PARENTAL EXPENDITURE OF TIME AND ENERGY IN THE ABERT'S TOWHEE (*PIPILO ABERTI*)

DEBORAH M. FINCH

Rocky Mountain Forest and Range Experiment Station, 222 South 22nd Street, Laramie, Wyoming 82070 USA

ABSTRACT.—Daily activity budgets of male and female Abert's Towhees (*Pipilo aberti*) were measured in 1980 during the reproductive cycle and then converted into energy budgets to determine the relative demands of different nesting phases. Mean daily energy expenditures (DEE_{tot}) in males reached a seasonal maximum of 126.7 kJ, or 2.16 times basal metabolic rate (*BMR*), in the prenesting phase. Thermoregulatory demands accounted for higher energy expenses in this phase. The cost for females was also high in the prenesting phase but was exceeded by DEE_{tot} in the egg-laying phase. Average DEE_{tot} was at a seasonal minimum of 103.8 kJ, or 1.8 times *BMR*, in incubating females. Females conserved energy in the incubation phase by minimizing activity, and 78% of the variation of DEE_{tot} in individual females was explained by mean daily air temperature. Activity costs (DEE_{act}) differed significantly between males and females during the incubation phase, but DEE_{tot} did not. Mean DEE_{act} and DEE_{tot} were significantly greater in females during the nestling period than during incubation. DEE_{act} explained 58% of the individual variation in female DEE_{tot} in the nestling phase, whereas air temperature explained only 28% of the variation. Interphasic variation in DEE_{act} was wider in females than males, because females closely tracked offspring requirements by attending at the nest. Males did not incubate or brood, and spare time spent "loafing" tended to minimize DEE_{act}. Excluding the egg-laying female, estimates of DEE_{tot} in individual towhees ranged from 1.6 to 2.18 times *BMR* and compare well with estimates of DEE_{tot} in the Northern Mockingbird (*Mimus polyglottos*), which is about the same size. *Received 5 August 1983, accepted 12 January 1984.*

CURRENT theory holds that parental investment patterns optimize the costs and benefits to the parents of raising one or more offspring (Trivers 1972, Goodman 1974, Pianka 1976, Wittenberger 1982). Efforts apportioned to survival and production depend on the availability of two resources: time and energy (King 1974). The availability of energy is dependent on its measured abundance and on the availability of time needed to acquire it. Intraspecific variation in parental expenditure of time and energy reflects not only environmental variation in resources, interspecific interactions, weather and climate, and day length, but also variation in sexes, phases of the breeding cycle, brood size, nestling age, and individual foraging skill.

Studies of flycatchers indicate that, despite numerous potential sources of variation, daily energy expenditure in activity remains quite stable through the reproductive cycle and that the obligatory costs of thermoregulation account for much of the variation in total energy expenditure (Walsberg 1977, 1978; Ettinger and King 1980). Perching, which comprises a large proportion of the daily activity of these sit-and-wait predators, conserves energy and stabilizes daily energy expenditure (Ettinger and King 1980). In contrast, thermoregulatory demands did not exceed basal level in the Purple Martin (*Progne subis*; Utter and LeFebvre 1970) and Common House-Martin (*Delichon urbica*; Hails and Bryant 1979), two species that spend much of the daytime on the wing; yet D_2O^{18} estimates of daily energy expenditure ranged from 2.3 to 3.7 times basal metabolic rate (*BMR*) in the Purple Martin and from 2.22 to 5.27 times *BMR* in the Common House-Martin. Activity costs for birds that forage on the ground also vary widely (e.g. Northern Mockingbird, *Mimus polyglottos*; Utter 1971, Biedenweg 1983). Mugaas and King (1981) showed that thermoregulatory demands were 5% or less of the daily energy expenditure of the Black-billed Magpie (*Pica pica hudsonia*), and that the cost of activity accounted for most of the considerable variation in the magpie's annual and reproductive cycles.

This study was undertaken to determine whether or not obligatory and activity costs caused variation in the reproductive energetics of the Abert's Towhee (*Pipilo aberti*), a nonmigratory, ground-foraging bird. This species is endemic to the Southwest and restricted in distribution to desert riparian habitats. To deter-

mine the obligatory and activity costs of this towhee, I timed its breeding activities in the lower Colorado River Valley. On my study site, predation and brood parasitism severely reduced reproductive success (Finch 1982, 1983a), and thermal stress was possible because of low air temperatures at the onset of reproduction in March and high temperatures in June and July (Finch 1983b). I asked the following questions: (1) Do males and females expend different amounts of energy during different breeding phases? (2) Does either sex show any variation in energy expenditure during the reproductive cycle? (3) If variation occurs, what is the source? (I tested for variation in activity and thermoregulatory demands.) (4) What similarities are there, if any, between patterns of energy expenditure in Abert's Towhees and those of other ground-foraging birds?

METHODS

The activity of the Abert's Towhee was studied in honey mesquite (*Prosopis glandulosa*) habitat along the lower Colorado River about 10 km north of Ehrenberg, Yuma County, Arizona, from March to July 1980. In the spring of 1980, 14 towhees were captured in mist nets and banded with U.S. Fish and Wildlife Service aluminum bands and colored bands. Five adults that I had banded the previous year were also present in the breeding population. The sex of each individual was determined by the presence of an incubation patch or by subsequent behavior. Body weights of towhees, measured on a Pesola Scale, averaged 46.8 g ($n = 13$), the same weight Dawson (1954) obtained for this towhee. Body weights of males and females were similar and assumed to be equal.

A panel of stopwatches was used to quantify the duration of four activities: perching, ground foraging, flying, and nest attendance. These data were transformed into percentages of the observation periods and the activity day. The mean percentage of the daily activity period ($\pm$ SE) spent in each activity was then calculated for both males and females in each phase of the reproductive cycle: prenesting, egg-laying, incubation, hatching, and nestling periods. The egg-laying period was not determined for the male. Towhees were extremely mobile and secretive during the prenesting, nest-construction, and post-fledging periods. Efforts to quantify activities during the latter two periods proved to be impossible. The activities of 3–4 different individuals were used to form composite budgets for male and female towhees during the prenesting phase. Data for those observation periods when the birds were lost were excluded unless visual contact was regained in less than

5 min. Males were more difficult to follow than females, and, thus, fewer male budgets were sampled.

I timed the activity of a towhee in a known phase of the breeding cycle for the first 20 min of each hour during an 11- to 13-h day. The towhee's activity generally began near the onset of civil twilight in the morning and extended through (about 25 min each) civil twilight in the evening. Day lengths varied through the season (Table 1) peaking at 15.35 h on 23 June. I used 13, 14, and 15 h as reasonable median estimates of the towhee's activity day in early (March), mid- (April, May), and late (June, July) seasons.

To ascertain whether or not the activity of female towhees changed as nestlings aged, I divided the 12-day nestling period into intervals of 2 days each, beginning with the day the first egg of each clutch hatched (Day 0) (see also Ettinger and King 1980), and I recorded the number of times during each 20-min observation period that the male and female brought food to the nestlings.

