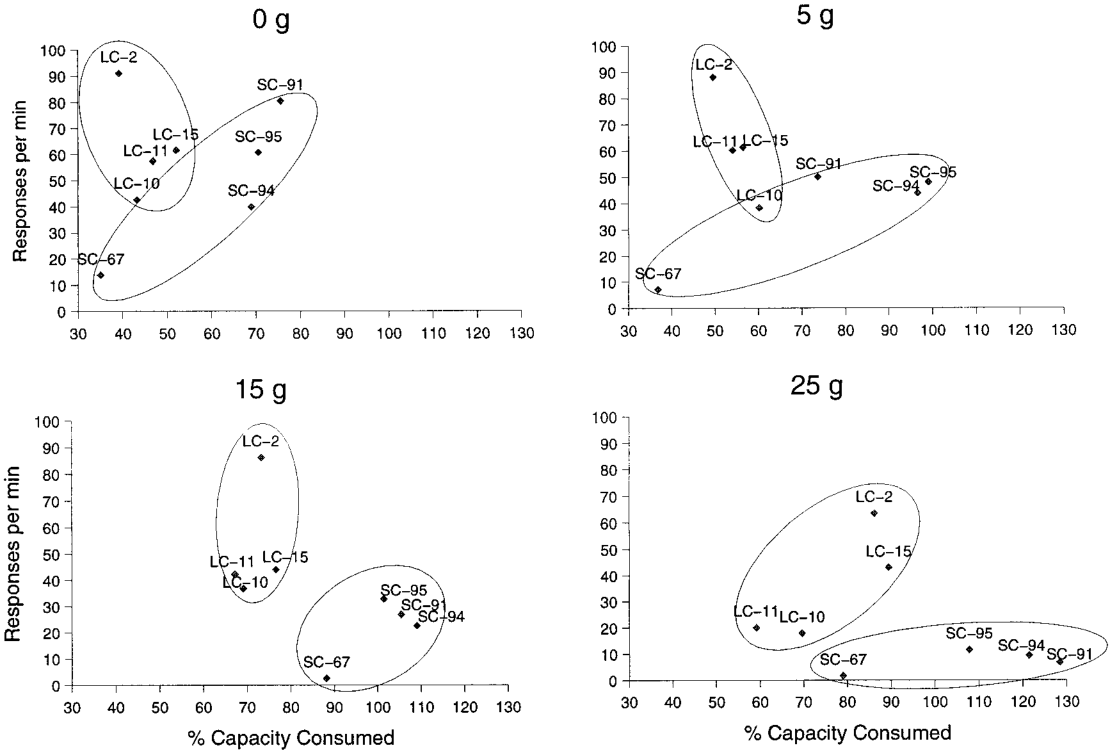

Fig. 9. Response rate versus percentage capacity consumed for each subject in Groups SC and LC during the 0-, 5-, 15-, and 25-g prefeeding conditions.

subjects and the corresponding fits to their data are shown in Figure 11. The independent variable, *t,* continued to represent the number of minutes into the session, but no longer predicted the amount of food consumed because some of these animals no longer ate. For this reason, the calculated average amount consumed per hopper presentation decreased from 0.14 g per hopper operation in the 0-g prefeed condition to 0.05 g per hopper operation in the 25-g prefeed condition, with some of the small-capacity animals ceasing to respond completely by the end of the latter condition. Therefore Equation 1 is at best an approximation to a dynamic situation in which the rate of repletion decreases with the amount prefed, and also as a function of the number of feedings through a session. (A better account might be provided if the amount of time with the head in the hopper was used as an estimate of the amount repleted on each trial, but that is not attempted here.)

The parameters of the group-based satiation curves are plotted against the residual deprivation at the start of the session (the empirically measured capacity minus the amount prefed) in Figure 12. The negative abscissae occur because the small-capacity birds consumed more than predicted from their capacity measurements (M = 20 g) in the 25-g prefeed condition. We believe that this happened because the session sometimes extended beyond the hour in which the capacity measurements were made (each session began only after a single peck), and because of the additional inducement to eat provided by a context in which the animals had habitually responded for food and eaten it (Neuringer, 1969).

The top panel shows that the rate at which the animals began responding increased with their residual deprivation, and the bottom panel shows that the rate of satiation decreased with their residual deprivation.

