

ulation males are often victims of extrapair fertilizations (Westneat 1987a, b; Westneat et al. 1987), yet the precise effect on reproductive success of these matings is unknown because parentage cannot be assigned. Nevertheless, polygyny in this species is associated with a decrease in male parental care, which probably affects female reproductive success by lengthening the time between fledging and reneating and makes it less likely that a female will attempt a second brood.

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Seasonal Changes in Food Preferences of American Robins in Captivity

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Virtually all birds change their diets over the course of the year (e.g. Martin et al. 1951, Hintz and Dyer 1970, Smith et al. 1978). Seasonal shifts in diet are

especially striking in birds that eat fruits. Fruits may comprise more than 95% of the diet in some seasons while in other seasons they are not eaten at all (Martin et al. 1951), despite the fact that in most habitats at least some fruits are available year-round (Jones and Wheelwright 1987, Skeate 1987). The simplest explanation for such diet shifts is that birds track food

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availability (e.g. Jordano 1986). As birds change habitats or as habitats change over time, and certain foods become rare or abundant, birds may consume them in general proportion to the rate at which they are encountered (changing-availability hypothesis). Thus, fruit-eating birds in the Temperate Zone may turn to fruits in fall and winter when invertebrates are scarce and favor invertebrates in the spring and summer when they are common (Morton 1973, Thompson and Willson 1979, Skeate 1987).

A second (and not necessarily mutually exclusive) explanation for diet shifts is that fruit-eating birds may change seasonally. For example, fruits may fulfill particular nutritional needs better than invertebrates at certain times of year (e.g. fat deposition for migration). According to this view, the seasonal shift to eating fruits reflects selective foraging on the part of birds rather than a simple response to changing food availability (changing-preference hypothesis; Snow 1971, Herrera 1982). Even if eating fruit conferred no particular advantage over eating insects at any time of the year, individual birds that anticipated changing food availability and shifted diets would be favored if fruit and invertebrate availability changed temporally in a predictable way. In other words, fruit-eating birds may have been selected to exploit limited opportunities, matching their preferences against the possibilities by choosing fruits when they are relatively abundant. In fact, birds could subsequently be "committed" to a particular food type, even if it unexpectedly became scarce, because of seasonal alterations in gut length, liver size, and other aspects of digestive morphology and physiology (see references given by Sibly 1981). The most likely hypothesis to explain seasonal diet shifts of fruit-eating birds is that they are due to changes in food availability, digestive capabilities and preferences, or both.

Disentangling the proximate and ultimate causation of diet shifts is complicated. For example, changes in gut length could be induced by diet changes (e.g. Moss 1972), they could be caused by responses to seasonally varying photoperiod (a reasonably reliable cue to estimate relative fruit availability), or they could result from endogenous circannual rhythms (which would indicate that fruit availability changes very predictably). Each situation implies an increasingly obligate, inflexible, and perhaps evolved commitment to seasonal fruit consumption. Coevolution between fruit-eating birds and plants, driven by the unique mutualistic relationship seed dispersers have with their "prey" (Snow 1971, Thompson 1982, Wheelwright and Orians 1982), opens the possibility of extensive and specialized adaptations to seasonal changes in fruit availability, such as endogenous changes in digestive morphology and physiology. Rather than consider the issue of proximate mechanism for diet shifts (i.e. whether they are induced, photoperiodic, or endogenous), I considered two extreme possibilities. Temporal changes in fruit con-

sumption by birds could reflect changes either in food availability or in food preference. Specifically, if fruit availability could be controlled so that it remained constant year-round, would birds eat a fixed amount of fruits each month, or would they show seasonal preferences that mirrored fruit consumption under natural conditions? The changing-availability hypothesis predicts that fruit consumption should remain similar throughout the year; the changing-preference hypothesis predicts that fruit consumption should be high in the fall and winter, and low in the spring and early summer, as it is in nature (Martin et al. 1951, Wheelwright 1986).

Previously, Berthold (1976a, b) reported that hand-raised Garden Warblers (*Sylvia borin*) showed regular spontaneous changes in their monthly intake of fruits relative to animal food even in the absence of photoperiodic cues. There was much intraspecific variation in the results, however, and the experimental protocol was not clear. Furthermore, related species (*S. atricapilla*, *Turdus merula*) showed different patterns from *S. borin* or no pattern at all (Berthold 1976a, b). That birds show intrinsic circannual rhythms in fruit preference remains uncertain as a result. I reexamined the question with American Robins (*Turdus migratorius*) because their diet is well known and they show marked seasonal dietary variation. They are also members of the same family (Muscicapidae) as *S. borin*. During the fall and winter, fruits comprise 80-99% (depending on the month and region) of robins' stomach contents by volume, vs. less than 10% in April and May (Wheelwright 1986).

