

FORAGING EFFICIENCY OF PARENT JUNCOS AND THEIR YOUNG¹

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Abstract. From measurements of metabolizable energy (ME) intake (doubly labeled water technique), prey capture rates, and time spent foraging, we calculated both foraging efficiency (FE) and rate of energy gained while foraging (\dot{E}_r) of adult Yellow-eyed Juncos (*Junco phaeonotus*) and their offspring throughout the breeding season. \dot{E}_r (kJ ME acquired per hr spent foraging) of adult Yellow-eyed Juncos varied 1.7 fold over the breeding cycle, as adults adjusted both the amount of time they spent foraging and their FE to meet changing energy demands and time constraints. Males paired to incubating females, and males and females feeding fledglings acquired energy at substantially lower rates (ca. 15–17 kJ/hr) than incubating females (26 kJ/hr) or than males and females feeding nestlings (21 kJ/hr). From this, we infer that adult juncos may reduce their FE when energy demands and/or time constraints are relaxed, either because the costs of inefficient foraging are negligible during these periods or because there are hidden costs or risks associated with foraging more efficiently. \dot{E}_r of juvenile juncos increased 2.1 fold from a low of 5.3 kJ/hr during their first week of parental independence (a period of marked juvenile mortality due to starvation) to 10.9 kJ/hr (about 75% of the lowest adult level) by six-weeks post-independence. Juvenile FE increased linearly with age as the young gained proficiency at foraging. By extrapolation, juvenile FE would not have reached adult levels until the young were about four months old.

Key words: Energetics; foraging efficiency; doubly labeled water; survivorship; breeding; parents; offspring.

INTRODUCTION

The widespread interest in foraging efficiency (FE) among behavioral ecologists stems partly from their desire to understand how organisms are designed for survival (Williams 1966, Stephens and Krebs 1986), their recognition of the considerable time that many animals devote to foraging (Krebs and McCleery 1984) and their cognizance that the various measures of FE (prey capture rate, rate of energy intake, net foraging efficiency, etc.) are usually easier to study than is reproductive success. Whereas numerous studies of diverse organisms have quantified foraging efficiency or proficiency and tested predictions from optimal foraging theory (see review by Pyke 1984), few have examined FE at more than one stage in an animal's life cycle. Accordingly, it is unclear: 1) whether animals always forage as efficiently as possible, given the constraints imposed by the need to avoid predators and reproduce, or whether they adjust their FE to changing

energy demands and time constraints, and 2) when individual differences in FE are most likely to affect survivorship or reproduction. To better understand selection on efficient foraging, we quantified FE among adult Yellow-eyed Juncos (*Junco phaeonotus*) over the breeding season and among their dependent fledglings and independent juveniles.

In our prior studies (Sullivan 1988a, 1988b, 1989, 1990; Weathers and Sullivan 1989a, 1989b, 1991), we measured (among other things) the allocation of time and energy by adult Yellow-eyed Juncos and their young (nestlings, fledglings, independent juveniles) throughout the breeding season using concurrent time-activity budgets and the doubly labeled water (DLW) technique. We examined diet selectivity among parents and their young, and quantified prey capture rates of select age classes. We found that adult juncos feeding young were neither food limited nor working maximally. Adults fulfilled their own energy demands, and those of their dependent young, while foraging for 75% or less of the daylight hours. In contrast, recently independent young, four to seven weeks after fledg-

¹ Received 31 July 1990. Final acceptance 26 November 1990.

ing, had to forage for over 90% of the daylight hours just to meet their own energy demands. Juncos younger than this could not attain energy balance in a 15-hr day, without supplemental feeding by their parents, even if they foraged continuously.

Our data suggested that if energy constraints are a major selective force in Yellow-eyed Juncos, they operate not through food limitation among adults but rather through the inefficient foraging of young juncos. In this paper, we employ our previous data together with new data on prey capture rates of additional age classes to examine further the foraging efficiency of adult juncos and their young.

