

SEASONAL VARIATION IN PIGEON BODY WEIGHT AND DELAYED
MATCHING-TO-SAMPLE PERFORMANCE

REBECCA J. SARGISSON, IAN G. McLEAN, GLENN S. BROWN, AND K. GEOFFREY WHITE

UNIVERSITY OF OTAGO, NEW ZEALAND

The weights of 5 pigeons with free access to food, monitored over 3 calendar years in the laboratory, were found to fluctuate with season. All pigeons were at their heaviest in the winter and were lightest in the summer. Five different pigeons performed a standard delayed matching-to-sample task for 44 weeks from January to November. Their weights were held at 85% of their summer free-feeding weights, making their predicted deprivation level higher in the winter relative to predicted winter free-feeding weights. Slopes of forgetting functions fit to weekly response totals for each pigeon were shallower in winter, showing an improvement in accuracy with longer delays. Thus, delayed matching-to-sample performance may have been affected by the practice of maintaining the pigeons at a constant body weight throughout the calendar year.

Key words: body weight, free-feeding, food deprivation, seasonal effects, delayed matching to sample, key peck, pigeon

Experimental subjects are typically maintained at weights below what is termed their “free-feeding weight”. A free-feeding weight is determined by providing a caged animal with unlimited access to food for some period under laboratory conditions. Poling, Nickel, and Alling (1990) showed that when wild pigeons were provided with unlimited access to food for 42 days in a laboratory, they gained between 9 and 30% of their body weight. Thus, a captive pigeon’s free-feeding body weight is higher than that of a wild pigeon. Once a free-feeding weight is established, the animal typically is gradually deprived of food until it weighs between 80 and 85% of its caged free-feeding weight. For example, in the *Journal of the Experimental Analysis of Behavior*, volumes 85 and 86, seven research laboratories used pigeons as experimental subjects. In six, pigeons were maintained at 80% and in one at 85% of free-feeding weights. Kangas and Branch (2006) point out that while it is a common practice to deprive experimental animals of food, there are no guidelines for establishing a free-feeding weight. Particularly, prior to the study by Kangas and Branch, there

were no published data on how long a pigeon with free access to food should be weighed before its weight is deemed to be stable.

Kangas and Branch (2006) weighed 27 pigeons for 30 consecutive days to determine the stability of pigeon weights across time. They reported that pigeon weights were very stable over this period, with the exception of some small variance in the case of female pigeons due to egg laying. They recommended a minimum free-feeding period of 7 days to calculate a pigeon’s base free-feeding weight.

In the course of running our experimental laboratory, we have sometimes maintained individual pigeons on free food for long periods. Free-feeding weights tend to be established, or reestablished, during the summer, as this is when the pigeons undergo molt and is a convenient time to suspend experiments while students and staff are on summer vacation. In a review of bird body weights, Clark (1979) described significant seasonal variation, with most species being heavier at times of environmental stress (winter in northern temperate areas and dry seasons in tropical areas). For example, wild screech owls (Henny & VanCamp, 1979) and titmice (Haftorn, 1989) gain weight in the spring and autumn to reach a maximum weight in the winter. If there is an effect of season on body weight in free-feeding pigeons, then the time of year at which free-feeding weights are determined could be important. In Study 1, we used data collected over three years to

The authors would like to thank the members of the laboratory team for maintaining weight records, and Dr. Fiona Wright for her contribution to early analyses. We would also like to thank Saralee Illingworth for ensuring the health of the pigeons. Experiments conducted in the authors’ laboratory (K.G.White, Principle Investigator) were approved by the University of Otago Animal Ethics Committee.

doi: 10.1901/jeab.2007.88-395

determine whether free-feeding body weights of pigeons housed in an indoor experimental laboratory change in relation to season. The colony room which housed the pigeons contained a frosted glass window which allowed natural light. There is evidence, however, that seasonal weight fluctuations persist in some bird species even in the absence of a natural light source (Barlein, 1986; Gifford & Odum, 1965; King, 1968; Lindgård, Näsland, & Stokkan, 1995).

Seasonal variation in body weight was found in Study 1, thus raising the question of whether variations in operant performance are associated with season. Study 2, therefore, investigated whether performance in a delayed matching-to-sample task varied across the seasons of a calendar year when pigeon weights were held at 85% of their summer free-feeding weights.

STUDY 1 METHOD

Subjects

Two female and 3 male homing pigeons were obtained from local fanciers and were of varying ages. Female Pigeons 1 and 2 were born in 1996 and 1998. Pigeons 3 and 4 were born in 1981 and 1983. The age of Pigeon 5 was unknown, but this pigeon was obtained in March 1993. Pigeons 3, 4, and 5 are believed to be male as they never laid an egg during their time in the laboratory.