I estimated daily energy expenditure (*DEE*, kJ/day) from the equation $DEE_{tot} = [h_d TR_d + h_n(BMR_n + TR_n)] + [4.69t_p + 6.46t_g + 16.63t_f + 4.39t_n]$, where DEE_{tot} = total daily energy expenditure (kJ/24 h), the first set of bracketed terms concerns basal and thermostatic requirements, and the second bracketed set includes the energy requirements for activity (DEE_{act}). BMR_n is the basal metabolic rate during the night, when towhees were assumed to be roosting, h_d and h_n are the hours of daytime (13- to 15-h day) and nighttime (9- to 11-h night), respectively, and TR is the daytime (TR_d) and nighttime (TR_n) thermostatic requirement (i.e. added cost above BMR) when air temperature is above the upper critical temperature (T_{uc}) or below the lower critical temperature (T_{lc}). BMR_d, the basal requirement during the daytime, is incorporated into the energy coefficients in the second bracketed set. Vleck (1981) demonstrated for Zebra Finches (*Poephila guttata*) that the increase in metabolic rate due to incubation was approximately compensated for by the ameliorating effects of the nest insulation, so I did not make any adjustments in $BMR_n + TR_n$ for incubating birds despite controversy on this subject (see Walsberg and King 1978a, b; Vleck 1981).

Basal and thermostatic requirements of the Abert's Towhee were measured during the daytime by Dawson (1954). I converted Dawson's data to kJ/h by assuming the energy equivalence of consumed O_2 to be 20.1×10^{-3} kJ/cc O_2 for an RQ of 0.8. The calculated value for BMR_d, 2.681 kJ/h, agrees well with the value derived from Aschoff and Pohl's (1970) equation ($BMR_d/1.25$; Aschoff and Pohl 1970). The thermoneutral zone of the Abert's Towhee is 25–35°C (Dawson 1954). Metabolic rates (i.e. $BMR + TR$) below the lower critical temperature (T_{lc}) were calculated as kJ/h = $5.0 - 0.094T_a$ (Dawson 1954). Because Dawson's values of metabolic rate (*MR*)

above the upper critical temperature (T_{uc}) were exceptionally high compared with the rates of other passerines of similar size (e.g. Weathers 1981), possibly because of elevated humidities in the metabolic chambers (e.g. 50.5% humidity at 42%C) or because towhees at high temperatures behaved unnaturally in an artificial environment, I used Weathers' (1981) allometric equation [log hs = log 12.5 $-$ 0.65 log m, where hs is the heat strain coefficient (mW/g°C) and m is body mass (g)] to predict heat stress above T_{uc} and calculated the metabolic rate for temperatures over 35°C from the equation $MR = -$ 3.372 + 0.173 (T_a), where MR is in kJ/h. Metabolism predicted from these equations includes both basal and thermoregulatory requirements. To insure that BMR_d is not counted twice, it is subtracted from total metabolism $(BMR_d + TR_d)$, and TR_d alone is included in the first set of bracketed terms of the DEE_{tot} equation. Roosting metabolism $(BMR_n + TR_n)$ is calculated as a single number from the regression equations.

I computed average air temperature (T_a) for daytime from readings made at the start of each 20-min observation period with Taylor dual scale minimum-maximum thermometers placed 30 cm above the ground in shaded microhabitat similar to that of the timed bird. Average nighttime T_a was computed from hourly meteorological recordings measured 1.2 m above the ground near Blythe, California by the California State Air Resources Board, Sacramento; the recordings are considered to be reasonable approximations of conditions at the study area. Average nighttime minimum and daytime maximum T_a per study month are listed in Table 1. Mahoney and King (1977) demonstrated in their study of White-crowned Sparrows (*Zonotrichia leucophrys*) that T_a was similar to equivalent temperature (T_e) (Robinson et al. 1976) when the birds were in the shade. Because towhees are active primarily in the shade (pers. obs.), I have assumed that the estimation of TR computed from T_a does not differ significantly from that computed from T_e (see also Ettinger and King 1980).

The energy requirements for DEE_{act} are denoted as numerical conversion coefficients (kJ/h), each being a multiplier for the time spent (h/day) in the related activity: active perching (t_p), ground foraging (t_g), flying (t_f), or in the nest incubating, brooding, or feeding the young (t_n). Variations in the cost of non-flight activity are small compared with differences between flight costs and nonflight costs, and it is probably not important to detail all of this activity (Mugaas and King 1981). The power consumption while preening, singing, or duetting is therefore included in the cost of perching (4.69 kJ/h). The cost of perching (including rest) for a 24-h cycle is about 1.5 × BMR for most altricial birds, but the cost for awake but quiescent birds is higher (King 1973). I have estimated t_p as 1.75 × BMR_d.

I used an average multiple of BMR_d to estimate the

TABLE 1. Average air temperature (°C) and hours of daylight and night for spring and summer months, 1980, in the lower Colorado River valley.

Month	Average temperature		Time (h)	
	Minimum	Maximum	Day[a]	Night
March	8.4	24.1	12.75	11.25
April	11.2	29.7	13.82	10.18
May	15.1	31.9	13.85	10.15
June	19.6	40.3	15.33	8.67
July	26.3	43.7	15.13	8.87

[a] Daylight time includes civil twilights at dawn and dusk.

power consumption while foraging. The cost of foraging for the Abert's Towhee includes the costs of bilateral scratching, hopping, standing, and running. These were estimated as 2.45 BMR_d, 1.9 BMR_d, 1.5 BMR_d, and 2.15 BMR_d, respectively, based on the discussion of Mugaas and King (1981) and on data for running bipeds (Paladino 1979, Paladino and King 1979). Based on nine 20-min samples (sexes combined), the proportions of time spent scratching, hopping, standing, and running were 95.1%, 2.0%, 1.8%, and 1.1%, respectively. As an average multiple, the power consumption while foraging was 2.41 BMR_d (6.46 kJ/h). I assumed that bilateral scratching, which averaged 62.8 scratches/min, consumed more energy than merely hopping, walking, or running.

Power consumption in flight for a towhee-sized bird was estimated from Berger and Hart's (1974) equation, which gave a value of 20.39 kJ/h or 7.61 × BMR_d. About 25% of the towhee's flight time was spent in gliding. To account for this, gliding was assumed to have the same cost as perching. This gives a final estimate of 16.63 kJ/h, or 6.20 × BMR_d, as the cost of flight for this towhee. This is very close to the value of 6.0 × BMR measured for the Purple Martin (Utter and LeFebvre 1970).

The cost of incubating (4.39 kJ/h) during the daytime, when temperatures are generally above the lower critical limit (see Vleck 1981), includes the cost of sitting in a nest (3.99 kJ/h, 15% less than perching) and the cost of rewarming the eggs after an inattentive bout (1.1 × 3.99 kJ/h) and was estimated as 1.64 × BMR_d (see Walsberg and King 1978b for rationale). Nest attendance by the male (i.e. feeding nestlings) was estimated to be the same as the cost of perching. The rationale for the selection of these conversion factors is discussed in general by King (1974) and Mugaas and King (1981).

DEE for females during oogenesis includes the costs of gonadal recrudesence and egg production. This is the most significant production cost during the reproductive period and was estimated by King (1973)

to be 45–58% of daily *BMR* for three species with altricial young and by Ricklefs (1974) to be 45–50% of *BMR*. I assigned it an energy equivalent of 45% of *BMR*, as did Mugaas and King (1981). For males, the costs of gonadal enlargement and sperm production are negligible (King 1973, Ricklefs 1974) and were, therefore, not assigned energy values.