METHODS AND ANALYSES

STUDY SPECIES

Yellow-eyed Juncos (*Junco phaeonotus*) are small (ca. 19 g), monogamous passerine birds. They maintain all-purpose breeding territories and have bi-parental care of the young (Moore 1972). At our study site in Arizona's Chiricahua Mountains, they begin nesting in late April and continue until late August, with pairs producing up to three successful clutches in a single season (for details, see Sullivan 1988a). Juncos conceal their nests on the ground, and females carry out all of the nest building, incubation, and brooding activities. Most nests contain three or four nestlings (Sullivan 1989) and both males and females feed the nestlings and fledglings. Insects are the primary food source of both young and adult juncos during the breeding season.

After fledging, immature juncos spend 22–28 days with one or both parents in a family flock. During this period the parents supplement the foraging efforts of their young. At the end of the 22- to 28-day fledgling period, the young juncos are evicted from the family territory. They then join juvenile flocks and remain in the general area for the rest of the breeding season. Thus the term fledgling denotes an immature junco that is still being fed by its parents, whereas the term juvenile is reserved for independent young no longer receiving parental care. We assigned immature juncos to age categories based on the time which had elapsed since fledging. The category 1-week fledgling thus denotes young during their first week out of the nest, 2-week fledgling, birds during their second week out of the nest, etc. For adults, the designations 1-week, 2-week, and

3-week denote adults feeding 1-week stage fledglings, etc. For further details see Weathers and Sullivan (1989a).

TERMS AND CONCEPTS

Foraging efficiency (FE) is a somewhat nebulous term, owing to the variety of ways in which it has been defined. We employed two of the term's more meaningful variants: net foraging efficiency (FE_n), as defined by Eq. 2; and the rate of energy gain (\dot{E}_p), which in our study is metabolized (=metabolizable) energy (ME) acquired per hour spent foraging. Although seemingly similar, these two measures of FE convey different information and permit different comparisons.

Brody (1945) recognized three categories of work efficiency, two of which can be applied by analogy to foraging:

Gross efficiency

$$= \frac{\text{energy gained while foraging}}{\text{total energy expended while foraging}} \quad (1)$$

Net efficiency

$$= \frac{\text{energy gained while foraging}}{\text{net energy cost of foraging}} \quad (2)$$

where the net energy cost of foraging (Eq. 2) is an animal's rate of energy expenditure while foraging minus its resting energy expenditure. Net efficiency (Eq. 2) was called "required foraging efficiency" by Wolf et al. (1975) and was used by Mugaas and King (1981) to examine seasonal changes in foraging of Black-billed Magpies (*Pica pica*). Efficiency, a dimensionless number, expresses the relative return on foraging effort. An efficiency of 10 signifies that the animal obtains 10 energy units for each energy unit spent foraging. A major advantage of net efficiency over other measures of foraging prowess, such as energy gained per unit time, is that one can compare directly the net efficiencies of different species. A disadvantage is that the net energy cost of foraging is often difficult to determine directly.

Determining either gross efficiency or net efficiency requires knowledge of the energy gained through foraging. This can represent either ingested food energy or metabolized energy (ME). Physiologically, animals eat to meet their ME demand. Hence FE calculated from ME provides an entirely satisfactory basis for comparing the physiologic performance of individuals.

ME of free-ranging animals can be measured

TABLE 1. Prey capture rate and energy content.

Age/stage ^a	Capture rate ^b insects/hr	Energy content ^c J/insect
Adults		
INC	240 ± 29.6 (11)	68
1 wk	251 ± 35.7 (12)	63
2 wk	254 ± 20.3 (19)	76
3 wk	320 ± 19.2 (24)	46
Immatures		
1 wk (3.1 ± 0.3)	3 ± 3.8 (31)	—
2 wk (11.3 ± 0.4)	83 ± 8.2 (39)	11
3 wk (20.9 ± 0.8)	180 ± 19.3 (21)	12
Juv. (41.8 ± 3.4)	222 ± 25.5 (16)	24

^a For adults: INC = incubating females and males paired to incubating females; Nestling = adults feeding nestlings; 1 wk, 2 wk and 3 wk = adults feeding, respectively, 1-wk old fledglings, 2-wk old fledglings, and 3-wk old fledglings. For immatures: 1 wk = fledglings during the first week out of the nest, etc. Mean days age ± SE in parentheses.