Procedure

All pigeons were housed in a laboratory in individual cages measuring 40 cm deep, 50 cm high, and 40 cm wide. The cages were made of wire mesh, and cages were stacked three wide \times three high. The pigeons could see and hear one another. The laboratory is located in the Psychology Department of the University of Otago, Dunedin, New Zealand. The room in which the pigeons were housed had a natural light source. Nine small frosted-glass windows, arranged three high \times three wide, each measuring 0.45 m high \times 1.05 m wide, were positioned on the back wall (3.5 m wide) of the rectangular colony room (3.5 \times 7 m). Throughout the year, artificial light was provided on a 12:12 hr cycle with lights on at 0600 and off at 1800. Thus, natural light patterns were buffered, with pigeons experiencing un-

naturally long day length in winter, but natural day length in summer. Temperature was maintained between 17 and 19° C year-round.

All pigeons had free access to a mixture of wheat, corn, peas, and pellets, as well as water and grit. The pigeons were weighed several times a week at approximately the same time in the morning for 3 years (2000, 2001, and 2002). Pigeon 3 was maintained on free food until 21 January 2001 when it began serving in an operant experiment. Pigeons 2, 4, and 5 had served in experiments until 25 January 2001, after which they were placed on free feeding (weight records began 28 January 2001). Pigeon 1 served in experiments until 15 February 2002 (weight records began 19 February 2002).

RESULTS AND DISCUSSION

The pigeons' weights varied between 368 and 706 g. A spreadsheet of weights may be obtained from the first author. Figure 1 shows the body weights (g) for 3 pigeons that were weighed over the same period in 2001 and 2002. The vertical dashed lines indicate winter solstice (June 21 in New Zealand). The body weight of the heaviest pigeon, Pigeon 5, peaked at the winter solstice, and the weights for the other two pigeons showed a similar pattern, with heaviest weights in winter. Pigeon 2, a female, showed systematic fluctuations in weight in November of each year, correlated with egg laying. The reason for the drop in body weight in September 2002 for Pigeon 4 is unknown.

In order to normalize fluctuations in weight across pigeons, each individual weight was converted into a proportion of the overall mean weight recorded for that pigeon. Figure 2 shows these proportions for all 5 pigeons plotted as a function of day over 2000, 2001, and 2002. Figure 2 shows a nearly sinusoidal pattern across the calendar year, with the highest proportion of mean weights occurring in winter, and the lowest in summer. In the southern hemisphere, winter runs from June to August, and summer from December to February.

All 5 pigeons with free access to food showed the same weight pattern across season. That is, all pigeons gained weight in the autumn and were at their heaviest in the winter. Weights fluctuated up to 17% above and below the mean body weight. Plots of absolute weights showed the same pattern.

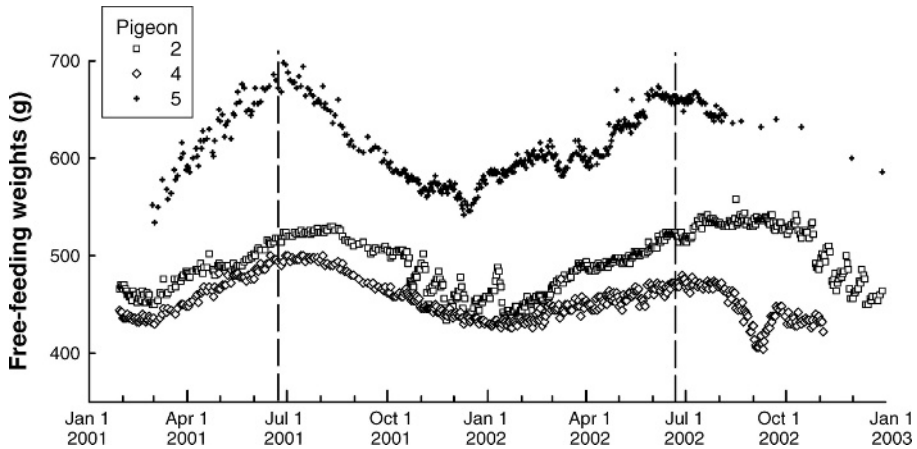


Fig. 1. Free-feeding weights (in g) for Pigeons 2, 4, and 5 for the years 2001 and 2002. Vertical dashed lines indicate winter solstice (June 21 in New Zealand). Note that the y-axis does not begin at zero.

Kangas and Branch (2006) do not state which 30 days of the year were used to record free-feeding weights for their pigeons, so we explored free-feeding weights in our data for 30 days in each of the four seasons. Figure 3 shows the weights of Pigeons 2, 4, and 5 for the months of April 2001 (autumn), July 2001 (winter), October 2001 (spring), and January 2002 (summer). The patterns are similar to those found by Kangas and Branch, that is, weights for Pigeons 2 and 4 would likely be regarded as stable on the basis of any of these months. However, there is some evidence of an increasing body weight trend in autumn for all 3 pigeons, and a decreasing trend for 2 of the 3 pigeons in spring. These trends suggest that 30 days is insufficient to detect a visual

trend in free-feeding body weight. Note that Pigeon 2 is a female bird and that egg laying occurs predominantly in the late spring/early summer, so the small variation in her weight in the summer plot was due to egg laying. The largest pigeon, Pigeon 5, showed an increasing body weight in autumn and a decreasing body weight in the spring and winter, but a stable summer weight (Figure 3, filled circles). If weights are compared across season in Figure 3, it is clear that the weights of all pigeons were lower in the summer than in the winter (bottom panels).