The costs of molt were not considered in the energy budgets because Abert's Towhees molted after my period of study. I have assumed that the heat increment of feeding (SDA) substitutes for the thermostatic requirement and thus does not represent an added cost of production (Calder and King 1974).

I used the *t*-statistic for comparing two means to test for differences in mean percentages of daytime spent in each activity and mean daily energy expenditures (DEE_{act} and DEE_{tot}) within and between phases and sexes. Probability values are given in the text, and the *t*-tests are provided in the appendix.

SENSITIVITY ANALYSIS

Walsberg's (1977) time-budget model of the Phainopepla (*Phainopepla nitens*) yielded underestimates of DEE_{tot}, when compared with $^3HH^{18}O$ measurements (Weathers and Nagy 1980). Using time-budget methods, Utter (1971) overestimated DEE_{tot} in the Mockingbird but found close agreement with D_2O^{18} estimates when he assigned a more realistic conversion coefficient to nonflight activities. Because errors in the selection of conversion factors can result in erroneous estimates of DEE_{tot}, I analyzed potential errors with a sensitivity test (e.g. Ettinger and King 1980).

Each conversion factor in the time budget of a male and female during the incubation phase was increased by 10–25%. The magnitude of error in DEE_{tot} associated with error in the estimation of conversion factors is shown in Table 2. The model was most sensitive to 10% errors in the estimation of body mass in males (+ 10% error in DEE_{tot} estimation) and basal and thermostatic power consumption in both sexes (+ 6% error) and to 25% error in the quantification of power consumption during perching in males (+ 8.6% error in DEE_{tot}) and during foraging in males and females (+ 8.4% and + 7.1% errors in DEE_{tot}, respectively).

Error in the conversion factor for perching had a greater effect on DEE_{tot} in males than did other activity coefficients, because perching comprised a large portion of the male's activity time. Errors in quantifying power consumption during flight resulted in errors of less than 2% in estimating DEE_{tot} in males and females.

Errors of 25% in additional factors affecting DEE_{tot} estimation in females such as nest attendance during the incubation phase and egg production produced 8.8% error and 4.9% error, respectively (Table 2). Nest attendance in females took the place of perching in males, which accounted for its relatively high error.

TABLE 2. Sensitivity of DEE_{tot} to errors in estimating conversion coefficients for males and females in the incubation phase (DEE_{tot} = 108.4 kJ/day and 103.8 kJ/day, respectively; 14 h daylight, 10 h night).

Percentage error in variable	Estimated DEE_{tot} (kJ/day)		Percentage deviation from original estimate	
	Males	Females	Males	Females
Mass + 10%	119.2	110.3	+10.0	+5.9
BMR + TR + 10%	114.9	110.6	+6.0	+6.6
Perching + 25%	117.7	104.8	+8.6	+0.1
Foraging + 25%	117.5	111.2	+8.4	+7.1
Flight + 25%	110.0	104.4	+1.5	+0.6
At nest + 25%		112.9		+8.8
Egg production + 25%[a]		143.0		+4.9

[a] DEE_{tot} in egg-laying phase is 136.3 kJ/day.

The model is most sensitive to errors in the estimates of mass, $BMR + TR$, and conversion factors of predominant activities. Because these errors are not likely to be simultaneously additive, I have confidence that my conversion factors are valid and yield estimates of DEE_{tot} that are accurate in the range of ±5–10% of the true value.

RESULTS AND DISCUSSION

INTERPHASIC VARIATION IN ACTIVITY BUDGETS

The prenesting phase.—The Abert's Towhee is a sedentary species that forms prolonged pair bonds on permanent territories (Marshall 1960, 1964). The prenesting phase was therefore not distinguished by initial courtship encounters and intense territorial altercations. Solitary male song was heard during this period, and pair duets appeared to increase in frequency. During the prenesting period, established pairs accompanied each other during all activities and generally foraged simultaneously on the ground. Females spent more time feeding and less time perching than did males, but both members of the pair spent about twice as much time feeding as perching (Table 3). Flight was typically brief, low to the ground, and usually synchronized between mates. A face-to-face simultaneous duet often immediately followed a paired flight. Time spent in flight was minimal compared with aerially foraging birds like swallows that spend 30% or more of their day in flight (e.g. Utter 1971; Utter and LeFebvre 1970, 1973; Withers 1977).

TABLE 3. Mean (± SE) percentage of daytime spent in different activities by Abert's Towhees during the breeding period.[a]

Phase of cycle	Number of budgets	Minutes of obser-vation	At nest	Perch	Forage	Fly
Females						
Prenesting[b]	1	160	—	26.9 (3.5)	71.4 (9.3)	1.7 (0.2)
Egg-laying[c]	1	240	33.1 (4.3)	10.3 (1.3)	55.5 (7.2)	1.1 (0.1)
Incubation	10	2,400	59.4 ± 2.6 (8.3)	6.6 ± 0.8 (0.9)	32.9 ± 2.6 (4.6)	1.1 ± 0.1 (0.1)
Hatching	3	720	42.2 ± 6.5 (6.0)	11.2 ± 2.2 (1.6)	44.9 ± 8.6 (6.2)	1.7 ± 0.1 (0.2)
Nestling	15	3,700	49.1 ± 4.1 (7.3)	10.4 ± 2.4 (1.5)	38.6 ± 2.2 (5.7)	1.9 ± 0.2 (0.3)
Males						
Prenesting[b]	1	160	—	32.1 (4.2)	66.2 (8.6)	1.7 (0.2)
Incubation	3	760	—	56.8 ± 2.6 (8.0)	40.3 ± 2.2 (5.7)	2.8 ± 0.4 (0.4)
Hatching	1	240	1.0 (0.1)	54.8 (7.7)	41.5 (5.8)	2.6 (0.4)
Nestling	3	720	3.7 ± 0.5 (0.5)	43.1 ± 3.8 (6.0)	49.7 ± 3.5 (7.0)	3.5 ± 0.7 (0.5)

[a] Hours spent in each activity are included in parentheses below each percentage.
[b] Shortly before nest construction.
[c] Specifically observed on the day the first egg was laid.

Ovulation phase.—The activity of one female was measured during this phase on the day the first egg was laid (Day 0) and did not include the activity of nest construction. By Day 0 of the egg-laying phase, the nest was already built, and flying time was further reduced to below that of the prenesting phase (Table 3). One-third of the daytime on Day 0 was spent incubating the egg and perching on the nest rim. Time spent in resting and foraging declined to 38% and 78%, respectively, of prenesting activities as the female restructured her activity pattern. The male continued to accompany the female during foraging bouts but did not visit the nest. While the female was at the nest, the male was usually resting solitarily in a mesquite or at the base of a small shrub.

Incubation phase.—Data for the incubation period were pooled without regard to stage of incubation, which is not likely to affect attentiveness. Female attentiveness at the nest during daytime averaged 59.4 ± 2.6% ($n = 10$) for the incubation phase (Table 3) and varied individually from 49.9% to 69.7%. Perching, for-

aging, and flight were at seasonal minima during the incubation phase.