^b Mean feeding rate ± SE; number of 5-min observation periods in parentheses.

^c Metabolized energy content of the average-sized insect eaten, determined by bomb calorimetry.

using the doubly labeled water (DLW) technique (Nagy 1983). In the absence of production, field metabolic rate (FMR) measured by DLW equals the total metabolized energy (TME). If production occurs during the DLW measurement period, the productive energy must be added to ME measured by DLW to yield TME. In the broadest sense, productive energy can include egg formation, growth or molt, fat accumulation, food storage, or food provided to dependent young or mates.

Ecologically, an animal's impact on lower trophic levels is proportional to the amount of food energy ingested. Hence, for some ecological studies it may be desirable to calculate FE based on food energy intake. Food energy intake of a free-living animal can be calculated from DLW measurements of CO₂ production provided: 1) the diet is known, 2) assimilation efficiency is known, and 3) one accounts for production or net utilization of body substance during the measurement period. Alternatively, food intake can be calculated from water flux, as measured by DLW, provided the water content of the food is known (Nagy 1975). Food energy intake can also be estimated from observations of feeding rate, provided prey size and energy content are known. Although both the DLW and food intake methods involve uncertainty, reasonable agreement between the two has been obtained with some species (Masman et al. 1988). We employ both methods in this study.

TABLE 2. Size of insects captured by fledgling juncos relative to their bill length.

Insect size	No. insects eaten (%)	
	2-wk old fledglings	3-wk old fledglings
Tiny	32 (46.4)	48 (52.2)
1/3 bill + small	27 (39.1)	31 (33.7)
1/2 bill	6 (8.7)	5 (5.4)
2/3 bill	0 (0)	1 (1.1)
1 bill	4 (5.8)	7 (7.6)
Total	69 (100)	92 (100)

PREY CAPTURE AND ENERGY CONTENT

We determined the prey capture rate of adult and young juncos from the number of insects consumed by focal individuals during 5-min observation periods (Table 1). We estimated the size of prey consumed by 2-week and 3-week old fledglings relative to the length of their bills, and assigned insects of one of five different size-classes (Table 2). We determined the gross energy content of 1-g samples of five additional size-classes (tiny, 1/4 bill, 1/2 bill, 1 bill, and 2 bill) by bomb calorimetry. Gross energy content (kJ/g dry insect) was not significantly correlated with insect size ($r^2 = 0.01$), and we used the mean (\pm SD) value (23 ± 1.3 kJ/g dry insect) in our calculations. We determined the average mass of dried insects in the original five size-classes and calculated the gross energy content per insect based on the above mean energy content per gram dry insect (Table 3).

FORAGING EFFICIENCY CALCULATION

We lack the data required to calculate the foraging efficiency of individual birds. Accordingly our calculations employ average values for time spent foraging and energy intake of the different

TABLE 3. Gross energy content of insect prey.

Prey size ^a	n ^b	Mass, ^c mg/insect	Energy content, ^d J/insect
Tiny	901	0.21	4.8
Small	942	0.43	9.9
1/3 bill	1,081	0.45	10.4
1/2 bill	664	1.05	24.2
2/3 bill	57	2.47	56.8
1 bill	261	4.70	108.1

^a Relative to fledgling bill length.

^b Number of insects sampled.

^c Mean dry mass of insects in this size class, determined from mass of n insects.

^d Gross energy content = 23 J/mg dry insect \times insect mass.

TABLE 4. Energy acquired by adult juncos and their dependent young. All energy values are kJ/day metabolizable energy.

Stage	Adult FMR ^a	Immature FMR	Brood size ^b	Brood energy demand ^c	Energy brood supplies ^d	Energy adult supplies ^e	Total energy adult acquires ^f
Nestling	74 (13)	53 (13)	1.8	92	0	92	166
Fledgling							
1 wk	75 (11)	60 (11)	1.7	102	0.1	102	177
2 wk	75 (6)	68 (10)	2.2	150	14	136	211
3 wk	79 (8)	74 (11)	1.6	118	42	76	155

^a FMR = field metabolic rate as measured with doubly labeled water, sample size in parentheses (Weathers and Sullivan 1989a).

