*COPING WITH RISING FOOD COSTS IN A CLOSED ECONOMY:
FEEDING BEHAVIOR AND NOCTURNAL
HYPOTHERMIA IN PIGEONS*

MICHAEL E. RASHOTTE AND DORI HENDERSON

FLORIDA STATE UNIVERSITY

The pigeon's response to increasing fixed-ratio schedules in a 24-hr closed economy is marked by changes in feeding behavior during the daily light phase and by changes in body temperature during the dark phase. The time course of these responses to increasing behavioral cost of obtaining food is very different. Feeding is most affected immediately, within the first day of exposure to moderate fixed ratios. The number of times the pigeons produce the food hopper each day decreases, and the rate at which they eat from the food hopper (grams per minute) when it is available increases, as the fixed ratio is raised. Body temperature is affected later, falling to progressively lower resting levels during the dark phase as body weight drops at the higher fixed ratios when food intake is reduced. The changes in feeding and in body temperature that occur as the fixed-ratio schedule increases seem to reduce daily energy expenditures, within the constraints imposed by the experiment. The ascending and descending limbs of the bitonic function obtained when total daily operant responding is plotted as a function of fixed-ratio schedule in the closed economy is possibly related to the occurrence of thermoregulatory strategies for energy conservation. The energetic analysis of performances in the closed economy requires consideration of a variety of energetic strategies available to the species being studied.

Key words: feeding behavior, closed economy, nocturnal hypothermia, economic analysis, energetic strategies, treadle press, pigeons

In experimental situations in which animals earn all food and water each day by performing operant responses, the animal can be viewed as dealing with the economic problem of striking a proper balance between its daily energy expenditures (e.g., behavioral output) and its daily energy gains (i.e., food obtained). Hursh (1980, 1984) has termed this type of procedure a "closed economy," which can be distinguished from the traditional "open economy" procedure in which the experimenter regulates the animal's total daily energy gain by providing supplementary food and water outside

the experimental situation to maintain a desired level of body weight. When an animal lives in the experimental situation on a continuous basis for several weeks, the closed economy procedure typically includes controlled daily photoperiods. In these cases, it is possible to monitor various aspects of the animal's behavior in both the diurnal and the nocturnal phases of the daily experimental cycle. We exploit this feature of the 24-hr closed economy to broaden the range of energetic strategies known to operate in these experimental situations.

One factor that figures prominently in economic analyses of operant behavior is the behavioral cost of gaining access to food. The methodology of operant reinforcement schedules makes it possible to impose costs in which the behavior required for food reinforcement is manipulated in a controlled way. For example, using fixed-ratio (FR) reinforcement schedules, the behavioral cost can be varied by changing the number of operant responses required for access to food. It is well known that animals cope with variations in food cost in the closed economy by altering their feeding behavior (e.g., Collier, 1983; Collier & Rovee-

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Collier, 1981). In the face of rising food costs, all species studied to date alter their feeding in ways that seem to maximize net energy gains within the constraints imposed by the environmental conditions. However, animals are likely to use a variety of energetic strategies to cope with rising food costs, and it is increasingly recognized that the closed economy can be a useful laboratory procedure for investigating at least some of those strategies and the interactions among them (Collier, Johnson, Hill, & Kaufman, 1986; Hayne, Rovee-Collier, & Gargano, 1986; Rashotte & O'Connell, 1986).

Many endothermic animals use thermoregulatory strategies that conserve energy during periods of reduced food availability (e.g., Hudson, 1978). An endotherm can greatly alter its daily energetic costs by varying the amount of heat lost from its body surface (Calder & King, 1974; Prothero & Jurgens, 1986). Greater heat loss in many circumstances is related to greater metabolic heat production and, therefore, to greater energy expenditure. Important factors determining metabolic heat production are identified in Equation 1:

$$H = c(Tb - Ta) \quad (1)$$

where H (heat production) is directly related to the metabolic rate, c is the thermal conductivity of the surface, and Tb and Ta are body temperature and ambient temperature, respectively (Calder & King, 1974). Equation 1 indicates that an endotherm can reduce its energetic expenditure by lowering the value of c and/or by reducing the $Tb - Ta$ gradient. The value of c can be lowered by increasing the surface insulation, for example when birds erect their feathers. The $Tb - Ta$ gradient can be reduced by lowering Tb (hypothermia) and/or by raising the normally lower Ta . Depending on the specific circumstances, some or all of these thermoregulatory strategies can be brought into play when an endotherm's net daily energy gain is reduced because environmental constraints make it more difficult to obtain food.