DISCUSSION

In this experiment pigeons in Group LC and Group SC were prefed with four differ-

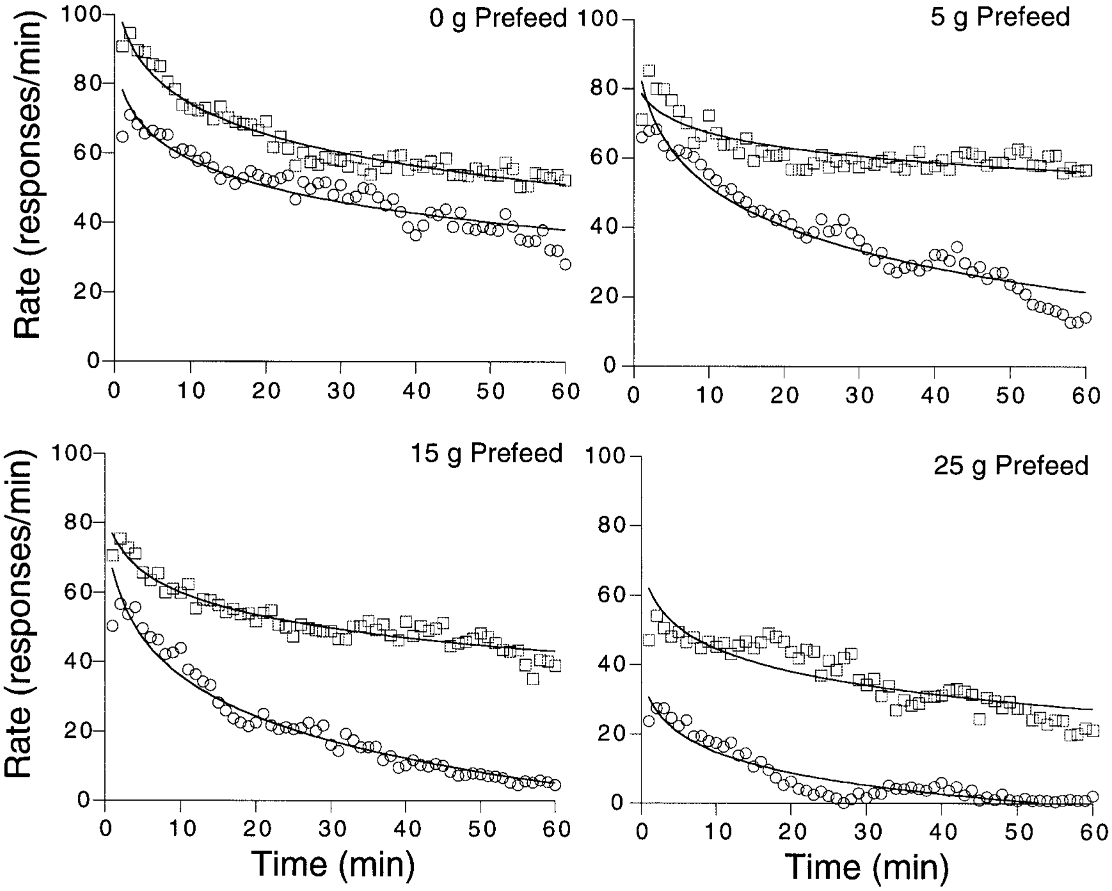

Fig. 10. Average response rates within each session for Group LC (squares) and Group SC (circles) during each prefeeding condition. The smooth curves are the best fitting lines from Equation 1.

ent amounts of food prior to each session. If satiation contributes to the within-session declines in responding, then subjects in Group SC should show the lowest overall response rates during each level of prefeeding. In fact, average response rates were lower in Group SC than in Group LC at each level of prefeeding, and this group consumed more food relative to their capacity (percentage capacity) than Group LC.