Six robins (3 adults and 3 juveniles) were mist-netted in August 1985 in Ithaca, New York, and maintained together in an aviary at Cornell University for 1 yr. The room measured 4 × 5 × 4 m and contained two 2-m-tall white pines (*Pinus strobus*) for perching, a 1-m² bathing/drinking area, and a one-way observation window. The birds were exposed to a natural photoperiod; temperatures varied from around 15°C in winter to 20°C in summer with a 2-3°C diurnal cycle. Birds were fed *ad libitum* a standard laboratory diet and water (see Jones and Wheelwright 1987). When the birds were released at the end of the experiment, their masses did not differ significantly from the beginning of the experiment (August 1985: \bar{x} = 73.0 g, SD = 5.9; September 1986: \bar{x} = 79.3 g, SD = 4.1; *t*-test, *P* = 0.056). The sex of the birds was not determined, but male and female robins have very similar diets at all times of year (Wheelwright 1986).

In the Ithaca area, robins favor the fruits of *Viburnum dentatum* (northern arrowwood) and *Lindera benzoin* (spicebush) over most other fruits (Wheelwright unpubl. data). Fruits of both species were picked in August 1985, frozen in the field in liquid nitrogen, and preserved at -60°C in triple plastic bags. On thawing, preserved fruits were a slightly different color (in *Lindera benzoin*) and were softer (in both species) than fresh fruits, but, as in other studies (Lee

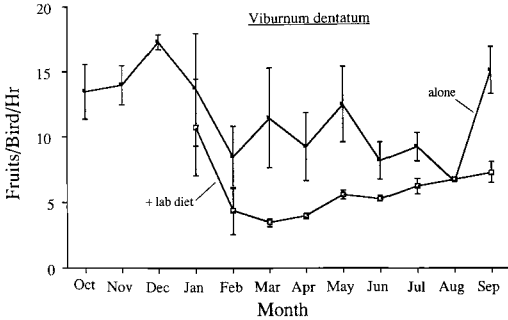


Fig. 1. Consumption rates of *Viburnum dentatum* fruits by 6 captive American Robins. Upper line (solid points) represents fruits presented alone. Lower line (open points) represents fruits presented with lab diet. Error bars represent 1 SD. Each point is the mean of 2 (lower) to 3 or 4 (upper) experiments.

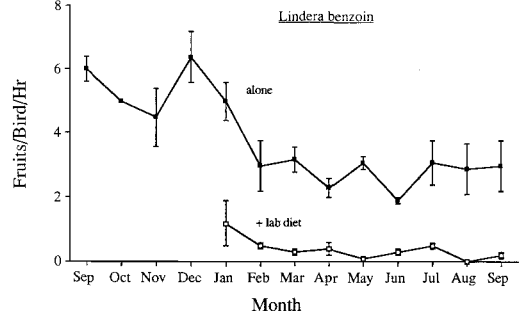


Fig. 2. Consumption rates of *Lindera benzoin* fruits by 6 captive American Robins. Upper line (solid points) represents fruits presented alone. Lower line (open points) represents fruits presented with lab diet. Error bars represent 1 SD. Each point is the mean of 2 (lower) to 3 or 4 (upper) experiments.

1970), there were no apparent nutritional changes over the year as judged by taste to humans and by the following experiment. When the robins were offered a choice between 1-yr-old preserved *V. dentatum* fruits and new *V. dentatum* fruits that were briefly frozen and thawed, they did not discriminate between them in 6 h of feeding trials carried out on 2 consecutive days (consumption of 1985 fruits: $\bar{x} = 29.8$ fruits/feeder, $SD = 6.8$, $n = 8$ feeders; 1986 fruits: $\bar{x} = 28.1$, $SD = 6.5$, $n = 8$; t -test, $P = 0.63$).

Given a choice, birds preferred fresh (unfrozen) fruits to preserved fruits by a ratio of 2.6:1 for *L. benzoin* and 5.4:1 for *V. dentatum* in 32 h of feeding trials. When only preserved fruits were presented, the birds ate them at about the same rates as fresh fruits. Faced with both fresh and preserved *L. benzoin* fruits *ad libitum*, robins consumed an average of 7.4 fruits·bird⁻¹·h⁻¹ (6 h of trials) vs. 7.3 fruits·bird⁻¹·h⁻¹ of preserved fruits alone (3 h of trials) in a series of experiments performed in September 1985. During the same month they ate 15.0 fresh *V. dentatum* fruits·bird⁻¹·h⁻¹ presented alone (6 h of trials) vs. 13.5 fruits·bird⁻¹·h⁻¹ of fresh plus preserved fruits (12 h of trials) vs. 13.5 fruits·bird⁻¹·h⁻¹ of preserved fruits alone (6 h of trials). Thus, captive robins remained healthy and ate preserved and fresh fruits at similar rates, and preserved fruits did not change detectably in palatability over time.