The male was not observed to incubate or to feed the female at the nest, although he occasionally visited the nest tree. During this phase, the male spent more of his time perching (56.8% ± 2.6%) (Table 3), but his foraging time exceeded that of the female. Many males congregated in the saltbush flats adjacent to my study grid in the early morning, perching openly on the mesquite snags and chasing other Abert's Towhees. Flight time of males during the incubation stage was 2.6 times greater than during the prenesting stage and was significantly higher than female flying time ($P < 0.001$). Male-female duets continued, but male solitary song stopped.

Hatching and nestling phases.—When the eggs hatch, the female takes responsibility for feeding the hatchlings and incubating the unhatched eggs. Her nest attentiveness decreased significantly from 59.4 ± 2.6% during incubation to 42.2 ± 6.5% at hatching ($P < 0.02$), and foraging time increased, but not significantly

($P > 0.1$). Males generally did not visit the nestlings for the first day or so of the hatching period, and the female typically fed the nestlings on her own. Female foraging time was significantly higher during the hatching phase than during the rest of the nestling period ($P < 0.05$), presumably because the male was not contributing time in gathering food for the young. Nevertheless, perching time significantly increased from incubation to hatching ($P < 0.05$), suggesting that females had time to spare. After the nestlings hatched, the female continued to brood or, occasionally, stand over them for $49.1 \pm 4.1\%$ of the day (Table 3).

During the nestling phase, the male did not brood but brought insects to the nest to feed to the female and young. Time spent by males in foraging increased from incubation to nestling period ($40.3 \pm 2.2\%$ vs. $49.7 \pm 3.5\%$, $P < 0.08$) as males foraged for themselves and their young. Male perching time during the nestling phase significantly declined ($P < 0.05$).

I assume that the small increase in time spent flying between the incubation and nestling stages was due to an increase in the number of flights from the nest to the foraging grounds during the nestling phase (females: $1.1 \pm 0.1\%$ to $1.9 \pm 0.2\%$, $P < 0.01$; males: $2.8 \pm 0.4\%$ to $3.5 \pm 0.7\%$, $P > 0.4$). The male's budget in the nestling phase was significantly different from the female's budget for perching time ($P < 0.001$), feeding time ($P < 0.05$), and flying time ($P < 0.01$).

INTERPHASIC AND INTRAPHASIC VARIATION IN BASAL AND THERMOSTATIC EXPENDITURE AND DEE_{tot}

Basal and thermostatic costs.—Air temperature increased through the reproductive cycle (Table 1), and the effect of this change on thermostatic power consumption had to be factored out of the energy budget so that any variation in energy expenditure among activities and phases could be recognized. For phases of the breeding cycle for which there were sufficient sample budgets, mean daily air temperature explained 78% ($r = 0.88$) of the variation of DEE_{tot} of females during the incubation phase but only 28% ($r = 0.53$) during the nestling phase. The residual variation among budgets was small during the incubation phase and suggests that the variation of power consumption by activity

was also small. During the nestling phase, residual variation was greater, much of which is explained by variation in DEE_{act}, as will be shown later.

Average obligatory basal and thermostatic power consumption for all phases of the reproductive cycle was 68.5 kJ/day (range 61.6–83.2) in females and 68.8 kJ/day (range 62.0–83.7) in males. Thermostatic power consumption alone comprised an average of 8.4% (range 2.3–18.8) of DEE_{tot} in females and 8.3% (range 2.7–19.0) in males. Basal metabolism consumed 54.9% (range 43.0–62.3) of DEE_{tot} in females and 52.4% (46.3–56.3) in males.

Prenesting phase.—Because of the large amount of time devoted to foraging, a more expensive activity than perching or attending the nest, DEE_{act} was high for females during the prenesting phase (Table 4). Furthermore, air temperatures were at their lowest in March (Table 1), causing thermostatic costs for both males and females to peak during the prenesting phase (Table 4). Thus, male DEE_{tot} was also at the seasonal maximum, and female DEE_{tot} was exceeded only by DEE_{tot} for the egg-laying phase. As a multiple of BMR_{tot}, DEE_{tot} was high for females ($2.18 \times BMR_{tot}$) and males ($2.16 \times BMR_{tot}$).

Egg-laying phase.—Because of the added cost of egg production, DEE_{tot} reached a seasonal high of 136.3 kJ/day for females during this phase (Table 4). For an altricial bird laying a 3-egg clutch (mean clutch size of the Abert's Towhee is 2.85, $n = 65$), energy allocated to oogenesis reaches a peak shortly before the first egg is laid and falls to zero after the third egg is laid (King 1973). For simplification, I have assumed that 26.6 kJ (0.45 BMR_{tot}/day) were allocated to egg production on Day 0. Egg production consumed 19.5% of DEE_{tot}, and activity consumed only 28.8% of DEE_{tot}. As a multiple of obligatory metabolism, DEE_{tot} was at a seasonal maximum of 2.32 BMR_{tot} (Table 4).

Incubation phase.—DEE_{tot} of female Abert's Towhees was at a seasonal minimum of 103.8 kJ/day during the incubation phase and ranged individually from 94.9 kJ/day (1.6 BMR_{tot}) to 112.7 kJ/day (1.9 BMR_{tot}). These low values were partly the result of a reduced thermoregulatory requirement and partly because the time and energy spent foraging was reduced (Tables 3, 4). Mean DEE_{act} was lowest in this phase (73 kJ/day; Table 4) and ranged from 66.6 to 77.5 kJ/day. Females spent more time and energy at

TABLE 4.   Energy allocation (kJ/day) by Abert's Towhees during different phases of the reproductive cycle.[a]

Phase of cycle	At nest	Perch	Forage	Fly	DEE_{act}[b]	TR_d	TR_n	BMR_n	DEE_{tot}
Females									
Prenesting	—	16.4	60.0	3.6	80.0	13.7	10.3	23.8	127.8
Egg-laying[c]	18.9	6.3	46.6	2.4	74.2	3.2	10.7	21.6	136.3
Incubation	36.4	4.3	29.7	2.6	73.0	3.2	6.0	21.6	103.8
Hatching	26.2	7.5	40.1	3.9	77.7	2.2	4.8	21.6	106.3
Nestling	31.8	7.2	36.6	4.8	80.4	6.1	2.2	20.1	108.8
Males									
Prenesting	—	19.5	55.6	3.7	78.8	12.7	11.4	23.8	126.7
Incubation	—	37.3	36.5	6.6	80.4	3.7	2.7	21.6	108.4
Hatching	0.7	36.0	37.5	6.1	80.3	2.2	3.9	21.6	108.0
Nestling	2.4	28.3	45.0	8.2	83.9	4.8	4.5	21.6	114.8

[a] $DEE_{tot} = DEE_{act} + TR_d + TR_n + BMR_n$.
[b] Includes basal metabolism (BMR_d).
[c] DEE_{tot} during egg-laying phase includes cost of oogenesis, 26.6 kJ/day.

the nest during incubation than during any other phase (Tables 3, 4). Although Vleck (1981) has demonstrated that energy is expended by Zebra Finches to rewarm eggs after a bout of inattentiveness or when air temperature is below T_{lc}, my results indicated that the incubation phase of Abert's Towhees was a period of reduced power consumption. Air temperature remained in the adult thermoneutral zone during most of the daytime, and the cost of rewarming eggs after an inattentive bout was the only major cause of increased energy expenditure beyond that of resting (the cost of rewarming eggs was included in the cost of incubation). The female incubated through the night, when thermostatic costs are higher, so inattentiveness was not a cause of energy stress at that time. My results support the premise of Walsberg and King (1978a, b) that the incubation phase is a period of reduced energy expenditure.