^b Number of young fed per adult.

^c Immature's FMR times brood size.

^d Energy brood gains due to the immature juncos' own foraging efforts (see text).

^e Brood energy demand minus energy brood supplies.

^f Sum of adult's FMR and energy adult supplies to the brood.

aged juncos that we studied. Because ratios of averages are subject to greater uncertainty than individual measurements, we have not analyzed our data statistically. Despite this limitation, we feel that the patterns exhibited by our "average" juncos are quite revealing.

We calculated foraging efficiency both as net foraging efficiency (FE_n , Eq. 2), and as the rate of ME gain while foraging (\dot{E}_f , kJ ME acquired/hour spent foraging). The numerator of Eq. 2 (energy gained while foraging) was determined from our DLW measurements of FMR (Weathers and Sullivan 1989a), subject to the adjustments described below for young being fed by parents and for parents feeding young. The net energy cost of foraging was calculated as $0.0636 \text{ kJ g}^{-1} \text{ hr}^{-1}$ (the unit cost of foraging, Weathers and Sullivan 1989a) times the bird's mean body mass times the hr/day that the bird spent foraging (for data see Weathers and Sullivan 1989a).

For birds in energy balance (juveniles and incubation stage adults), the rate of energy gain while foraging (kJ/hr) is equal to their FMR (kJ/day) divided by the hr/day spent foraging. Although 10- to 12-week old juveniles were molting, they did not exhibit a net accumulation of new tissue during the DLW measurements, as evidenced by their lack of change in body mass during the DLW measurements (mean mass change = $-0.42 \pm 3.28 \text{ g}$; range -5.31 to 5.63 g). Molt did increase the juveniles' FMR (Weathers and Sullivan 1989a), but the bulk of the increase was due to increased heat loss. Consequently, the DLW method accurately gauged this age group's total ME. Some birds were not in energy balance, despite being in mass balance, either because they obtained less ME through foraging than required to meet their FMR (i.e.,

nestlings and fledglings being fed by their parents), or because they acquired more ME by foraging than required to meet their FMR (i.e., adults feeding young). Calculating the foraging efficiency of these two groups involves accounting for the auxiliary ME.

BROOD ENERGY DEMAND

The ME obtained by each adult of a pair feeding dependent young (nestlings or fledglings) equals their own FMR plus one half of the brood's ME demand (males and females provision their young equally, Sullivan 1988a). The brood's ME demand in turn depends upon the age and number of young being fed (brood size), and the extent to which the young forage on their own. Using data in Tables 1-3 and 5, we can calculate how much energy adults supply to their broods (Table 4). We based our calculations of brood energy demand on the number of young actually fed by the adults whose FMR we determined by DLW, rather than on the mean brood size for the different age classes, because some males fed nestlings by themselves.

Nestling energy demand varies with nestling size; increasing from about 2 kJ/day on the day of hatching to a plateau of 54 kJ/day by the time nestlings weigh about 17 g (day 9) (Weathers and Sullivan 1991). The nestling stage adults whose FMR we determined by DLW were feeding nestlings with an average mass of $14.5 \pm 2.0 \text{ g}$ ($n = 24$; mean \pm SD). The ME of nestlings this size averages 51 kJ/day (Weathers and Sullivan 1991), which represents the sum of their FMR (about 38 kJ/day) and the energy accumulated as new tissue (growth). The adult pairs that we measured with DLW fed broods that averaged 3.6 nestlings. Hence, each parent had to acquire an

TABLE 5. Foraging efficiency of adult and immature juncos.