The causal mechanism of the seasonal variation in body weights of these pigeons is unknown, but the pattern makes ecological and evolutionary sense as increased weight

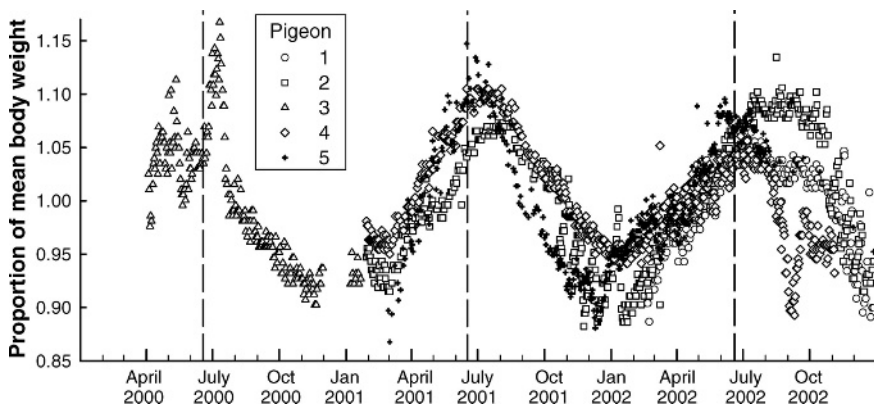


Fig. 2. Proportion of mean free-feeding body weights for all pigeons for the years 2000–2002. Tick marks on the x-axis represent the 1st of each month. Vertical dashed lines indicate winter solstice (June 21 in New Zealand). Note that the y-axis does not begin at zero.

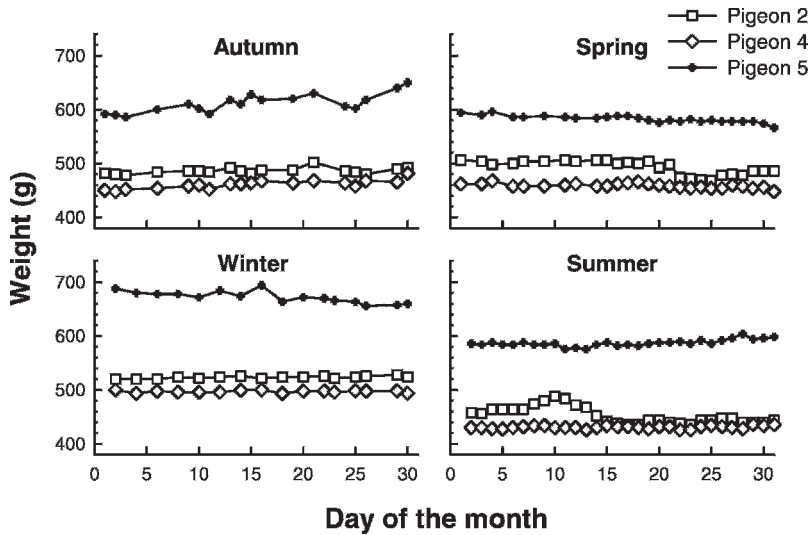


Fig. 3. Free-feeding weights (in g) for Pigeons 2, 4, and 5 for the months of April 2001 (autumn), July 2001 (winter), October 2001 (spring), and January 2002 (summer).

provides a buffer against stressful periods in the year. The most plausible causal agent for the seasonal weight fluctuations was the external light source, which allowed natural variation in light patterns across the seasons. Male chickens housed in rooms devoid of natural light gained more weight when the room was illuminated for less than 9 hr in every 24-hr period than when it was illuminated for longer than 9 hr (Lamoreux, 1943), showing that the length of the light cycle could be important in determining the weight of birds. Thus, it is possible that pigeons housed in rooms devoid of natural light would not show seasonal weight fluctuations.

There are several studies, however, that show that birds housed in rooms devoid of natural light continue to gain and lose weight according to season. For example, white-crowned sparrows housed in rooms with strictly controlled light/dark cycles gained weight in winter and lost it in summer (King, 1968). Similarly, weight changes in bobolink exposed to either simulated natural light or a constant 12-hr photoperiod paralleled those of wild birds in both timing and magnitude (Gifford & Odum, 1965). Barlein (1986) found seasonal weight gains in garden warblers housed in conditions of artificial light (LD 12:12) for 2 consecutive years. Captive Svalbard ptarmigan birds housed in conditions of simulated natural light and in contin-

uous light all gained weight in the autumn, although the birds in simulated natural light gained weight faster than the birds exposed to continuous light, and those birds in continuous light conditions did not lose the winter weight in the spring (Lindgård *et al.*, 1995). Whether, and for how long, seasonal weight fluctuations persist in pigeons housed in rooms devoid of natural light should be the subject of further investigation.

Operant experimenters maintain working animals at reduced weights to ensure that they respond consistently for food during experimental sessions. As Study 1 suggests, the relative level of food deprivation of an individual animal maintained at a constant weight varies across the year due to natural seasonal variation. However, it may be that this degree of food deprivation has little effect on response strength or accuracy. In order to determine the effect of food deprivation levels on operant performance, pigeons need to be run in daily experimental sessions and the experimental procedure held constant across a period sufficiently long to encompass the range of natural seasonal weight fluctuation.