There was a reduction in the male's DEE_{tot}, mostly because of lower thermostatic costs (Table 4) but also as a result of a substantial decline in foraging activity (Tables 3, 4). This extra time and energy were reallocated to perching. During the incubation phase, the male spent more time and energy in feeding and resting than the female did, because he did not attend the nest. During incubation, DEE_{act} of males was significantly different from DEE_{act} of females ($P < 0.01$), but DEE_{tot} was not ($P > 0.2$).

Hatching phase.—Female Abert's Towhees spent more energy foraging during the brief hatching phase than during either the incubation or the nestling phase (Table 4). Females received little initial help from males during the hatching phase, and their flight energy increased by about one-third compared with the incubation phase. Consequently, DEE_{act} of females in the hatching period was almost significantly greater than that of females during the incubation phase ($P < 0.07$). Thermostatic costs during the hatching phase remained relatively constant for both males and females (Table 4). DEE_{act} and DEE_{tot} did not change substantially in the male during the hatching phase (Table 4). The male visited the nest infrequently, often without food, and energy spent in nest attendance was, therefore, minimal. Data for males during the hatching phase were inadequate to test for significant differences.

Nestling phase.—Mean DEE_{act} was significantly greater ($P < 0.001$) in females during the nestling period than during incubation (Table 4). Mean DEE_{tot} was also significantly greater ($P < 0.02$), with a mean of 108.8 kJ and a range of 105.7 kJ (1.71 BMR_{tot}) to 120.6 kJ (2.02 BMR_{tot}). DEE_{act} explains 58% ($r = 0.76$) of the variation in DEE_{tot}. An interpretation of energy expenditure during this phase was complicated by the variables of nestling growth and brood size. Mean DEE_{act} and mean DEE_{tot} increased gradually as nestlings aged and as time expended in flying and foraging activity increased commensurately (Table 5). There was a significant difference ($P < 0.02$) in DEE_{act}, but not DEE_{tot} ($P > 0.2$), between the mean value for Days 0–5 and the mean value for Days 6–10+ of the nestling

TABLE 5. Mean percentage of daytime spent in four activities and mean daily energy expenditure by female Abert's Towhees during the nestling phase.[a]

Days	Number of budgets	Activity (%)				kJ/day				
		At nest	Perch	Forage	Fly	DEE_{act}[b]	TR_d	TR_n	BMR_n	DEE_{tot}
0-1[c]	3	42.2 (25.9)	11.2 (7.9)	44.9 (40.6)	1.7 (3.9)	77.7	2.6	4.8	21.6	106.7
2-3	3	57.3 (36.1)	6.1 (4.1)	34.7 (32.2)	1.9 (4.5)	76.9	3.6	5.3	20.9	106.7
4-5	5	53.5 (34.7)	6.8 (4.7)	38.2 (36.5)	1.5 (3.7)	79.6	7.3	1.9	19.9	108.6
6-7	2	45.1 (29.7)	9.5 (6.7)	42.8 (41.5)	2.6 (6.5)	84.4	8.1	0.5	19.5	112.4
8-9	3	36.4 (23.4)	18.8 (12.9)	43.1 (40.8)	1.7 (4.1)	81.2	4.3	2.3	20.1	107.9
10+	2	41.6 (27.4)	15.8 (11.1)	39.9 (38.7)	2.7 (6.7)	83.9	7.4	0.2	19.4	110.9

[a] Energy expenditure (kJ/day) in each activity is included below each percentage.
[b] Includes basal metabolism (BMR_d).
[c] Days 0-1 and Hatching Phase (Tables 3, 4) are same budgets.

period. Nest attendance declined as nestlings became feathered and able to thermoregulate to some degree. Unlike most flycatching birds that fledge at or close to adult weight (Ricklefs 1968), towhees fledge at 70% adult size (Finch 1981a). This may explain why brooding time remained as high as 36.4% and 41.6% at ages of 8 days and older. In contrast, Willow Flycatchers (*Empidonax traillii*) spend only 10–15% of their time brooding when the nestlings are 8 days and older (Ettinger and King 1980). Because 8–12-day-old towhees are not close to adult weight, they may not be entirely homeothermic near the time of fledging and, therefore, may require more brooding protection (e.g. body warmth, shade), particularly from the extreme mid-day heat of the desert summer.

By the time of fledging (age 10+), nestling growth has slowed considerably (Finch 1981a), which possibly accounts for the apparent decline in female foraging time (Table 5). Parents may purposefully reduce feeding to force nestlings to fledge. The slight increase in nest attendance at this age may be explained by high air temperatures on the days the budgets were measured. High air temperatures caused increases in daytime thermostatic power consumption, and, consequently, females spent more time resting at the nest than feeding.

Paralleling the increase in female DEE_{act} through the nestling phase was an increase in female feeding rate from 27 visits per 14-h day

(9.0 ± 4.6 visits/280 min) at the start of the nestling phase to 73.5 visits/day (24.5 ± 2.9 visits/280 min) by the time of fledging (Fig. 1). The male's feeding rate changed from 5.1 visits per 14-h day (1.7 ± 1.5 visits/280 min) to 82.5 visits/day (27.5 ± 0.7 visits/280 min) (Fig. 1) and exceeded the female's rate near the end of the nestling phase. Male and female feeding rates through the nestling phase were exponentially increasing similar to towhee nestling growth, which is also exponential (Finch 1981a).

Although males share feeding responsibilities, they allocated only 2.4 kJ/day in actual nest attendance (Table 4). Mean DEE_{act} in males showed an apparent increase of 3.5 kJ/day from the incubation and hatching phases to the nestling phase, but the difference was not significant ($P > 0.2$). A shift in power consumption of perching to energy spent in foraging and flying accounted for this slight increase in DEE_{act}. Mean DEE_{tot} increased about 7 kJ from the incubation and hatching phases to the nestling phase. Air temperature frequently exceeded T_{uc} even after dusk during the nestling phase, and TR_{tot} alone accounted for 8.1% of DEE_{tot} in males. Mean DEE_{tot} was 1.93 BMR_{tot} in males and ranged from 1.82 to 2.04 BMR_{tot}. There was no significant difference in mean DEE_{act} ($P > 0.2$) or mean DEE_{tot} ($P > 0.2$) of males and females during the nestling phase. My data were inadequate for testing of male budgets in relation to nestling age.
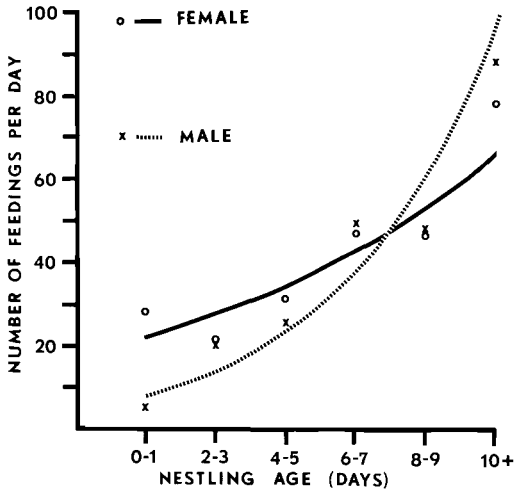
Fig. 1.   Rate of feeding nestlings by male and female Abert's Towhees as a function of nestling age. For females, $y = 19.96^{0.11x}$; $r^2 = 0.82$; for males, $y = 6.89^{0.24x}$, $r^2 = 0.88$.