Age/stage ^a	Energy acquired ^b kJ/day	Foraging			
		Time ^c hr/day	Cost ^d kJ/day	Efficiency	
				FE _n ^e	E _r , kJ/hr
Adults					
INC. ♂	71	4.7 (72)	5.8	12.2	15.1
INC. ♀	67	2.6 (18)	3.3	20.3	25.8
Nestling	166	8.0 (149)	9.7	17.1	20.8
1 wk	177	11.2 (89)	14.6	12.1	15.8
2 wk	211	10.9 (81)	13.6	15.5	19.4
3 wk	155	10.2 (69)	12.6	12.3	15.2
Fledglings					
1 wk	0.1	1.2 (70)	1.5	0.1	0.1
2 wk	6.6	7.2 (75)	8.8	0.8	0.9
3 wk	26	12.0 (84)	14.3	1.8	2.2
Juveniles					
4-5 wk	73	13.7 (73)	16.6	4.4	5.3
6-7 wk	93	13.9 (69)	17.5	5.3	6.7
10-12 wk	100	9.2 (70)	12.6	7.9	10.9

^a For explanation of symbols, see Table 1 footnote.

^b Metabolizable energy acquired through foraging. From Table 4 for nonincubating adults.

^c Hours foraging/day based on the number of 15-min observation periods indicated in parentheses (Sullivan 1990).

^d Calculated as: $(63.6 \text{ J g}^{-1} \text{ hr}^{-1}) \times \text{mass} \times \text{hr spent foraging per day} \times 0.001 \text{ J/kJ}$; where the first term is the unit cost of foraging.

^e FE_n = net foraging efficiency calculated as energy acquired through foraging divided by net cost of foraging.

^f E_r = energy acquired through foraging (kJ/day) divided by foraging time (hr/day).

amount of ME equal to the demand of 1.8 nestlings ($1.8 \times 51 \text{ kJ/day} = 92 \text{ kJ/day}$) plus their own FMR of 74 kJ/day, or a total of 166 kJ/day of acquired ME (Table 4).

Determining how much energy adults supply to their fledglings is complicated because fledglings obtain some energy through their own foraging efforts. Initially the amount of this energy is very small, but as fledglings age and become more proficient at foraging it increases. We estimated the energy fledglings gathered on their own by observing their prey capture rates (Table 1) and calculating the prey's energy content (Table 3) as follows. To calculate gross energy of the average-sized insect eaten by fledglings, we multiplied the number of prey eaten per size class (Table 2) by the energy content of that size prey (Table 3), summed the products, and divided by the total number of prey eaten (Table 2). By this calculation, 2-week old fledglings and 3-week old fledglings consumed insects containing on average 14.6 and 16.1 J gross energy per insect, respectively. Assuming a metabolizable energy coefficient of ca. 77% for an insect diet (Levey and Karasov 1989; Karasov, in press), the fledglings would have obtained, respectively, about 11 and 12 J ME per insect consumed (Table 1).

Two-week old fledglings captured an average

of 83 insects per hour spent foraging (Table 1) and foraged for 7.2 hr/day (Table 5). Thus they obtained a total of 6.6 kJ/day from their own foraging efforts ($83 \text{ insects/hr} \times 11 \text{ J/insect} \times 7.2 \text{ hr/day} \times 0.001 \text{ kJ/J}$). This represents about 10% of their daily requirement of 68 kJ ME (Table 4). The remaining 61.4 kJ must have been supplied by their parents. On average, each adult fed 2.2 2-week old fledglings, for a total brood demand of 136 kJ/parent per day ($61.4 \text{ kJ/fledgling} \times 2.2 \text{ fledglings/parent}$) (Table 4). Brood energy demand calculated in this manner increased from a minimum of 92 kJ/day for nestlings, through a maximum of 136 kJ/day for 2-week old fledglings and declined to 76 kJ/day for 3-week old fledglings (Table 4).

DISCUSSION

FORAGING EFFICIENCY OF IMMATURE JUNCOS

The foraging efficiency (FE) of immature juncos improves with age and appears to be a major factor in both age-specific survivorship and breeding season phenology. FE of fledglings during their first week out of the nest is essentially nil (Table 5). Fledglings this age capture an average of only 3 insects per hour, spent foraging (Table 1) and forage for only 1.2 hr/day (Table

5); both statistics reflect their primitive stage of development. In many respects, 1-week stage fledglings are functionally still nestlings—they have left the nest, but cannot fly and their coordination has not matured enough to permit effective prey capture.