Hypothermia during the inactive part of the day is a common response to energy deficits; it helps many small birds and mammals conserve energy by reducing the $Tb - Ta$ gradient (e.g., Hainsworth & Wolf, 1978; Hudson, 1978). There are several reports of fasting-induced nocturnal hypothermia in Columbi-

forme species. The Inca dove (*Scardafella inca*), the ringed turtle dove (*Streptopelia risoria*), and the domestic pigeon (*Columba livia*) all show a progressive decline in nocturnal Tb when the fasting period extends across several days (MacMillen & Trost, 1967; Walker, Walker, Palca, & Berger, 1983).¹ During the daily light phase, Tb returns to its usual high value (about 41 °C), with rewarming occurring shortly before the light phase begins. In Columbiformes, as well as many other types of birds, nocturnal hypothermia is a response to the depletion of energy reserves, the depth of hypothermia becoming greater in proportion to the loss of the reserves. According to some estimates, a bird with body mass approximating that of domestic pigeons will reduce its energy expenditure by about 10% for each degree drop in Tb (Chaplin, Diesel, & Kasparie, 1984). It might be expected, therefore, that pigeons would use this kind of thermoregulatory strategy under some energetically demanding conditions in the closed economy, such as when the behavioral cost of obtaining food is high. This possibility has not been investigated.

In contrast to the lack of knowledge about hypothermia in the closed economy, there is a good deal of information about the ways in which feeding behavior is affected by food costs. Collier's data, from several species, have led him to distinguish between costs associated with gaining access to a meal and costs associated with obtaining portions of a meal (e.g., Collier, 1983; Collier & Rovee-Collier, 1981; Collier et al., 1986). This distinction is made because the primary effect of meal cost appears in the frequency and size of meals, whereas the primary effect of portion cost appears in the rate of consuming the portions that make up a meal. When meal cost increases, the frequency of meals per day decreases and the size of meals increases. When portion cost increases, it is the rate of consummatory behavior that increases. These changes in feeding behavior are readily conceptualized within an economic

¹ Also: Rashotte, M. E. (1985). *A hard day's night: Nocturnal hypothermia in response to high food costs in the 24-hr closed economy*. Paper delivered at the 26th annual meeting of the Psychonomic Society, Boston; Rashotte, M. E., Rautenberg, W., Henderson, D., & Ostheim, J. (1986). *Thermal, metabolic and feeding reactions of pigeons when food is scarce*. Paper delivered at the 27th annual meeting of the Psychonomic Society, New Orleans.

framework because, in each case, they appear to maximize the animal's net energy returns under circumstances in which the environment imposes constraints (i.e., high prices) on food availability (Collier & Rovee-Collier, 1981). When costs become sufficiently high, however, animals greatly reduce their daily food intake, even ceasing to eat.

The effects of food cost on the feeding behavior of pigeons in the 24-hr closed economy have been investigated in several experiments (Lucas, 1981; O'Connell, 1985, 1988; Rashotte & O'Connell, 1986; Rashotte, O'Connell, & Beidler, 1982; Rashotte, O'Connell, & Djuric, 1987). The present paper is concerned with variations in the cost of portions of meals, operationally defined by the number of responses required by the FR schedule (cost) to gain access to 10 s of food reinforcement in a hopper (meal portion). There are sizable changes in feeding behavior when the FR is increased from a low value (FR 6) to a moderate value (FR 30 to FR 100) for even a single day (O'Connell, 1988; unpublished observations). Specifically, when the FR is increased, the rate (grams per minute) at which pigeons eat from the food hopper increases within a few exposures to the higher cost, and the number of portions obtained during the day decreases. Although daily food intake is reduced at the moderate FRs, there is not much effect on body weight. At higher FRs, however, there is a greater reduction in food intake which eventually results in greater loss of body weight.

These findings suggest a way to evaluate the three main questions of interest here. First, by increasing the FR from low to moderate values, and by measuring T_b as well as feeding behavior, it should be possible to determine whether hypothermia is used in concert with the cost-induced changes in feeding behavior, well before body weight loss indicates any significant depletion of energy reserves. Second, by continuing to increase the FR beyond the moderate range, it should be possible to determine whether the pigeon resorts to hypothermia in the closed economy when the cost of food is so high that feeding behavior fails to maintain energy reserves. The available literature on fasting-induced nocturnal hypothermia in Columbiformes suggests an affirmative answer to this second question. Finally, it has been reported that the total amount of behavior per day increases to a peak value and

then declines as the FR increases from low to high values in a closed economy (e.g., Hursh, 1980, 1984; Timberlake & Peden, 1987). The determinants of peak performance are not well understood, but it is possible that the occurrence of energy conservation through hypothermia is related in some way to the occurrence of the peak (Timberlake & Peden, 1987). The present experiment provides information on this possibility.