Effects of brood size on DEE_{act} *and* DEE_{tot}.—Contrary to theory, females did not show a clearcut trend of increasing DEE_{act} with increasing brood size (Table 6). DEE_{act} remained remarkably constant, and DEE_{tot} varied largely in response to thermoregulatory costs. Nevertheless, when each activity component was examined separately, it was apparent that time spent in feeding activity increased as brood size increased (Table 6). Trends in other activity components were not as clear, possibly because (1) sample size was insufficient for broods of 1 and 4, (2) the effects of nestling age overrode the effects

of brood size, thereby complicating interpretation, or (3) there were complex tradeoffs among allocations of energy to nest attendance, perching, and feeding, allocations that may vary in response to variation in extraneous factors such as day length, temperature, weather, food supply, competition, or predator density.

The daily energy expenditure of Common House-Martins was positively correlated with brood number (Hails and Bryant 1979). Walsberg (1978) found only a 7% difference in DEE_{tot} of Phainopeplas feeding broods of 2 or 3. Towhees feed by an energetically less expensive method than do Common House-Martins or flycatching Phainopeplas, and a change in foraging time of towhees should not affect power consumption as greatly as a change in flying time. Walsberg (1980) has pointed out that birds that feed in flight spend more energy on average than do ground-foraging birds, because flying is costly. Feeding method may therefore account for the negligible variation in DEE_{tot} of towhees feeding broods of 2, 3, or 4.

SUMMARY OF INTERPHASIC VARIATION
AND PARENTAL INVESTMENT

Variation in DEE_{tot} through the reproductive cycle was due to variation in both obligatory and activity costs. Variation in DEE_{tot} in males was primarily caused by variation in thermostatic requirements, which were most costly in the prenesting phase. During the nestling phase, thermostatic costs were elevated in some individuals in late summer on days when T_a

TABLE 6.   Mean percentage of daytime spent in four activities and mean daily energy expenditure by female Abert's Towhees with different brood sizes.[a]

Brood size	Number of budgets	Mean age	Activity (%)				kJ/day				
			At nest	Perch	Forage	Fly	DEE_{act}	TR_d	TR_n	BMR_n	DEE_{tot}
1	1	4.0	53.2 (35.0)	11.3 (7.9)	33.5 (32.5)	2.0 (5.0)	80.4	1.1	1.3	19.4	102.2
2	6	4.0	57.3 (37.2)	6.4 (4.5)	34.7 (33.3)	1.6 (4.1)	79.1	8.1	3.0	19.8	110.0
3	5	5.0	50.3 (32.5)	7.2 (5.0)	40.6 (38.4)	1.9 (4.7)	80.6	5.3	2.9	20.3	109.1
4	1	8.0	4.9 (3.0)	37.9 (24.9)	55.1 (49.8)	2.1 (5.0)	82.7	6.7	0.1	21.6	111.1

[a] Energy expenditure (kJ/day) in each activity is included below each percentage.

exceeded T_{uc}, but even in these cases thermostatic costs were less than those during the prenesting phase. A small but steady increase in male DEE_{act} throughout the reproductive cycle contributed to the slight increase in DEE_{tot} in the nestling phase. Variation in DEE_{tot} in females was caused by variation in thermostatic costs, production costs (oogenesis), and activity costs. With the exception of the prenesting period, females spent less energy in activity than did males. DEE_{tot} was consequently lower during the last three phases of the reproductive cycle in females than in males.

Towhees used flight time very conservatively during all phases, and, as a consequence, the daily power consumption by flying was reduced to a minimum despite its high unit costs (see also Mugaas and King 1981, Biedenweg 1983). In general, activity was adjusted in response to changes in reproductive demands on time and energy. These behavioral adaptations tended to minimize DEE_{act} and DEE_{tot}. Male towhees perched quietly for extended periods, a behavior that minimizes energy expenditure. Females conserved movement by spending large amounts of time at the nest, even through the nestling period. It is difficult to gauge how much nest attendance time was actually required for incubating or brooding. Because sitting in a nest conserves energy (Walsberg and King 1978a, b), females may spend some "free" time (i.e. time not specifically needed for foraging, flying, incubating, and brooding) in nest attendance rather than in perching. Spending time in a shaded nest benefits females by reducing thermal stress during hot times of the day. When days are cold, nest insulation warms females.

The cost of parental investment cannot be measured solely by quantifying power consumption by parental activity. The advantages of producing progeny must outweigh the immediate risks (Trivers 1972). In 1980, nesting predation of Abert's Towhees was high in my study area (Finch 1981a, 1982). Tree-climbing snakes were major nest predators (Finch 1981b), and one was observed to swallow an adult towhee (Tim Brush pers. comm.). Female towhees therefore risked predation by staying at the nest, but at the same time they were in a position to protect their offspring from predation. The twofold benefit of conserving movement and energy and protecting the young apparently outweighed the risk of predation, because towhees spent close to half of their time in nest attendance.

Parental effort was divided between the sexes. Females produced and incubated the eggs and brooded the nestlings. Both sexes fed the nestlings, but the male also fed the female when she was brooding. In the nestling phase, male foraging time was significantly greater than that of the female, and the rate at which the male fed nestlings exceeded that of the female by Day 8 of the nestling phase. Although males did not invest much time in solitary territorial singing after the incubation phase (see Marshall 1964), mate duetting was heard throughout the annual cycle and probably served to reinforce the pair bond. Perhaps the best evidence of male commitment is seen in the pair relationship itself. By maintaining a prolonged, possibly permanent pair bond (Marshall 1960), the male Abert's Towhee demonstrates a greater investment in his mate and offspring than most North American passerines. Towhees do not migrate to avoid unfavorable conditions, and consequently each pair has a long breeding period to invest time and energy in reproduction. A long breeding period that allows several nesting attempts may be necessary to outweigh the poor nesting success caused by predation and brood parasitism (Finch 1981a, 1983a).

Like Willow Flycatchers and Black-billed Magpies (Ettinger and King 1980, Mugaas and King 1981), Abert's Towhees can be classified as "time minimizers" rather than "energy maximizers," at least during the breeding cycle. Increases in day length and a probable increase in food supply (see Cohan et al. 1978, Anderson et al. 1982) created more time for energy acquisition; yet towhees responded with a reduction in foraging time and an increase in either perching time (males) or nest attendance (females). Female foraging time did increase during the hatching phase, when males were not helping to feed the young, but decreased again during the nestling phase, when males began to help. Foraging time was highest in males and females in the prenesting phase, when thermostatic costs were elevated. Foraging time altered in response to varying energy demands, yet there was still time for other activities, even perching. Minimization of flying time, alteration of foraging time, and time allocation to perching support the idea that foraging behavior is regulated on the basis of a

fixed energy requirement. If there is no gain in fitness when the energy requirement is exceeded, individuals in the group are behaving like time minimizers (Schoener 1971).