STUDY 2

Study 2 addressed whether the performance of pigeons varies with season when their weights are held constant. If free-feeding

weights are established during the summer minimum (as occurs in our laboratory), and then weights are reduced to 85%, the deprivation level reached during the winter would be greater than 85% of the winter free-feeding weight of the same pigeon. Conversely, if the free-feeding weight were established in the winter, then the deprivation level of that pigeon during the summer would be less than 85%. We predicted effects on performance because the natural variation in weight demonstrated in Figure 1, combined with the standard protocol of holding weights of subjects constant, implies that deprivation was absolutely, but not relatively, constant through time. If birds are relatively more or less food deprived through time, their performance could be affected. For example, when Cumming, Berryman, and Nevin (1965) fed pigeons 10% of their working weights prior to a delayed matching-to-sample session, accuracy with long delays improved. Such a prefeeding manipulation may have a different effect on operant performance, however, compared to longer-term maintenance of body weights at a constant level. A standard delayed matching-to-sample procedure was used in Study 2 because the pigeons had extensive experience with this task. The task was held constant over 44 weeks, and the pigeons' weights were maintained at a constant value.

METHOD

Subjects

Five homing pigeons, numbered F1 to F5 and aged between 4 and 11 years, were individually housed in wire cages measuring 40 cm deep, 50 cm high, and 40 cm wide, with free access to water and grit. The pigeons were weighed daily and maintained at $85\% \pm 10\%$ of their summer free-feeding weights (see *Procedure*) through postexperimental feeding of a mixture of wheat, corn, peas, and pellets. If a pigeon's weight fell outside the range, it was excluded from experimental sessions until its weight was within the range.

Apparatus

Five Med Associates Inc. chambers were used, measuring 29.5 cm high, 29.5 cm wide, and 24.5 cm deep. The side walls of the chambers were made of black plastic. Three translucent plastic response keys, 2.1 cm in

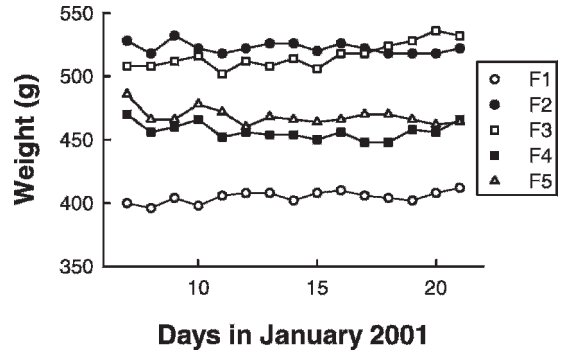


Fig. 4. Free-feeding weights (in g) for Pigeons F1 to F5 recorded from January 7–21, 2001 (summer) and used to calculate 85% deprivation levels.

diameter, were recessed 1 cm into the front panel of each chamber, 21 cm from the grid floor, and 6 cm apart. All three keys could be illuminated red, green, or white. The keys required a force of at least 0.15 N to be operated. A hopper situated behind an aperture 12.5 cm below the center key provided access to wheat when raised. An infrared beam was broken when the pigeon placed its head in the hopper aperture, allowing precise timing of the reinforcement period. The hopper was illuminated with a 1-W white bulb when raised.

Procedure

The pigeons were given free access to food from 07 January 2001 until 21 January 2001 (summer). Figure 4 shows that their weights were stable through this period. The mean weight for each pigeon for the period 11 January 2001 to 15 January 2001 (inclusive) was used to calculate a weight that was 85% of the free-feeding weight (350, 444, 456, 396, and 400 g for Pigeons F1, F2, F3, F4, and F5, respectively). The pigeons were then deprived of food until within 10 g of their target weight.

All 5 pigeons had had previous experience with delayed matching-to-sample tasks (Pigeons F1 to F5 were T3, T4, P2, P3, and P4, respectively, in Sargisson & White, 2001, 2003, and F1 to F5 in Wright & White, 2003), so required no training. Each daily session was terminated after 50 min, or after 82 trials had been completed, whichever came first. Sessions were run 7 days per week, at approximately the same time each day, from 13 January 2003 until 28 November 2003.

The first two trials of each session were treated as warm-up trials and were not included in analyses. Each trial began with the center key lit either red or green (the sample stimulus). Five responses to the center key turned it off and initiated a retention interval. After the retention interval, one of the side keys was lit red and the other green (the comparison stimuli). A peck to the red key was deemed correct following presentation of the red sample, and a peck to the green key correct following presentation of the green sample. Correct red and green responses produced 2.5-s access to wheat, timed from the moment the pigeon first placed its head into the hopper. Wheat was used as the reinforcer rather than the maintenance diet because peas, pellets, and corn tend to clog the hopper. Incorrect responses produced a 2.5-s blackout. The blackout and the reinforcer period were followed by a 15-s inter-trial interval, during which all keys were dark. Five different retention intervals (0.2, 1, 3, 6, and 12 s) were arranged within each session, giving 16 trials per retention interval per session. The five retention intervals occurred in a quasirandom order equally often in combination with each sample stimulus and comparison stimulus location on left and right keys.