Although FE increases as fledglings age (Fig. 1), it remains very low compared with that of adults (Table 5). The fact that juvenile juncos are poor foragers, despite strong selection for efficient foraging at this stage, implies some type of “constraint” on maximization of FE by juveniles. This constraint is the time needed to learn how to capture and handle prey with proficiency (Sullivan 1988b), and young juncos require four months of experience before their foraging proficiency reaches adult levels (Fig. 1, by extrapolation). As in the Spotted Flycatcher (*Muscicapa striata*) (Davies 1976), Reed Warbler (*Acrocephalus scirpaceus*) (Davies and Green 1976), and White-winged Chough (*Corcorax melanorhamphos*) (Heinshon, in press), fledgling FE is a major factor determining the length of parental care and the number of broods that can be successfully reared each year.

The first few weeks of independence from their parents is a critical period in the life of a Yellow-eyed Junco. During this period, an individual's FE may determine whether it survives to reproduce or perishes as an adolescent. FE of juveniles during their first week of independence from parental care (i.e., 4–5 week age) is only one-third to one-fifth that of their parents (Fig. 1, Table 5). These recently independent juveniles capture nearly the same number of insects per unit time as their parents (Table 1), but because they take smaller prey they spend a greater proportion of their time searching for and handling food items than the adults (Sullivan 1988a). Consequently they incur greater energy costs for each prey item obtained, with correspondingly diminished FE.

The consequences of inefficient foraging are severe for juvenile juncos. Whereas only 8.4% of adult juncos die during the breeding season (daily mortality rate = 0.11%, Sullivan 1989), 46.3% of independent juveniles die during their first two weeks of independence (daily mortality rate = 3.85%, Sullivan 1989). Adults meet their own daily energy demands while foraging for only 28.2% of the daylight hours (Sullivan 1990). Furthermore, they maintain their body mass over the breeding season and do not face time and energy constraints when afternoon storms lim-

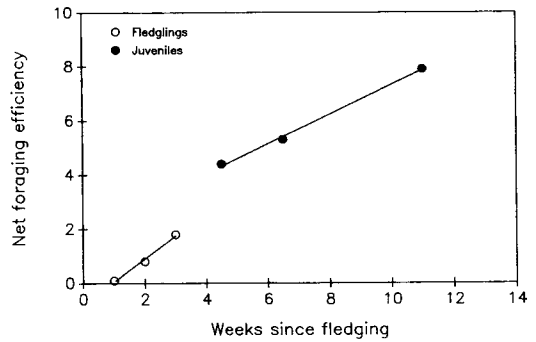


FIGURE 1. Net foraging efficiency of immature juncos as a function of time since fledging. Mean times used for 4–5 week, 6–7 week, and 10–12 week fledglings.

it the time available for foraging (Sullivan 1990). In striking contrast, recently independent juveniles forage for almost all of the daylight hours (>90%) and still often fail to achieve energy balance (Sullivan 1990, Weathers and Sullivan 1989a). All juveniles lose mass during their first two weeks of independence, and the decrease in body mass is a significant predictor of survival to the end of the breeding season (Sullivan 1989).

During the first few weeks of independence young juncos must quickly gain proficiency at foraging or die. Juveniles that survive their first month of independence have shorter handling times (especially for large prey items) and incorporate more large prey into their diet than do recently independent juveniles (Sullivan 1988b). Compared with younger independent juveniles, these older juveniles are twice as efficient at foraging (Table 5), spend fewer hours foraging, and most importantly have much higher survivorship (daily mortality rate = 0.55%, Sullivan 1989).