Without further knowledge of the food supply in my study area, I cannot establish whether or not time and energy were limiting for Abert's Towhees. The prenesting phase (or before) seems like the most probable period for time and energy limitations, because (1) obligatory demands were highest during the prenesting phase and (2) time available for finding and ingesting food was reduced by the photoperiod. Also, food supply in and near my study area has been shown to be less in March than later in the season (Cohan et al. 1978, Anderson et al. 1982). Nevertheless, males and females still had time to spare for perching. Based on my estimates of average DEE_{act} and DEE_{tot}, it would seem that both males and females have some surplus time for inactivity during all phases. Perhaps the best way to find evidence of time and energy limitations is by considering the daily budgets of individuals. One female brooding 5-day-old nestlings on 17 June alloted only 3.3% of the daytime to perching (compared to a mean of 8.3% for 4 other females with 4–5-day-old nestlings), the perching periods ranging from 0 to 108 s per 20-min interval. On this particular day, T_a exceeded T_{uc} from 1000 to 1900, and the female spent these hours primarily sitting in the shaded nest, panting. It therefore seems likely that time can be restricted in response to high T_a, and, consequently, females during the nestling phase may occasionally be time-stressed.

Many animals spend a large proportion of their active day in inactivity (Herbers 1981). If animals regulate their food intake like a thermostat, whereby an individual feeds when it is hungry and ceases when it is satiated, then surplus time often results (Herbers 1981). Inactivity is an energetically inexpensive means of spending spare time between foraging periods. Energy conservation serves an immediate advantage to the animal. Excess time is advantageous, because it can be used in some other way in the future and, as such, provides a buffer against periods of high time and energy demands. Ettinger and King (1980) applied Wilson's (1975) "principle of stringency" to explain loafing activity and the stability of DEE_{act} of the Willow Flycatcher. According to Wilson, time and energy budgets have been selected to accommodate periods when metabolic demands are high, when food supplies are poor, or when young are being fed. The time-energy budgets of the Abert's Towhee support the principle of stringency, because towhees tended to conserve energy by minimizing power consumption in all phases even though increased energy expenditure was possible (witness the wider range in individual variation of DEE_{act}).

INTERSPECIFIC COMPARISONS

Comparing values of DEE_{tot} between Abert's Towhees and mockingbirds is useful, because mockingbirds (1) do not feed on the wing, (2) weigh approximately the same as Abert's Towhees (range: 44.4 g–50.9 g, Utter 1971), and (3) have been studied with both D_2O^{18} estimates and time-budget methods. Utter's (1971) D_2O^{18} estimates of DEE_{tot} in mockingbirds ranged from 1.35 to 2.10 × BMR_{tot}. Extrapolating from Biedenweg's (1983) data, time-budget estimates of DEE_{tot} in mockingbirds ranged from approximately 1.43 to 2.15 × BMR_n. Excluding the egg-laying female, my estimates of DEE_{tot} in the Abert's Towhee ranged from 1.6 to 2.1 × BMR_{tot} and thus compare well with those of the mockingbird. The magpie, another ground-foraging bird, had values that ranged from 1.2 to 2.08 × BMR_{tot} (Mugaas and King 1981).

Comparing the reproductive phases that were measured in common among these three ground-foraging species indicated several similarities. DEE_{act} and DEE_{tot} were at seasonal minimums in the incubation phase for all three species. The ovulation and nestling periods were most energetically expensive. Nevertheless, the magpie expended maximum energy in winter, a period not measured in mockingbirds and towhees. In mockingbirds, the most expensive phase was the fledging period, a period not measured in magpies and towhees.

The thermostatic costs of all three species declined through the reproductive season, with the exception that obligatory costs were elevated in the towhee in response to high air temperatures during the nestling period. The domed nest of the magpie, which provides protection from wind, sun, and cold, possibly explains why magpie thermostatic costs were generally lower than those of towhees.

Males of all three species devoted a large proportion of time to perching through the breeding cycle. Unlike towhees, female mag-

pies spend more time perching during the nestling period than attending the nest (Mugaas and King 1981). Biedenweg (1983) suggested that the large percentage of time mockingbirds spent in perching was a response to high predation pressure and that predation pressure rather than time-minimization determined the "loafing" component. Predation was high in my study area also and may explain why females spent large amounts of time in nest attendance throughout the nestling stage. By sitting still in a nest females do not attract attention to themselves, and they have a better chance of detecting nest predators. Brooding also quiets the begging calls of nestlings, thus possibly reducing the probability of nestling predation.

In conclusion, ground-foraging birds like Abert's Towhees, mockingbirds, and magpies expend less energy than do birds that feed in flight (Walsberg 1980). Bilateral scratching, the foraging method practiced by towhees, is presumably more costly than the foraging activities (standing, walking, running) of magpies and mockingbirds, which may explain the slightly higher range of towhee DEE_{tot}. Despite these differences in the activities of towhees, mockingbirds, and magpies, the pattern that classifies them into a group is energy conservation via minimization of flight.

LITERATURE CITED

ANDERSON, B. W., R. D. OHMART, & S. D. FRETWELL. 1982. Evidence for social regulation in some riparian bird populations. Amer. Natur. 102: 340–352.

ASCHOFF, J., & H. POHL. 1970. Der Ruheumsatz von Vogeln als Funktion der Tageszeit und der Korpergrosse. J. Ornithol. 111: 38–47.

BERGER, M., & J. S. HART. 1974. Physiology and energetics of flight. Pp. 415–477 in Avian biology, vol. 4 (D. S. Farner and J. R. King, Eds.). New York, Academic Press.

BIEDENWEG, D. W. 1983. Time and energy budgets of the Mockingbird (Mimus polyglottos) during the breeding season. Auk 100: 149–160.

CALDER, W. A., & J. R. KING. 1974. Thermal and caloric relations of birds. Pp. 259–413 in Avian biology, vol. 4 (D. S. Farner and J. R. King, Eds.). New York, Academic Press.

COHAN, D. R., B. W. ANDERSON, & R. D. OHMART. 1978. Avian population responses to salt cedar along the lower Colorado River. Pp. 371–381 in Symposium, Strategies for protection and management of floodplain wetlands and other riparian ecosystems. USDA For. Serv. Gen. Tech. Rep. WO-12.

DAWSON, W. R. 1954. Temperature regulation and water requirements of the Brown and Abert's towhees, Pipilo fuscus and Pipilo aberti. Univ. California Publ. Zool. 59: 81–124.

ETTINGER, A. O., & J. R. KING. 1980. Time and energy budgets of the Willow Flycatcher (Empidonax traillii) during the breeding season. Auk 97: 533–546.

FINCH, D. M. 1981a. Variation in the reproductive ecology of the Abert Towhee. Unpublished M.S. thesis. Tempe, Arizona, Arizona State Univ.