In our experiment, individual pigeons lived for several weeks in a chamber maintained at room temperature where they experienced a daily 10:14 hr light/dark cycle. The pigeons were able to drink water at any time from a freely available cup. They could eat only during the daily light phase, and to do so they were required to press a foot-treadle on an FR schedule of reinforcement. Each completion of the FR provided access to a food hopper for 10 s. There were two FR series. The first was designed to impose moderate costs for a short period, with the goal of creating large changes in feeding behavior without having much effect on body weight. This series began at FR 6 and increased every 3 days, first to FR 30, then to FR 60, and finally to FR 120. In the second series, each FR was imposed for 6-day periods. This series began at FR 6 and progressed to FR 60, FR 120, FR 240, FR 480, FR 960, and FR 1,920, terminating for individual pigeons when they lost about 20% of baseline body weight. Subcutaneous temperature (T_s) was measured continuously by a thermocouple surgically implanted between the skin and muscle in the interscapular region. With this arrangement, it was possible to determine how T_s was affected during the manipulation of food cost.

METHOD

Subjects

Six adult pigeons (*Columbia livia*) were purchased from a local supplier who maintains a loft of free-flying birds in a rural environment. Two of the pigeons (P4 and P7) participated in an earlier experiment in which the number of treadle presses required to gain access to food in a 24-hr closed economy varied between 3 and 60 during several months of training with a procedure that involved a hierarchy of visual signals for feeding opportunities (O'-

Connell, 1985). The other pigeons had no prior experience in a closed economy. Before the experiment began, the pigeons were acclimated to the colony room conditions: a 10:14 hr light/dark cycle, ambient temperature approximating 20 °C, and free access to water and to a commercially available diet of mixed grains (Purina Pro Grains) in individual cages. In the data reported below, there were no systematic differences between birds related to their prior experience in the closed economy. Accordingly, the different backgrounds of the birds will not be discussed further.

Apparatus

During the experiment, individual pigeons lived continuously in one of two identical chambers, 38.5 by 40 by 42.5 cm in size. The ambient temperature in the chambers averaged about 22 ± 3 °C. Water and food were located behind openings (5.2 by 5.8 cm) on one wall. The midpoints of the openings were 8.5 cm to the left and right of the wall centerpoint, with bottom edges 10 cm above the floor. Water was available in a cup mounted behind the left opening. Food (the grain mixture used in the colony housing) was available behind the other opening whenever a solenoid-operated hopper was raised. An infrared photobeam in the food-hopper assembly detected the pigeon's head at the hopper and was the means by which time spent eating was quantified. A pecking key that was normally dark but that could be lighted red by a rear-projection device was mounted 25 cm above the floor midway between the openings.

The pigeons gained access to the food by pressing on a T-shaped, foot-operated treadle mounted at the opposite end of the chamber, 2.5 cm above the floor and 27.5 cm from the wall that housed the food, water, and pecking key. The treadle, which extended 9 cm into the chamber and operated when a force of about 0.90 N was applied, had a 7.5-cm long metal rod as the shaft and a 4.5-cm long metal tube (1.5 cm diameter) as the crosspiece.

The 10-hr daily light period was provided by a 25-W bulb (at 90 V) located in a roof-top housing outside each chamber. The bulb illuminated the chamber through an opening in the ceiling covered with frosted acrylic. An exhaust fan ventilated each chamber and provided masking noise. The chambers were located in an isolated room in such a way that

visual interactions between the pigeons were precluded and auditory interactions were minimal. Experimental events were controlled and recorded by a computer located in a nearby room.

The pigeons' subcutaneous body temperature was measured by means of an implantable thermocouple (Sensortek, Model IT 18) sutured to muscle under a skin flap in the interscapular region. The thermocouple exited the skin and passed through a metal plate held midway on the pigeon's back by a harness arrangement comprised of flexible tubing that was wrapped loosely around the base of each wing and connected to the plate. The thermocouple exited from the plate and passed through flexible plastic tubing that was connected through an opening in the top of the chamber to a slip-ring assembly located outside. This arrangement allowed the pigeon to move comfortably about the chamber and to rest in a natural position. The thermocouple exited the slip-ring assembly and was connected to a multichannel polygraph (Grass) located in another room. The polygraph provided continuous chart recordings of T_s from the pigeons in each experimental chamber, the ambient temperature in one of the chambers, the occurrence of treadle pressing and hopper presentation in one of the chambers, and the light/dark phase transitions in the daily cycle. The speed of the chart drive on the polygraph was set at 0.25 mm/s.

Procedure

The experimentally naive pigeons were placed individually in the chambers with food available continuously in the raised hopper. All pigeons ate for sustained periods from the raised hopper and drank from the water cup within 4 to 6 hr of being placed in the chamber. The pigeons were then removed from the chambers while food and water supplies were replenished, and were finally returned with the hopper available for 60-s presentations on a FR 1 schedule. The full sequence of events following completion of the FR schedule consisted of illumination of the pecking key (red) for 10 s followed by presentation of the hopper. In this experiment, the red keylight simply signaled the impending presentation of food. Such signals for food, which attract the pigeon to the vicinity and evoke directed pecking responses, have been of interest in other closed

economy experiments in this laboratory (e.g., Rashotte et al., 1987). In the present case, the keylight signal is not of interest and will be ignored in the presentation. The pigeons were kept on this FR 1 schedule for 1 or 2 days until they were feeding from the hopper on a regular basis. The duration of the hopper presentation was then decreased to 30 s and subsequently to 10 s. Finally, the FR was increased to the final baseline condition, FR 6 for 10-s hopper presentations, which remained in effect for about 2 weeks. The experimentally experienced pigeons were placed directly in this final baseline condition for approximately 2 weeks. Because there were 6 pigeons and only two experimental chambers, the experiment was conducted in three successive replications.