Data Analysis

The number of correct and incorrect red and green responses with each retention interval was summed in 7-day blocks from 13 January 2003 (summer) to 28 November 2003 (spring). The first 7-day block, labelled Week 3 to match closely the weeks of the calendar year, was discarded as accuracy levels were lower than in subsequent weeks due to a break from the previous experiment over the summer. The first week used for analysis was thus labelled Week 4, making the last full week in the datum set Week 47.

Summed responses were converted to a measure of discriminability, $\log d$. $\log d$ is a bias-free measure of discriminability described by Davison and Tustin (1978), and is calculated according to $\log d = \frac{1}{2} \log [(c_r/e_r)(c_g/e_g)]$, where c and e are correct and error responses for red (r) and green (g) sample stimuli. A correction factor of 0.25 was added to all cells (Brown & White, 2005) to avoid infinite $\log d$ values. Due to extensive experience with the

task, many pigeons made no errors with the shorter delays. Additionally, because pigeons were not run if their weight fell outside $85\% \pm 10$ g of their free-feeding base weight, the number of sessions completed in each 7-day block varied for some pigeons. Thus, the resulting $\log d$ values, which are based on ratios of correct responses to error responses, were affected by the number of trials included in the analysis (see Brown & White). For example, a pigeon whose responses were perfectly correct at a particular delay over seven sessions would produce a $\log d$ value of 2.35 ($= \frac{1}{2} \log [(56.25/0.25)(56.25/0.25)]$), whereas perfect responses at a particular delay over five sessions would produce a $\log d$ value of 2.21 ($= \frac{1}{2} \log [(40.25/0.25)(40.25/0.25)]$). Therefore, in order to keep constant the number of trials for each week across the year for each pigeon, only a certain number of sessions per week contributed to the data analysis for each pigeon. For Pigeons F1, F2, F3, and F4, the first five, seven, seven, and four sessions, respectively, of each 7-day block were used for analysis. For Pigeon F5, the first five sessions in each 7-day block were used, after elimination of sessions in which fewer than 50 trials were completed. Weeks containing fewer than the determined number of sessions for each pigeon were excluded from analysis. Data for Pigeon F4 for Weeks 19–22 were omitted from the analyses owing to equipment failure for this pigeon.

For each week, and each pigeon, $\log d$ was plotted as a function of retention interval. Forgetting functions were then fit to these data using an exponential function in the square root of time (White, 2001), $y = a \exp^{-b/\sqrt{t}}$. The resulting parameter values yield two independent measures of remembering performance (White, 1985). Firstly, the intercept, a , is a measure of initial discriminability, or of accuracy in the absence of a retention interval. Secondly, the slope, b , is a measure of the rate of forgetting, or how rapidly accuracy decreases with increasing retention-interval duration.

RESULTS

Figure 5 shows forgetting functions for each pigeon for Week 4 (summer; solid curve) and Week 25 (winter; dashed curve). Figure 5 illustrates the comparable intercepts of the functions for the two most extreme times of

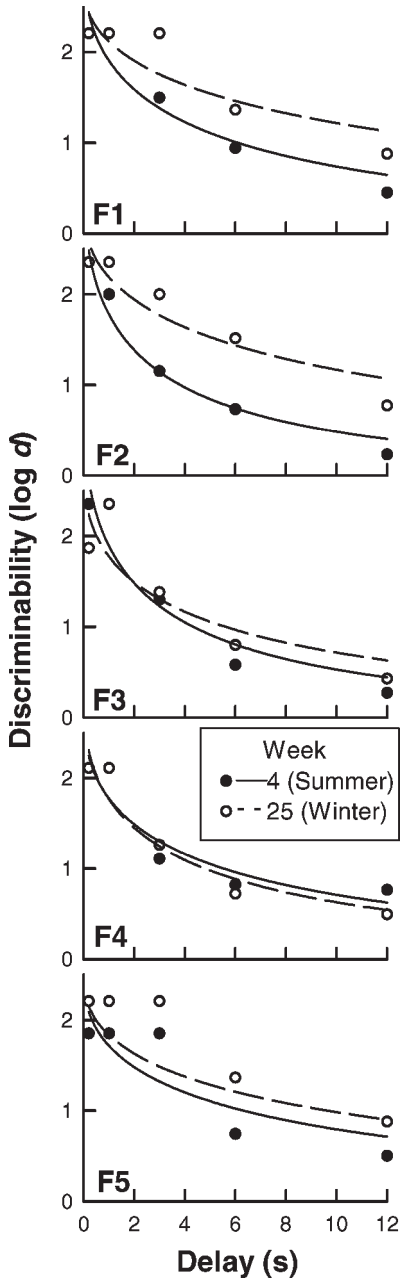


Fig. 5. Discriminability ($\log d$) as a function of delay (in s) for all 5 pigeons for Week 4 (summer) and Week 25 (winter). Forgetting functions were fit to the data using $y = a \cdot \exp^{-b \cdot t}$.

the year with respect to predicted deprivation, and the steeper slope of the function in summer (filled circles, solid curve) for 4 of the 5 pigeons.