GENERAL DISCUSSION

According to the satiation hypothesis, within-session changes in responding represent the contribution of satiation and hence, changes in arousal, over the course of each session. As the session progresses, the animal should gradually become more sated, and because of this, the overall level of arousal and hence the overall level of responding should decline. To assess this hypothesis, various tests of capacity to consume food were conducted. These tests indicated that each of the three methods produces a relatively reliable measure of capacity, but the simple expedient of measuring the amount consumed during a 1-hr free access to food was preferred. In Experiment 2 pigeons were divided into two groups on the basis of the amount of food they consumed during a free-food capacity test. The satiation hypothesis predicts, and the experiment found, that greater within-session decreases occurred in small-capacity subjects compared with the large-capacity subjects at two different hopper durations. When the overall amount consumed during the course of a session was manipulated during Experiment 3 by providing food prior to the

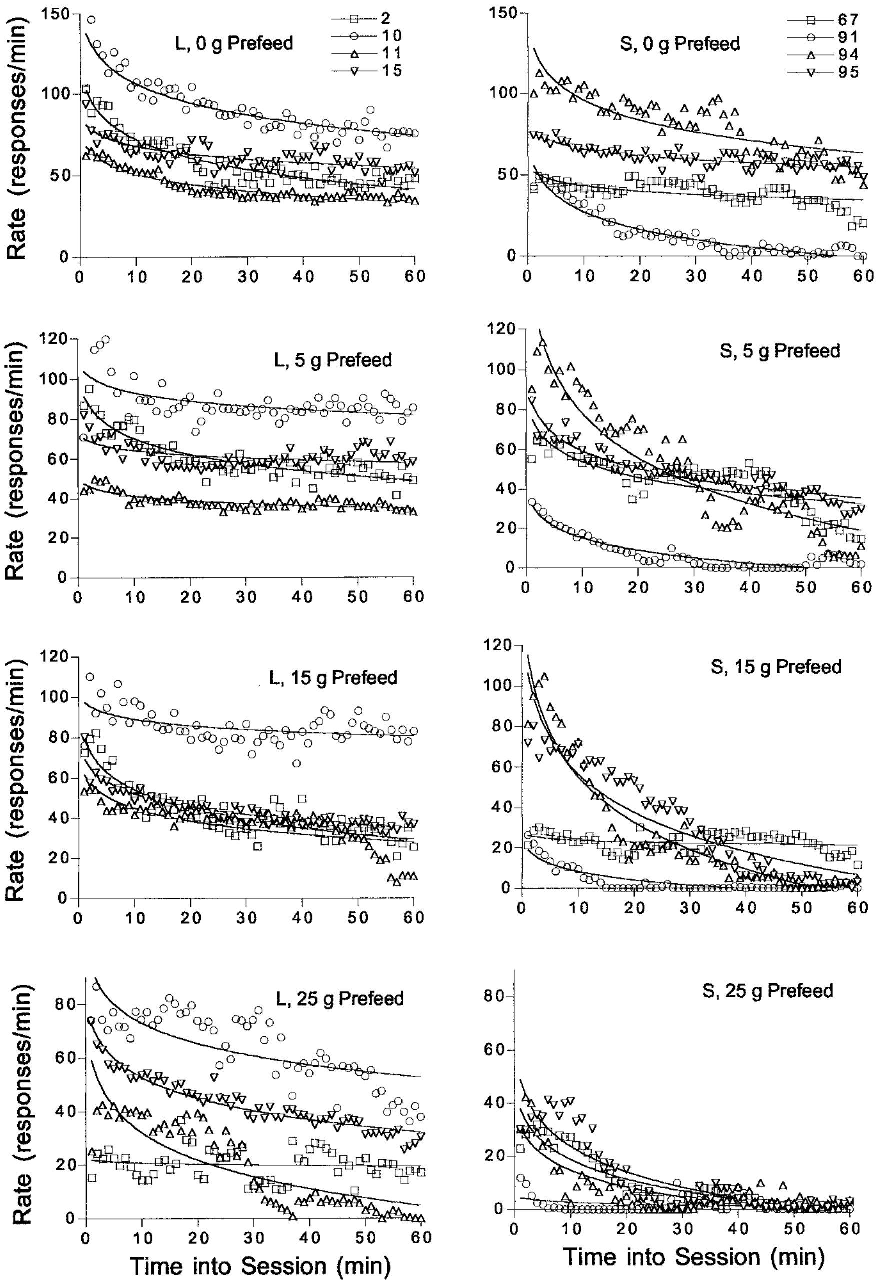

Fig. 11. Average response rates within each session for each subject in Groups LC and SC during each prefeeding condition. The curves represent the best fitting lines from Equation 1 for each subject.