The pretraining and baseline conditions described above, and all other parts of the experiment, were carried out on a 10:14 hr light/dark cycle, with lights on at 8:00 a.m. The food hopper could be operated by presses on the foot-treadle only during the daily light phase. This arrangement did not impose a functional restriction on the pigeons' feeding time, because in other experiments in which the treadle could always be operated, we found that pigeons do not produce food during the dark phase (Rashotte et al., 1982). Each day, the birds were removed from the chambers for about 10 min immediately after the light phase of the cycle began. During this period, body weight was measured and the previous day's consumption of food and water (corrected for evaporation) was determined by weighing the amount of food and water remaining in the hopper and cup, respectively. Also, at this time chamber maintenance was carried out, and the food and water dispensers were refilled.

After about a week of exposure to the FR 6 baseline condition, the pigeons were fitted with the harness and returned to the chamber to adapt to the harness and its slip-ring connection. The birds seemed to be comfortable in the harness after a short time and showed essentially no disruption of baseline eating and drinking levels. After a few more days, the birds were removed from the chamber for about an hour while the thermocouple was implanted. Under local anesthesia (Lidocaine), a small skin flap was made to one side of the spine in the interscapular region to expose the underlying muscle. The thermocouple was su-

tured to the muscle and the skin flap was sutured closed. The thermocouple and harness assembly were then replaced on the bird, and the bird was returned immediately to the chamber on the FR 6 baseline schedule. The birds showed very little disruption of the baseline feeding pattern following surgery.

The main experimental treatment began 1 or 2 days after surgery. All birds were exposed to a sequence of conditions in which the FR for treadle pressing was increased from FR 6 to FR 30, FR 60, and finally to FR 120. Each schedule was in effect for 3 days. Then, with 1 bird discontinued for reasons unrelated to its performance in the experiment, the remaining 5 pigeons returned to the FR 6 baseline condition for 4 days prior to entering the second phase of the experiment. In the second phase, each of a sequence of FR schedules was in effect for 6 days. This series began with the FR 6 baseline, then FR 60, FR 120, FR 240, FR 480, FR 960, and FR 1,920. The reinforcement was always 10-s presentation of the food hopper. Each bird continued in the series until it lost about 20% of its body weight. One bird ended the series at FR 240, 2 ended at FR 480, and 1 each at FR 960 and FR 1,920. In each condition, a time criterion was in effect that encouraged the pigeons to complete the required number of presses without long breaks in responding. The criterion imposed a time limit between successive pairs of treadle presses that, if exceeded, caused the number of presses already completed to be ignored and the entire required number of presses to be reimposed. The value of the criterion was 30 s at FR 6 and FR 30, 600 s at FR 60, FR 120, and FR 240, and 1,200 s at higher FRs. The actual behavior of the pigeons indicated that the criterion was rarely invoked. The pigeons usually responded continuously on the treadle to complete the FR, occasionally interrupting high FRs for brief trips to inspect the (inoperative) food hopper and peck on the (darkened) response key. Following completion of the last series, 3 pigeons were returned to the FR 6 baseline for a few days. The scheduling of the chamber prevented the return of all birds to the baseline condition.

RESULTS

As the FR increased in both the 3-day and 6-day series, the pigeons completed fewer FRs

Fig. 1. Number of feeding opportunities obtained during the 10-hr light phase by individual pigeons on the last day at each FR. (Because of technical problems while running the experiment, data for P14 at FR 240 in the 6-day series are not plotted in any figure.)

each day and, therefore, had fewer opportunities to eat each day (Figure 1), and they ate from the hopper at a higher rate when it became available (Figure 2). The figures show the performance of individual pigeons on the final day of each FR schedule. In some cases, there was a changing trend in performance across the first day or two on a schedule. For example, at the very high FRs in the 6-day series, some pigeons produced the hopper more often on the first day than on later days. In contrast, the rate-of-eating measure was essentially constant across days on an FR schedule. There are insufficient data to allow gen-

Fig. 2. Rate of eating (grams per minute) from the food hopper during the 10-hr light phase for individual pigeons on the last day at each FR, computed by dividing the total food intake for the light phase (in grams) by the total amount of time (in minutes) the photobeam in the food hopper was broken while the hopper was presented. No point is plotted on days when a pigeon failed to eat.

Fig. 3. Total food intake (grams) by individual pigeons during the 10-hr light phase on the last day at each FR.

eralizations about these trends, however. The robust effects of the FR schedule on these two measures of feeding behavior are best characterized by the data in Figures 1 and 2. Unfortunately, limitations on computer memory made it impossible to record sufficient data to permit a satisfactory analysis of the feeding data in terms of meal patterns.