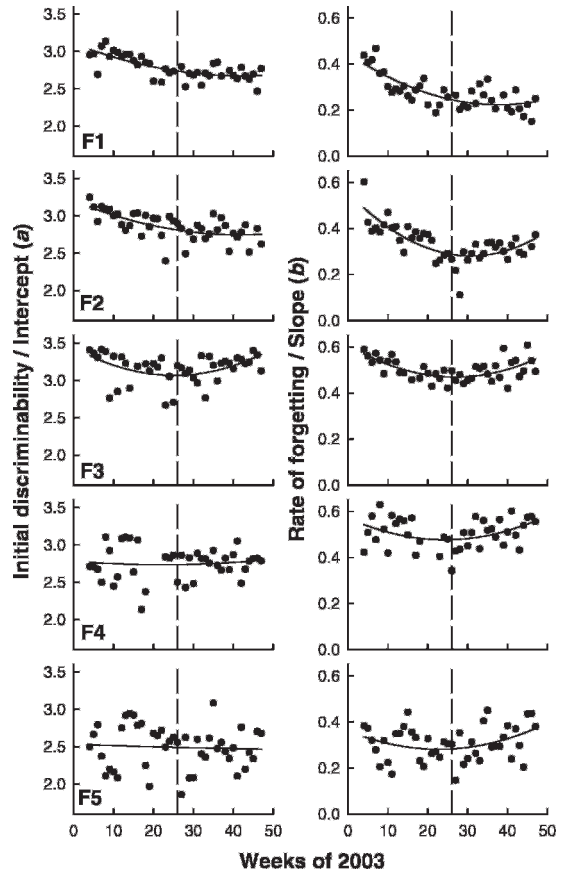


Fig. 6. Initial discriminability (intercept; left panel) and rate of forgetting (slope; right panel) for each pigeon obtained by plotting $\log d$ against weeks in 2003. Vertical dashed lines indicate winter solstice (Week 26).

Figure 6 shows initial discriminability (*a*) and rate of forgetting (*b*) as a function of week for each pigeon. Quadratic polynomial functions were fit to the data to highlight the pattern in each graph. Intercepts (left panel) for Pigeons F1 and F2 decreased across weeks of the year. The intercepts for Pigeon F3 first decreased, and then increased towards the end of the year. For Pigeons F4 and F5, intercept values were constant across the weeks of the year. A dependent-measures *t*-test showed that, in terms of variance accounted for, linear functions (not shown) fit the intercept data (Figure 6, left panel) equally as well as the polynomial functions ($t(4) = -1.63, p = .18$).

Slope, or rate of forgetting (Figure 6, right panel), for 4 of the 5 pigeons (F2, F3, F4, and F5) showed a U-shaped pattern. Rate of forgetting decreased towards the middle of

the year (winter) and increased at the end of the year (summer). Slope values for Pigeon F1 decreased across the year, without a distinct recovery at the end of the year. In contrast to the intercept values, a dependent-measures *t*-test showed that the polynomial functions shown in the right panel of Figure 6 accounted for a higher proportion of variance (mean $R^2 = 36.46$) than did linear functions (mean $r^2 = 16.75$; $t(4) = -3.41$, $p = .03$).

Depending on the season, the difference between the pigeons' 85% target weight and their projected free-feeding weight will change. If the target weight is established in winter when free-feeding weights peak, then the difference will tend to be a negative value in summer when pigeons naturally weigh less. If the target weight is established in the summer, then the difference will tend to be a positive value in winter when pigeons naturally weigh more.

To investigate the trends in Figure 6, two multiple regressions were conducted. In separate analyses, intercept and slope values for all 5 pigeons were used as dependent variables and body weights relative to expected free-feeding weights as the independent variable. Expected free-feeding weights were based on mean across-subjects weights obtained in Study 1. From these values we calculated the proportion of the predicted free-feeding weight represented by the target weight. A significant regression was found for slope (*b*) ($r = .59$, $F(1, 12) = 6.27$, $p = .03$). The positive *r* value indicates that the slope became shallower as the pigeons became relatively more deprived. The regression for intercept was not significant ($r = .01$, $F(1, 12) < 1$, $p = .98$). The same intercept and slope variables were regressed against the independent measure of week, with weeks incrementing from 4 to a maximum of 26, and then decreasing to Week 47 (Week 26 is equivalent to the winter solstice). Thus, in the analysis, high numbers represented winter, whereas low numbers represented summer. As previously, there was an effect for slope ($r = .58$, $F(1, 12) = 6.02$, $p = .03$), but not for intercept ($r = .17$, $F(1, 12) = 0.34$, $p = .57$).

In any one week, each pigeon could be run in a maximum of seven sessions. If the pigeon's weight was more than 10 g above or below 85% of its summer free-feeding weight prior to any session, the pigeon was not run in that day's session. Where a pigeon was not run,

it was almost always because the pigeon was too heavy, and not because it was too light. There was no pattern of inclusion in sessions across the year for any pigeon.

Trials completed per session did not vary as a function of week in Study 2. Pigeons F1, F3, and F4 completed every trial in every session that they were run in. Pigeon F2 completed every trial in each session, except for Weeks 26–29 (mid-winter), when it completed 89, 94, 86, and 98% of the sessions. Pigeon F5 rarely completed all the trials but its pattern of session completion was not related to the week of the year.