ADULT FORAGING EFFICIENCY

Because incubation stage adults were in energy balance (no net mass change, no ME allocated to young), they acquired an amount of energy while foraging equal to their FMR requirement, which averaged 71 kJ/day for males and 67 kJ/day for females (Table 5). Although the FMR of incubation stage males and females was similar, the time that they devoted to foraging was vastly different (4.7 vs. 2.6 hr/day) (Table 5). As a consequence, incubating females had a much higher FE_n than their mates (20.3 vs. 12.2) (Table 5). The high FE_n exhibited by incubating females reflects their time constraints. Female juncos car-

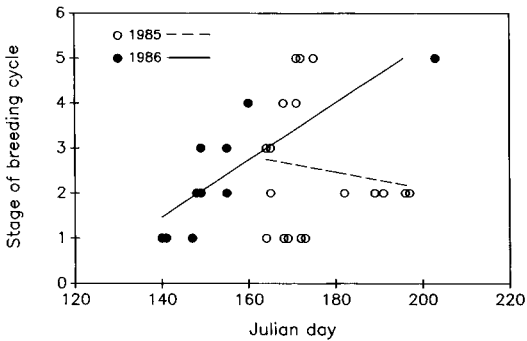


FIGURE 2. Relation between the date that an adult's field metabolic rate was measured by doubly labeled water and stage of the breeding cycle (1 = incubation, 2 = feeding nestlings, 3 = feeding 1-week old fledglings, 4 = feeding 2-week old fledglings, 5 = feeding 3-week old fledglings). Lines were fitted to the 1985 ($n = 31$) and 1986 ($n = 20$) data by the method of least squares.

ry out all of the incubation and brooding activities (males lack brood patches). Because male juncos rarely feed their mates, incubating females must periodically leave the nest to forage. In the juncos' montane environment, eggs cool rapidly during "off-bouts" and this factor effectively limits foraging bout length (Weathers and Sullivan 1989b). How incubating females are able to increase their FE in the face of intense time constraints is unknown, yet intriguing. Presumably, the FE of incubating females represents the maximum that juncos can attain. If so, our data reveal that other breeding stage adults typically do not maximize their FE.

E_r of adults varied 1.7 fold over the breeding cycle (Table 5). Males paired to incubating females, and males and females feeding fledglings acquired energy at substantially lower rates (ca. 15 kJ/hr) than incubating females (26 kJ/hr) or males and females feeding nestlings (21 kJ/hr). Although FE_n of parents feeding fledglings was lower than that of adults feeding nestlings, it varied slightly depending upon the fledgling's age because of variations in the brood size of the different age classes. Overall, FE_n of adults feeding fledglings averaged 13.3, which is roughly equivalent to that of incubation stage males that foraged to meet only their own energy needs.

We discount the possibility that seasonal changes in prey availability underlie the differences in adult foraging efficiency. Such was clearly not the case for incubation stage males and females, for whom DLW measurements were

made at the same time of year. For other breeding stages, DLW measurements varied temporally. Breeding stage and date that adult FMR was measured were significantly correlated in 1986 ($r = 0.838$, $P < 0.01$, $n = 20$), but not in 1985 ($r = 0.100$, $P > 0.05$, $n = 31$) (Fig. 2). Although seasonal changes in prey availability might thus have affected the 1986 FE data (but not the 1985 data), we found no correlation between FE and breeding stage for the 1986 data, as would have been expected if seasonal changes in prey availability were responsible for the observed changes in adult FE.

INFERENCES

A basic tenet of optimal foraging theory holds that fitness is a function of FE (Schoener 1971, Pyke et al. 1977, Krebs 1978). Animals that maximize their net energy gain when foraging should produce more surviving offspring on average than less efficient individuals, because less efficient individuals will either accumulate less energy for growth and reproduction or spend more time foraging. Implicit in this stagement is the idea that animals should always forage as efficiently as possible given the constraints imposed upon them by the need to avoid predators (Holmes 1984, Lima 1987), meet nutritional demands (Belovsky 1981), defend territories and mates, and provide parental care. Adult Yellow-eyed Juncos adjust both the amount of time they spend foraging and their FE to meet their changing energy demands and time constraints during the breeding cycle. From this, we infer that animals may reduce their FE when energy demands and time constraints are relaxed, either because the costs of inefficient foraging are negligible during these periods or because there are hidden costs or risks associated with foraging more efficiently.

ACKNOWLEDGMENTS

Many individuals and organizations contributed to the studies upon which this paper is based. Most are acknowledged in our publications cited below. In addition to them, D. Anderson and D. Spiller provided useful comments on this manuscript and Barbara Askröba did the bomb calorimetry determinations.

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