Figures 3 and 4 summarize changes in the pigeons' food intake and body weight that accompanied the changes in feeding. In the 3-day series, P4 and P6 showed the greatest effects, eating no food at all on the last day of FR 120 and showing the greatest loss in body weight (4.8% and 7.4% for P4 and P6, respectively). In the subsequent 6-day series, the FR increased for individual pigeons until their weight loss approximated 20% of the value at the (6-day) FR 6 baseline. The amount of food eaten decreased as the FR increased, and at the final FR no food (or very little for P6) was consumed for several days. The percentage of body weight lost when the FR series was terminated was 23%, 16%, 21.1%, 19.6%, and 18.8% for P4, P6, P7, P14, and P20, respectively. The

gradual reduction in food intake and body weight as the FR increased, especially in the 6-day series, indicates conditions of growing food scarcity and depletion of energy reserves for the pigeons.

A summary of the dark-phase T_s data for each pigeon in the experiment is provided in Figure 5, which shows, for the last day on each FR schedule, the mean of all T_s readings taken every 20 min during Hours 3 to 11 of the dark phase. These means characterize the resting level of T_s in the dark phase, ignoring the periods of cooling and rewarming at the beginning and end of the dark phase (see Figures 6 and 7). In both the 3-day and 6-day series, it is clear that there were individual differences in the point at which the resting level of the dark-phase T_s began to decrease as the FR requirement increased. It is noteworthy that the increasing FR affected feeding behavior sooner than it affected T_s (cf. Figures 1, 2, and 3).

Correlations between body weight and resting level of nocturnal T_s are summarized in Table 1. The outcome in the 6-day series is

Fig. 4. Body weight (grams) of individual pigeons at the end of the dark phase on the last day at each FR.

very clear: For each pigeon, over 90% of the variance in resting level of the dark-phase T_s is accounted for by variation in body weight. In the 3-day series, the 3 pigeons for which T_s decreased in the dark phase (P1, P4, and P6; see Figure 5) also experienced the largest decreases in body weight (their largest individual weight losses in this series were 4.7%, 4.8%, and 7.9%, respectively). Table 1 shows that in these three cases there was a strong relationship between body weight and dark-

phase T_s in the 3-day series. Additional computations indicated that the resting level of T_s was related to the amount of food eaten during the previous light phase for all birds in the 6-day series and for P1, P4, and P7 in the 3-day series. However, across birds the correlations were uniformly lower than when body weight was used in the analysis (range, $r = .68$ to $.90$).

Figures 6 and 7 present two representative examples of the T_s data plotted at 20-min in-

Fig. 5. Mean subcutaneous temperatures averaged over the middle 8 hr of the dark phase for individual pigeons on the last day of each FR.

tervals during several complete 24-hr cycles. The dotted-line curve in each panel of Figure 6 shows T_s for P6 on the last day of the FR 6 baseline schedule in the 3-day series. This curve provides a common reference point for the solid-line curves, which show T_s on the last day of the other FR schedules during the 3-day series and on the first day of return to the FR 6 baseline schedule immediately after the FR 120 condition was completed (bottom panel). The FR 6 reference curve (dotted line) illustrates several features of the typical day-night cycle in body temperature found in birds and mammals. Specifically, the nocturnal body temperature is about 1 to 2 °C lower than in the light phase (dark mean = 39.0 °C; light mean = 40.4 °C), which is characteristic of well-fed animals maintained in ambient temperatures within the thermoneutral zone (Hainsworth & Wolf, 1978; Walker et al., 1983). Also, the beginning of the drop in nocturnal T_s coincides with the onset of darkness, but the rise in T_s to its light-phase level is completed before the lights are turned on (Graf, 1980). Under the present experimental conditions, this late-night rewarming in T_s occurred without coincident external stimulation.

There are four points to note about the T_s data plotted as the solid lines in Figure 6. First, the resting level of the dark-phase T_s fell as the FR increased from FR 30 to FR 60 to FR 120. Second, the nocturnal T_s immediately recovered to its reference level in the first dark phase after the pigeon was returned to FR 6. Third, examination of the polygraph charts and intermittent remote observation of the pigeons revealed that fluctuations in T_s during the light phase were associated with periods of activity and inactivity. At FR 30 and FR 60, high T_s associated with treadle pressing and eating were usually followed by periods in which T_s fell sharply to 40 °C or less. The pigeon was observed directly during these periods on several occasions and was seen to drink water, to be inactive, or even to be behaviorally asleep. The relatively high T_s at the beginning of each light phase was associated with the aftereffects of the daily maintenance period. Finally, as shown in the bottom two panels, T_s was relatively low during most of Hours 1 to 6 of the light phase, but increased in the remaining light-phase hours when P6 became active (walking about, looking in the food hopper, pecking the dark key, pressing the trea-

Table 1
Regression of mean dark-phase subcutaneous temperatures on percentage of body weight for individual pigeons.