DISCUSSION

In Study 2, the target weights of 5 pigeons were established in the summer. The pigeons began Study 2 at 85% of their summer free-feeding weights and presumably became more deprived relative to winter free-feeding weights, after which their presumed level of deprivation approached the summer level. The predicted higher level of deprivation in winter was correlated with a lowered rate of forgetting (Figures 5 and 6). There was no effect of time of year on response rate or proportion of sessions completed but none was expected because number of trials completed per session is usually only lowered in conditions of satiation, not deprivation (e.g. DeMarse, Killeen & Baker, 1999; Nevin, Milo, Odum, & Shahan, 2003).

While presumed deprivation level was correlated with rate of forgetting, it does not necessarily follow that the effects on DMTS performance were caused by seasonal effects on deprivation levels. Other natural processes also occur seasonally, such as hormonal fluctuations, molt, and egg laying. For example, many researchers have found seasonal changes in the testicular development of birds (Engels, 1962; Jones, 1970; Tewary & Kumar, 1982; Tsutsui, Kawashima, Saxena, & Ishii, 1994). Therefore, it is possible that the timing of some of these processes affected DMTS performance.

The intercept of a forgetting function is thought to reflect the overall difficulty of the discrimination (White, 2001). For example, Roberts (1972) found that the accuracy of pigeons' responses increased with all retention intervals (producing an increase in initial

discriminability with no change in the rate of forgetting) when the pigeons responded 15 times to the sample stimulus, rather than 5 times. Increasing the wavelength difference between sample stimuli (White, 1985) or the duration of the sample stimulus presentation (Foster, Temple, MacKenzie, DeMello, & Poling, 1995) also increases initial discriminability. In Study 2, there was no significant association between intercept and predicted body weight. Discrimination of the sample stimulus or overall difficulty, therefore, may not be correlated with relative body weight. Extensive experience with the delayed matching-to-sample procedure in Study 2 drove accuracy levels with the shorter delays to a ceiling, thus there could be no further improvement in accuracy with short delays as a result of deprivation level. Conversely, the pattern of intercept values in Figure 6 (left panel) show that for at least 3 pigeons, the intercept decreased across the year (and recovered for Pigeon F3), rather than remaining at a ceiling level. Thus, there is some suggestion that initial discriminability may decline with increasing deprivation levels, although the trend was not statistically significant.

The result for rate of forgetting (Figure 6, right panel) indicates that the slopes of forgetting functions became shallower in the winter, when the pigeons were predicted to be most food deprived. Spetch (1985) found that when free food was offered to pigeons at three separate times during a delayed matching-to-sample session, performance was only affected in conditions where food was offered all three times, or only near the end of the session. In these conditions, matching accuracy decreased with long delays, but not with short delays, compared to conditions with no free food, or where free food was offered only in the early part of the session. This result supports the present finding that greater levels of deprivation produce shallower forgetting functions, with no change in intercept.

It is common practice for operant experimenters to deprive pigeons of food when investigating discrimination, remembering, and choice behavior, but none report the time of the year at which target weights were established. As operant experiments are often conducted over many months (or even years), seasonal weight fluctuations may affect the results when weights are held constant for the

duration of the experiment. The results of Study 2 showed that accuracy in a delayed matching-to-sample task varied seasonally when pigeons were maintained at 85% of their summer free-feeding weight. It is likely that the accuracy of pigeons in other types of discrimination tasks will also be affected if their weights are similarly controlled. It also is possible that if the target weight were calculated at a different time of the year, the effects on response rate and accuracy may differ from those found here. For example, if the target weight were established in the winter, when the pigeons are at their heaviest weight of the year, then during the summer months relative weights would be higher than 85% of the summer free-feeding weight. Under such conditions, we might expect that the pigeons would respond at a lower rate (e.g. as under prefeeding conditions, in DeMarse et al., 1999; Nevin et al., 2003), or indeed, may not respond at all because they are effectively satiated (Reese & Hogenson, 1962). The effect on delayed matching-to-sample accuracy is unknown, but, given the trends in Figure 6, it is possible that accuracy would suffer, given that greater predicted levels of deprivation produced higher discriminability with longer delays.

We recommend that when pigeons used in operant experiments are deprived of food, each experimenter must decide whether seasonal deprivation levels might affect response rate or accuracy measures. To achieve stable response rate and accuracy throughout the calendar year, our results indicate that deprivation level should be adjusted to match natural weight fluctuations, or reassessed at different times of the year. A compromise could be to establish the free-feeding weight, and hence the 85% target weight, in the spring or autumn, these being intermediate months in terms of natural weight variation.

The present results reinforce the importance of within-subject experimental design, especially where the independent variables (such as delay-interval duration in the present experiment) are manipulated within session. Where the independent variables are manipulated across conditions, the patterns of seasonal variation observed in the present study underline the importance of conducting replications or arranging balanced orders of conditions across subjects in order to take account of potential order effects.