beginning of each session, overall responding decreased as the amount of food prefed increased. In fact, this effect was largest in Group SC, whose average overall response rates were lower than those of Group LC, which is also consistent with the satiation hypothesis. Finally, Experiments 2 and 3 also showed that it is not the amount of food consumed that determines whether decreases in responding will be observed; rather, it is the amount of food consumed relative to the subject's capacity that is important. In other

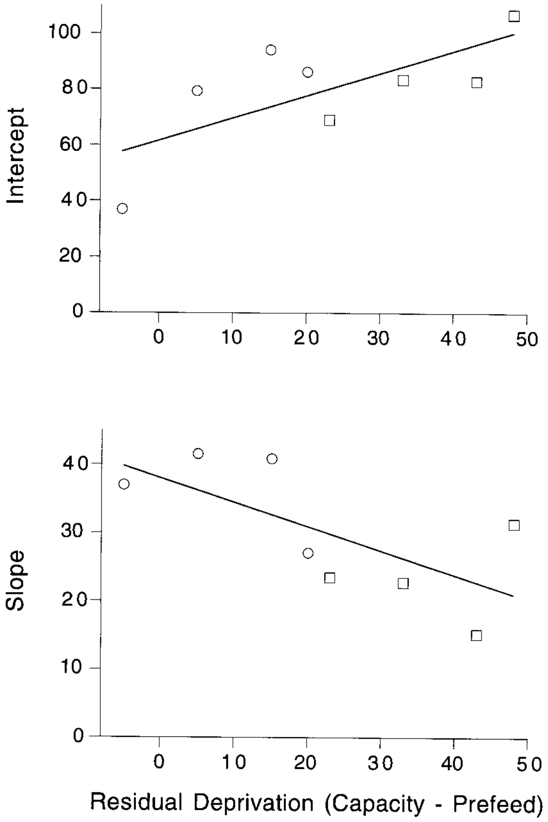

Fig. 12. Top panel: The intercepts of the satiation curves shown in Figure 10, B_0, in units of responses per minute, are plotted against the residual deprivation level of the pigeons in Group SC (circles) and Group LC (squares). Bottom panel: the slopes of the satiation curves, *k,* plotted against the residual deprivation levels.

words, the controlling variable is the amount the animal has become sated.

In contrast, McSweeney, Hinson, and Cannon (1996) suggest that the within-session increases or declines may represent the contribution of sensitization and habituation to the reinforcers: Within-session changes in responding may be produced by an initial sensitization to the reinforcer during the first few trials, followed by habituation to that reinforcer after repeated presentations, so that its ability to support responding declines over the course of the session. In fact, these authors argue that these effects are not due to satiation, because manipulations that affect satiation (e.g., reinforcement duration) do not seem to influence within-session patterns of responding (e.g., Cannon & McSweeney, 1995; McSweeney, 1992).

It is not clear, however, how an explanation in terms of habituation might explain the between-group differences reported here. In Experiments 1 and 2, pigeons were initially divided into groups simply on the basis of the amount they consumed during an FF session. The habituation hypothesis does not obviously predict any of the differences in response rates or within-session decreases in responding between subjects in the two groups: Both groups of subjects received reinforcers at the same rate, and there is no apparent reason to expect these capacity differences to predict the rate at which the pigeons habituate to the reinforcer during the experimental session. Moreover, the pigeons in Group LC consumed more grain per session, which might be expected to lead to faster habituation, yet this group showed significantly smaller within-session decreases than Group SC. Thus, unless habituation depends on capacities, this result is inconsistent with the habituation hypothesis for within-session decreases. Although both habituation and satiation may play significant roles in the development of within-session changes in responding, the data from this experiment, like those from Bizo et al. (1998), clearly support the satiation hypothesis.

Possibly the most important contribution of these experiments, however, is the demonstration of a factor that will affect all experiments using food-reinforced pigeons. What we have called *capacity* can be easily measured and may have significant effects on within-session and between-subject response rates. Experimenters may wish to control this source of variance in their experimental designs, and report capacities routinely in the *Subjects* section of their reports.

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Received March 8, 1999
Final acceptance July 31, 1999