Pigeon	<i>r</i>	Slope	Intercept	<i>n</i>
3-day series				
1	.950	0.472	-7.89	9
4	.952	0.207	18.63	10
6	.907	0.166	22.36	10
7	.701	0.212	17.85	10
14	.567	0.068	32.45	9
20	.605	0.079	31.37	9
6-day series				
4	.959	0.132	25.83	25
6	.973	0.295	10.14	14
7	.959	0.144	24.98	33
14	.965	0.192	20.01	27
20	.965	0.235	16.63	26

Note: Mean subcutaneous temperature during the middle 8 hr of each dark phase was correlated with body weight measured just after each dark phase ended. Body weights expressed as a percentage of the pigeons' final body weight (2- or 3-day mean) on FR 6 were computed separately for the 3-day and 6-day series.

The values in the column headed *n* indicate the number of pairs of observations in each analysis. In the 3-day series, the maximum number was 10 (one for FR 6; three for each of the others). In the 6-day series, there was one pair for FR 6 and six for each of the others. Missing data were caused by equipment failures, most of which were attributable to brief power outages that resulted in the entire day's temperature data being unusable.

dle). Its treadle-pressing activity was not sufficient to produce the food hopper on the FR 120 day shown, but it was successful on the day of return to FR 6 (bottom panel). The pigeon first ate on that day between 6 hr 40 min and 7 hr in the light phase (marked by an arrow), and it produced the hopper a total of 49 times and ate 20 g of food.

Figure 7 presents 24-hr T_s data for P7 during the higher FRs in the 6-day series. The dotted-line curve in each panel shows T_s on the final day of the FR 6 baseline schedule immediately preceding the series of FR exposures in the 6-day series. The solid-line curves indicate that the resting level of the dark-phase T_s was not greatly influenced until FR 960 and FR 1,920 were reached. Unlike P6, the dark-phase T_s of P7 was not affected by the FR schedules in the 3-day series. During the light phase, T_s was related to activity level, which was normally most pronounced in the later hours of the light phase when the pigeon was working for food. On the FR 1,920 day shown, however, the drop in T_s during

P6 (3-DAY SERIES)

these late-day hours was associated with inactivity and apparent sleep.

The total number of operant responses made each day to produce food rose to a peak and then declined as the 6-day FR series progressed. The data for individual animals in Table 2 indicate that there were large differences among the birds in the point at which peak responding occurred in the FR series. It is clear, however, that up to the FR at which the peak occurred, the birds were relatively successful in defending body weight, despite a sizable reduction in food intake. The unit cost of food (responses made to obtain a gram of food) increased with increases in FR.

Computations based on the data in Table 2 indicate that, with reference to the FR 6 baseline, body weight at the peak FR averaged 96.1% of the baseline, whereas food intake averaged only 48.9% of baseline. The ability of pigeons to maintain high body weight despite several days of greatly reduced food intake implicates significant energetic strategies for dealing with food scarcity. The body temperature data indicate that nocturnal hypothermia plays a relatively small role in this prepeak period. That is, at the FR in which peak responding occurred, mean nocturnal T_s was 0.7 °C below the FR 6 baseline (baseline mean: 39.5 °C; peak mean: 38.8 °C). However, at the FR immediately following the peak, mean nocturnal T_s was 2.1 °C below the FR 6 baseline, suggesting the involvement of nocturnal hypothermia as an important energy-saving strategy in the postpeak period. Of course, the postpeak deepening of nocturnal hypothermia coincided with a greater reduction in body weight and food intake. Mean weight at the postpeak FR was 89.6% of the FR 6 baseline, and mean food intake was 15% of the baseline.

DISCUSSION

Pigeons react to increasing food costs in the 24-hr closed economy by altering their feeding

behavior during the light phase and by lowering their body temperature during the dark phase. The time course of these effects is very different. Changes in feeding behavior occur within a single day of exposure to a moderate rise in cost. Nocturnal hypothermia, on the other hand, is closely related to the loss of body weight, which typically occurs at relatively high costs when food intake is greatly reduced for several days. Apparently, of the thermoregulatory strategies available to the pigeon (see Equation 1), the lowering of body temperature plays only a small role, at best, in situations in which the cost of food increases to moderate values and the ambient temperature is in the thermoneutral zone.

The changes in feeding behavior and in nocturnal T_b documented here seem to help the pigeons cope with increasingly severe energetic challenges posed by rising food costs. That is, as the cost of food rises, the changes in feeding behavior seem to be aimed at reducing the cost of feeding in the sense that the pigeons work to produce the food hopper less frequently each day, and they eat at a higher rate when the hopper is available. Of course, the experimental conditions impose an important constraint on the absolute level of efficiency the pigeons can achieve in feeding. In particular, because the animals were working for fixed durations of access to a food hopper, a rise in the cost of food necessitated a steep rise in the unit cost of a gram of food (Table 2).