REFERENCES

- Barlein, F. (1986). Spontaneous, approximately semi-monthly rhythmic variations of body weight in the migratory garden warbler (*Sylvia borin* Boddaert). *Journal of Comparative Physiology B*, *156*, 859–865.
- Brown, G. S., & White, K. G. (2005). The optimal correction for estimating extreme discriminability. *Behavior Research Methods*, *37*, 436–449.
- Clark, G. A. (1979). Body weights of birds: A review. *Condor*, *81*, 193–202.
- Cumming, W. W., Berryman, R., & Nevin, J. A. (1965). Search for an effect of satiation on delayed matching-to-sample performance. *Psychological Reports*, *16*, 645–652.
- Davison, M. C., & Tustin, R. D. (1978). The relation between the generalized matching law and signal-detection theory. *Journal of the Experimental Analysis of Behavior*, *29*, 331–336.
- DeMarse, T. B., Killeen, P. R., & Baker, D. (1999). Satiation, capacity, and within session responding. *Journal of the Experimental Analysis of Behavior*, *72*, 407–423.
- Engels, W. L. (1962). Day-length and termination of photorefractoriness in the annual testicular cycle of the transequatorial migrant *Dolichonyx* (the Bobolink). *Biological Bulletin*, *123*, 94–104.
- Foster, T. M., Temple, W., MacKenzie, C., DeMello, L. R., & Poling, A. (1995). Delayed matching-to-sample performance of hens: Effects of sample duration and response requirement during the sample. *Journal of the Experimental Analysis of Behavior*, *64*, 19–31.
- Gifford, C. E., & Odum, E. P. (1965). Bioenergetics of lipid deposition in the bobolink, a trans-equatorial migrant. *The Condor*, *67*, 383–403.
- Haftorn, S. (1989). Seasonal and diurnal body weight variations in titmice, based on analyses of individual birds. *Wilson Bulletin*, *101*, 217–235.
- Henny, C. J., & VanCamp, L. F. (1979). Annual weight cycle in wild Screech Owls. *Auk*, *96*, 795–796.
- Jones, R. E. (1970). Effect of season and gonadotropin on testicular interstitial cells of California Quail. *The Auk*, *87*, 729–737.
- Kangas, B. D., & Branch, M. N. (2006). Stability of pigeon body weight under free-feeding conditions. *Journal of the Experimental Analysis of Behavior*, *86*, 393–396.
- King, J. R. (1968). Cycles of fat deposition and molt in White-crowned Sparrows in constant environmental conditions. *Comparative Biochemistry and Physiology*, *24*, 827–837.
- Lamoreux, W. F. (1943). The influence of different amounts of illumination upon the body weight of birds. *Ecology*, *24*, 79–84.
- Lindgård, K., Näslund, S., & Stokkan, K. A. (1995). Annual changes in body mass in captive Svalbard ptarmigan: Role of changes in locomotor activity and food intake. *Journal of Comparative Physiology B*, *165*, 445–449.
- Nevin, J. A., Milo, J., Odum, A. L., & Shahan, T. A. (2003). Accuracy of discrimination, rate of responding, and resistance to change. *Journal of the Experimental Analysis of Behavior*, *79*, 307–321.
- Poling, A., Nickel, M., & Alling, K. (1990). Free birds aren't fat: Weight gain in captured wild pigeons maintained under laboratory conditions. *Journal of the Experimental Analysis of Behavior*, *53*, 423–424.
- Reese, T. W., & Hogenson, M. J. (1962). Food satiation in the pigeon. *Journal of the Experimental Analysis of Behavior*, *5*, 239–245.
- Roberts, W. A. (1972). Short-term memory in the pigeon: Effects of repetition and spacing. *Journal of Experimental Psychology*, *94*, 74–83.
- Sargisson, R. J., & White, K. G. (2001). Generalization of delayed matching to sample following training at different delays. *Journal of the Experimental Analysis of Behavior*, *75*, 1–14.
- Sargisson, R. J., & White, K. G. (2003). The effect of reinforcer delays on the form of the forgetting function. *Journal of the Experimental Analysis of Behavior*, *80*, 77–94.
- Spetch, M. L. (1985). The effect of intertrial interval food presentation on pigeons' delayed matching to sample accuracy. *Behavioural Processes*, *11*, 309–315.
- Tewary, P. D., & Kumar, V. (1982). Photoperiodic responses of a subtropical migratory finch, the black-headed bunting (*Emberiza melanocephala*). *Condor*, *84*, 168–171.
- Tsutsui, K., Kawashima, S., Saxena, R. N., & Ishii, S. (1994). Effect of season and photoperiod on the follicle-stimulating hormone receptors in a subtropical bird. *Journal of Bioscience*, *19*, 485–489.
- White, K. G. (1985). Characteristics of forgetting functions in delayed matching to sample. *Journal of the Experimental Analysis of Behavior*, *44*, 15–34.
- White, K. G. (2001). Forgetting functions. *Animal Learning & Behavior*, *29*, 193–207.
- Wright, F. K., & White, K. G. (2003). Effects of methylphenidate on working memory in pigeons. *Cognitive, Affective & Behavioral Neuroscience*, *3*, 300–308.

Received: March 29, 2007

Final acceptance: July 12, 2007