Four types of feeding trials were performed to distinguish the changing-availability hypothesis from the changing-preference hypothesis: (1) *V. dentatum* fruits alone (*Vd* trials), (2) *V. dentatum* fruits with the laboratory diet (*Vd* + diet trials), (3) *L. benzoin* fruits alone (*Lb* trials), and (4) *L. benzoin* fruits with the laboratory diet (*Lb* + diet trials). I used two species of fruits to determine whether any seasonal pattern of fruit consumption that robins might have shown was a function of fruit species. Comparison of the results of fruit alone with fruit plus diet trials indicated birds' preference for fruits relative to the standard labora-

tory diet. Fruits were thawed to room temperature and presented *ad libitum* in petri dishes placed on the floor in circles with 5 dishes each. Experiments began between 0900 and 1000 and lasted 3 h. In the *Vd* and *Lb* trials all other food was removed at the beginning of the experiment and replaced at the end. *Vd* and *Lb* trials were repeated on a minimum of 3 consecutive days/month; monthly data points thus represent at least 54 bird-hours of feeding (6 birds × 3 h × 3 replicates). In the *Vd* trials each of 10 petri dishes contained 50 fruits; in the *Lb* trials each of 10 petri dishes contained 15 fruits (*L. benzoin* fruits contain about 4 times as much pulp by mass and 4 times the caloric content per fruit as *V. dentatum* fruits). The *Vd* + diet trials and *Lb* + diet trials were repeated at least 2 times/month and did not begin until January. Because birds ate relatively few fruits when the laboratory diet was also present (see below), only 5 dishes were presented, each with 50 (*Vd*) or 15 (*Lb*) fruits, to conserve fruits. Uneaten fruits were discarded at the end of all experiments.

In the *Vd* trials robins initially appeared to show a seasonal rhythm in fruit-consumption rates that paralleled fruit consumption in nature (Martin et al. 1951). Fall fruit consumption was high, rose to a peak of about 18 fruits·bird⁻¹·h⁻¹ in December, and fell rapidly in February (Fig. 1; cf. Wheelwright 1986: Fig. 1). Fruit-consumption rates fluctuated thereafter around 10 fruits·bird⁻¹·h⁻¹ through August, rather than diminishing from February until June or July as in nature. In September *V. dentatum* fruit-consumption rates again rose to over 15 fruits·bird⁻¹·h⁻¹. Fruit consumption was not significantly correlated with time from March through September (Spearman rank correlation, $P = 0.15$). In the *Lb* trials fruit consumption peaked in December and declined steeply in February, as in the field (Fig. 2; cf. Wheelwright 1986). Fruit-consumption rates then leveled off, but did not increase even by September (Spearman rank correlation, $P = 0.93$).

When simultaneously offered fruits and laboratory diets, robins always ate fewer fruits than when presented with fruits alone. The sole exception was the August trials involving *V. dentatum* (Figs. 1 and 2). The seasonal pattern of the *Lb* + diet trials resembled that of the *Lb* trials (Fig. 2). Of the four types of feeding trials, only the *Vd* + diet trials (and, to a lesser extent, the *Vd* trials) showed a basic seasonal pattern similar to the pattern in nature. Fruit-consumption rates increased steadily and significantly (although not sharply, as in the field) from April onward (Spearman rank correlation, $P < 0.001$; Fig. 1).

These experiments demonstrate circannual changes in fruit consumption by captive American Robins even when food quality and availability were held constant. Temporal changes in fruit preference were shown in two different fruit species (as well as a third species, *Viburnum opulus*; Jones and Wheelwright 1987). In at least one fruit species (*V. dentatum*), the seasonal change in diet roughly paralleled shifts in nature, which gives some credence to the changing-preference hypothesis.

The reduced magnitude and the inconsistency of seasonal shifts under constant laboratory conditions relative to the field suggest that seasonal changes in diet in nature are influenced by both food availability and preference, including photoperiodically induced or possibly endogenous annual rhythms in behavior, morphology, or physiology. Even though a close match between the behavior of fruit-eating birds and the natural seasonal availability of fruits might be predicted as a result of general coevolution with fruiting plants, the match seems weak.