The lowering of T_b for several hours during the dark phase when the cost of food is very high is one of the thermoregulatory strategies endotherms can use to reduce energetic costs, as shown by Equation 1. The close relation between body weight loss and the depth of nocturnal hypothermia found here is similar to the findings of experiments in which Columbiformes (MacMillen & Trost, 1967; Walker et al., 1983) and small birds of other orders (e.g., Hainsworth, Collins, & Wolf, 1972; Hainsworth & Wolf, 1978) are made to fast by the complete withdrawal of food. An

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Fig. 6. Subcutaneous temperature throughout the daily cycle for P6 in the 3-day series. The transition from light phase to dark phase is marked by the broken line at Hour 10. Temperature is shown on the last day of FR 30, FR 60, and FR 120, and on the first day of return to FR 6 (bottom panel). The three numbers in parentheses in the heading of each panel indicate, respectively, body weight at the end of the dark phase (expressed as a percentage of the weight at FR 6), total amount of food consumed (grams) during the light phase, and total amount of water consumed (mL corrected for evaporation) during the light phase. The comparable numbers for the dotted-line curves are 100%, 20.9, and 28.5. See text for further details.

P7 (6-DAY SERIES)

Table 2

Individual data for the 6-day series of FR schedules. Each entry is the mean value over all days studied at each FR: number of responses (treadle presses) per day, food intake as a percentage of the intake at FR 6, unit cost of food expressed as the number of treadle presses made to obtain 1 g of food, body weight as a percentage of the weight at FR 6, and nocturnal (mid-8 hr) subcutaneous temperature in °C. The point at which the highest number of responses per day occurred is underlined for each bird.

	FR 6	FR 60	FR 120	FR 240	FR 480	FR 960	FR 1,920
P4							
Responses	270	<u>710</u>	456	600	548.6		
Food	100	<u>61.8</u>	28.4	20.4	10.2		
Unit cost	12	51.1	71.3	130.4	238.4		
Body weight	100	102.4	97.6	92.6	84.5		
Subcutaneous temperature	39.6	39.1	38.8	38.2	36.8		
P6							
Responses	591	<u>1,053</u>	520	285			
Food	100	<u>53.6</u>	32.2	2.7			
Unit cost	25.4	84.1	99.6	452.3			
Body weight	100	98.8	94.6	86.4			
Subcutaneous temperature	39.3	39.2	38.6	35.4			
P7							
Responses	317	1,000	1,310	1,866.7	2,194.3	<u>4,480</u>	1,440
Food	100	74.4	65.4	52.1	33.6	<u>38</u>	7.6
Unit cost	15.1	63.8	94.6	169.7	309	560	900
Body weight	100	100.1	99	96.4	93.4	89.1	82.8
Subcutaneous temperature	39.4	39.1	39.1	38.9	38.5	37.9	36.6
P14							
Responses	487	1,280	1,480	1,824	<u>2,800</u>	960	
Food	100	78.8	64.4	50.7	41.8	3.8	
Unit cost	16.7	55.7	78.7	123.2	226.7	888.9	
Body weight	100	102.6	103.5	101.8	93.9	86.2	
Subcutaneous temperature	39.4	39	39.7	39.2	38.4	36.1	
P20							
Responses	363	1,320	1,350	<u>2,240</u>	240		
Food	100	79.6	57.8	49.5	2.9		
Unit cost	17.6	92.7	113.5	219.6	381		
Body weight	100	100.2	98.9	96.3	87.2		
Subcutaneous temperature	39.8	39.8	39.9	39.5	36.9		

Note: Entries for food intake and body weight are expressed as a percentage of the value at FR 6. The mean food intake (in grams) at FR 6 was 22.5, 23.3, 21.1, 29.2, and 20.6 for P4, P6, P7, P14, and P20, respectively. The mean body weight (in grams) at FR 6 was 348.2, 346.0, 371.8, 395.8, and 375.6 for P4, P6, P7, P14, and P20, respectively.

interesting aspect of the present result is that, in a sense, the pigeons underwent a self-imposed fast. That is, food was available at all times in the light phase, and there was sufficient time to earn a full (i.e., baseline) level of intake except perhaps at the very highest FR

imposed. Instead of working for the baseline level of food, however, the pigeons became decreasingly likely to pay the price as it rose, with the consequence that food intake and body weight fell. It seems, therefore, that nocturnal hypothermia is an energetic strategy called into

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Fig. 7. Subcutaneous temperature throughout selected daily cycles for P7 in the 6-day series. Data are presented as in Figure 6. The body weight/food intake/water intake numbers for the dotted line curves are 100%, 20.3, and 24.5. See text for details.

play when cost-induced changes in feeding behavior fail to maintain body weight.