In captivity the birds in these experiments were not subject to the special nutritional demands of migration or reproduction (e.g. egg production or territorial defense). This may have minimized their need for protein during the feeding season (April through July) and enabled them to eat more fruits than they would in nature. Furthermore, the robins' standard laboratory diet may have had a long-term effect on their digestive morphology and physiology, and subsequently on their diet preferences. The guts of Red Grouse (*Lagopus lagopus scoticus*), for example, shrink when fed a rich artificial diet in captivity (Moss 1972). Efficient digestion of fruits apparently requires relatively longer guts in passerines (Al-Joborae in Sibly 1981). This may explain why fruit consumption did not dramatically increase in August and September. To avoid these problems, future studies should be longer and begin in the spring rather than the fall (E. Morton pers. comm.). If possible, birds should be maintained on a natural diet of fruits and invertebrates between experiments. Finally, the possibility of circannual changes in gut morphology or physiology (cf. Al-Joborae in Sibly 1981) should be explored. Such changes would have the effect of reordering the profitabilities of different foods for birds and complicating the interpretation of foraging studies conducted at different times of the year.

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On the Danger of Using Dummy Nests to Study Predation

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Because the nests of ground-nesting birds are often hard to find, dummy nests were used in many early studies of egg predation (e.g. Balser et al. 1968, Chessness et al. 1968, Henry 1969, Jones and Hungerford 1972). Predation on dummy nests is different from natural waterfowl nests (Dwernychuk and Boag 1972), and dummy nests often are used without verifying that the results are similar for natural nests (e.g. Göransson and Loman 1982, Andrén et al. 1985, Angelstam 1986, Müller 1986, Sugden and Beyersbergen 1986).

Storaas (1988) showed that predation on dummy nests differed from that on real nests of Common Capercaillie (*Tetrao urogallus*) and suggested that dummy nests were more vulnerable than natural nests to visual predators. We found that predation on dummy nests was an unreliable index of predation on natural nests of Eurasian Black-Grouse (*Tetrao tetrix*) and used radio-tagged eggs to show that dummy nests were robbed mainly by birds, whereas natural nests attracted more mammalian predators.

In 1984-1987 natural black-grouse nests were found by radio-tagging 18-25 hens before or during the mating period each year in a 32-km² study area (61°N, 16°E). Dummy nests, each with 5 or 6 eggs, were established 20-100 m from forest roads in a similar way each year. Fifty dummy nests were laid out each year from 1984 to 1986, and 25 were used in 1987. Pheasant eggs were used in 1984 and similar-colored chicken eggs in the other years. Nests were placed in sites that resembled natural nest sites as nearly as possible, were exposed for 20-24 days, and were revisited on the last day of exposure. The comparison of natural and dummy nests was confined to hens that either hatched eggs or had their nests disturbed during the exposure period. This was the period when most natural egg predation took place.

Radio-tagged eggs were prepared by carefully cutting a 10-15-mm-wide cap from the blunt end of the egg and removing the fluid content. After the transmitter (Biotrack, U.K.) was inserted, the egg was filled with paraffin and sealed with the removed cap. In 1985-1987, 1 radio-tagged egg was placed in 12-20 natural nests each year and checked daily by recording its position. In 1987, 1 radio-tagged egg was placed

in each of the 25 dummy nests and checked 5 times during exposure.

When radio-tagged eggs were found within 10 m of robbed nests, bite marks or beak marks could always be used to distinguish between mammal and bird predation. All of the 25 eggs taken farther away were cached by the predator. Fifteen had been covered with earth in a way typical for mammals; 5 of these eggs had bite marks or were from nests where the hen had been killed by a mammal, and 10 eggs were without marks. Of 10 eggs hidden in the vegetative layer of the ground and covered by grass and debris, 3 had beak marks. Because none of the other 7 eggs had bite marks, we assumed that they too had been taken by birds.

About 50% of natural nests were subject to predation each year (Table 1), with no significant between-year differences (Chi-square, $P > 0.25$, two-tailed). Predation on dummy nests was significantly higher in 1986 and 1987 than in 1984 and 1985 (Chi-square, $P < 0.005$, two-tailed). In 1984-1985 predation on natural nests significantly exceeded that on dummy nests (Chi-square, $P < 0.01$, two-tailed). Predation on both natural and dummy nests was similar in 1986 and 1987, however, because of the increase in predation on dummy nests without a similar increase on natural nests.

In 1987 dummy nests were robbed mainly by birds (2 taken by mammals, 9 by birds). The natural nests attracted mainly mammalian predators (8 by mammals, 1 by birds) (Fisher exact, $P < 0.02$, two-tailed). The predator that destroyed 2 dummy nests was not identified because the radios failed. Mammals were also important predators on natural nests with radio-tagged eggs in 1985 (4 by mammals, 2 by birds) and 1986 (4 by mammals, 3 by birds).

Previous studies have stressed the importance of bird predation on dummy nests. Andrén et al. (1985) reported that predation on dummy nests was correlated with corvid abundance, and Angelstam (1986) found that dummy nests, set on boards smeared with grease to identify predators, were destroyed mainly by birds. Correlations between predation and nest cover have also suggested that birds are important predators on dummy nests (e.g. Jones and Hunger-