It is likely that the energy savings resulting from nocturnal hypothermia play a significant role in allowing the pigeon to survive extended periods of relatively low food intake induced by high food prices. Based on Chaplin et al.'s (1984) equation, the pigeon should achieve an approximately 10% energy saving for each degree drop in T_b . Computations made on the individual animal data in Table 2 indicate that average body temperature during the final FR in the 6-day series was 36.4 °C, compared to 39.5 °C on the FR 6 baseline. This 3.1 °C difference in resting nocturnal temperature represents an approximately 31% energy saving. The actual saving for the entire night is difficult to estimate because costs associated with rewarming prior to the light phase would likely reduce the net saving, whereas changes in conductance (e.g., insulative feather posture) would increase energy saving. All that can be said with certainty, on the basis of the present findings, is that the pigeon increasingly engages at least one of the possible thermoregulatory strategies (hypothermia) during the nocturnal phase of the daily cycle when it experiences increasing loss of body weight in the closed economy.

It is important to note that body weight loss is not always a good predictor of nocturnal hypothermia. The 3 pigeons returned to the FR 6 baseline after they had completed the 6-day series of FRs required several days to recover their body weight from its value near 80% of baseline. Nevertheless, the nocturnal T_s of these birds recovered to its high baseline level on the first night after exposure to FR 6. It is likely that nocturnal T_s was influenced by the thermogenic effects of food in these cases, but there are other instances in which T_b is known to be unrelated to body weight loss. Perhaps the most dramatic examples occur in birds that lose a large percentage of their body mass during incubation (as much as 45%) but do not become hypothermic (Cherel, Robin, & Le Maho, 1988).

In several closed economy experiments, a bitonic function relating number of operant responses to size of the FR schedule has been reported (Hursh, 1984; Timberlake & Peden, 1987). The data in Table 2 suggest some considerations for an energetic analysis of that function. It is possible that the ascending limb

of the bitonic function reflects a strategy in which the animal expends increasing amounts of energy in an attempt to defend energy income. The descending limb, coupled with increased loss of body weight and deepening nocturnal hypothermia, seems to reflect a clear shift to energy conservation mechanisms in the face of increasing energy deficit. It is noteworthy, however, that the body weight of the pigeons was defended at relatively high levels during the ascending limb of the function, despite the considerable reduction in food intake. This finding implicates energy conservation mechanisms during the ascending limb of the function, and Equation 1 identifies a thermoregulatory strategy other than hypothermia that might have been operative. Specifically, it is possible for the pigeons to achieve energy savings by decreasing conductance through changes in insulation. Some Columbiformes achieve significant energy savings by changing their feather posture when food intake is restricted (McFarland & Budgell, 1970), and it is also possible to reduce heat loss by making postural changes (e.g., crouching) that reduce the amount of body surface exposed to the surrounding medium. If these thermoregulatory strategies were used in our experiment, they would have been undetected. It is possible that such strategies are preferentially used during relatively mild energetic challenges, to be joined by hypothermia in more difficult circumstances.

We note that the bitonic function identified in experiments in which animals are maintained chronically at low body weight (see Timberlake & Peden, 1987) may not be related to the present energetic considerations. Highly deprived animals might use a relatively full complement of strategies to conserve energy at all times and, therefore, might not have the flexibility to use individual strategies selectively when the FR increases, as our account implies. Because the energetic consequences of extended periods of reduced food intake in birds are complex (e.g., Cherel et al., 1988), the energetics of performance in traditional operant experiments are difficult to conceptualize.

Equation 1 indicates that energy savings might also be achieved by raising T_a . The pigeons in our experiment might have used this thermoregulatory strategy when the FR increased if they had been able to control T_a .

Recent data obtained in the closed economy have begun to indicate some of the conditions under which pigeons will utilize this thermoregulatory strategy during rising food costs (Ostheim & Rautenberg, in press).

It is clear that a complete picture of the thermoregulatory strategies used by animals in dealing with rising food costs will require a variety of experimental and observational approaches. It should also be noted that birds are able to improve their energetic situation by means other than the thermoregulatory strategies discussed here. For example, reduced locomotor activity during periods of reduced food intake can result in significant energy savings, even to the point of allowing body weight to increase during reduced intake (Stokkan, Mortensen, & Blix, 1986). Improved digestive efficiency arising from more complete extraction of nutrients from ingested food and other changes in digestive physiology are important considerations, as are structural changes in the digestive system during periods of reduced food intake (Cherel et al., 1988; Fabry, 1967). Clearly, the energetic analysis of closed economy experiments must include a range of strategies beyond the traditional emphasis on feeding strategies.

With proper instrumentation, the 24-hr closed economy should provide a useful experimental setting in which to study the conditions under which various energetic defenses are activated, singly and in combination, when pigeons and other birds and mammals are faced with energetic threats. Information from such investigations will improve the understanding of how animals defend against food scarcity and may suggest new directions for research on the physiology of energetic defenses in demanding environmental conditions.

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