———. 1981b. Nest predation of Abert's Towhees by coachwhips and roadrunners. Condor 83: 389.

———. 1982. Rejection of cowbird eggs by Crissal Thrashers. Auk 99: 719–724.

———. 1983a. Brood parasitism of the Abert's Towhee: timing, frequency, and effects. Condor 85: 355–359.

———. 1983b. Seasonal variation in nest placement of Abert's Towhees. Condor 85: 111–113.

GOODMAN, D. 1974. Natural selection and a cost ceiling on reproductive effort. Amer. Natur. 108: 247–268.

HAILS, C. J., & D. M. BRYANT. 1979. Reproductive energetics of a freeliving bird. J. Anim. Ecol. 48: 471–482.

HERBERS, J. M. 1981. Time resources and laziness in animals. Oecologia 49: 252–262.

KING, J. R. 1973. Energetics of reproduction in birds. Pp. 78–117 in Breeding biology of birds (D. S. Farner, Ed.). Washington, D.C., Natl. Acad. Sci.

———. 1974. Seasonal allocation of time and energy resources in birds. Pp. 4–70 in Avian energetics (R. A. Paynter, Jr., Ed.). Publ. Nuttall Ornithol. Club No. 15.

MAHONEY, S. A., & J. R. KING. 1977. The use of the equivalent black-body temperature in the thermal energetics of small birds. J. Thermal Biol. 1977: 115–120.

MARSHALL, J. T., JR. 1960. Interrelations of Abert and Brown towhees. Condor 62: 49–64.

———. 1964. Voice in communication and relationships among Brown Towhees. Condor 66: 345–356.

MUGAAS, J. N., & J. R. KING. 1981. Annual variation of daily energy expenditure by the Black-billed Magpie: a study of thermal and behavioral energetics. Studies in Avian Biol. No. 5.

PALADINO, F. V. 1979. Energetics of terrestrial locomotion in White-crowned Sparrows (*Zonotrichia leucophrys gambelii*). Unpublished Ph.D. dissertation. Pullman, Washington State Univ.

———, & J. R. KING. 1979. Energetic cost of terrestrial locomotion: biped and quadruped runners compared. Rev. Canadian Biol. 38(4): 321–323.

PIANKA, E. R. 1976. Natural selection of optimal reproductive tactics. Amer. Zool. 16: 775–784.

RICKLEFS, R. E. 1968. Patterns of growth in birds. Ibis 110: 419–451.

———. 1974. Energetics of reproduction in birds. Pp. 152–292 *in* Avian energetics (R. A. Paynter, Jr., Ed.). Publ. Nuttall Ornithol. Club No. 15.

ROBINSON, D. E., G. S. CAMPBELL, & J. R. KING. 1976. An evaluation of heat exchange in small birds. J. Comp. Physiol. 105: 153–166.

SCHOENER, T. W. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst. 2: 369–404.

TRIVERS, R. L. 1972. Parental investment and sexual selection. Pp. 136–179 *in* Sexual selection and the descent of man, 1871–1971 (B. G. Campbell, Ed.). Chicago, Aldine.

UTTER, J. M. 1971. Daily energy expenditure of free-living Purple Martins (*Progne subis*) and Mockingbirds (*Mimus polyglottos*) with comparison of two northern populations of Mockingbirds. Unpublished Ph.D dissertation. Rutgers Univ., New Brunswick, New Jersey.

———, & E. A. LeFEBVRE. 1970. Energy expenditure for free flight by the Purple Martin (*Progne subis*). Comp. Biochem. Physiol. 35: 713–719.

———, & ———. 1973. Daily energy expenditure of Purple Martins (*Progne subis*) during the breeding season: estimates using D_2O^{18} and time budget methods. Ecology 54: 597–603.

VLECK, C. M. 1981. Energetic cost of incubation in the Zebra Finch. Condor 83: 229–237.

WALSBERG, G. E. 1977. Ecology and energetics of contrasting social systems in *Phainopepla nitens* (Aves: Ptilogonatidae). Univ. Calif. Publ. Zool. 108: 1–63.

———. 1978. Brood size and the use of time and energy by the Phainopepla. Ecology 59: 147–153.

———. 1980. Energy expenditure in free-living birds: patterns and diversity. Proc. 17th Intern. Ornithol. Congr.: 300–305.

———, & J. R. KING. 1978a. The heat budget of incubating White-crowned Sparrows (*Zonotrichia leucophyrys oriantha*) in Oregon. Physiol. Zool. 51: 92–103.

———, & ———. 1978b. The energetic consequences of incubation for two passerine species. Auk 95: 644–655.

WEATHERS, W. W. 1981. Physiological thermoregulation in heat-stressed birds: consequences of body size. Physiol. Zool. 54: 345–361.

———, & K. A. NAGY. 1980. Simultaneous doubly labeled water ($^3HH^{18}O$) and time-budget estimates of daily energy expenditure in *Phainopepla nitens*. Auk 97: 861–867.

WILSON, E. O. 1975. Sociobiology. Cambridge, Massachusetts, Belknap.

WITHERS, P. C. 1977. Energetic aspects of reproduction by the Cliff Swallow. Auk 94: 718–725.

WITTENBERGER, J. R. 1982. Factors affecting how male and female Bobolinks apportion parental investments. Condor 84: 22–39.

APPENDIX.   *t*-tests comparing mean percentages of daytime spent by Abert's Towhees in each activity, mean DEE_{act}, and mean DEE_{tot}.

Comparison[a]	Timed activity				Energy expenditure	
	At nest	Perch	Feed	Fly	DEE_{act}	DEE_{tot}
Female × Female						
I × N						
t	1.91	1.31	1.57	3.34	4.99	2.74
df	23	23	23	23	23	23
P	<0.08	<0.4	<0.2	<0.01	<0.001	<0.02
I × H						
t	2.97	2.43	1.78	2.24	2.13	1.11
df	11	11	11	11	11	11
P	<0.02	<0.05	<0.2	<0.05	<0.07	<0.4
H × N						
t	0.08	0.34	2.60	0.05	1.19	0.55
df	14	14	14	14	16	16
P	<0.5	<0.9	<0.05	<1.0	<0.4	<0.9
Nestling age[b]						
t	2.32	2.22	1.79	1.72	2.89	1.26
df	13	13	13	13	16	16
P	<0.05	<0.05	<0.1	<0.2	<0.02	<0.4
Brood size						
t	1.53	0.92	1.98	0.72	0.74	1.81
df	11	11	11	11	11	11
P	<0.2	<0.4	<0.075	<0.5	<0.5	<0.1
Male × Male						
I × N						
t	—	3.01	2.29	0.86	1.20	1.38
df	—	4	4	4	4	4
P	—	<0.05	<0.08	<0.5	<0.4	<0.4
Male × Female						
I × I						
t	—	24.66	1.37	5.41	3.45	1.21
df	—	11	11	11	11	11
P	—	<0.001	<0.3	<0.001	<0.01	<0.4
N × N						
t	—	5.97	2.34	3.25	1.10	0.87
df	—	16	16	16	16	16
P	—	<0.001	<0.05	<0.01	<0.4	<0.4

[a] I = incubation phase; N = nestling phase; H = hatching phase.

[b] Average of days 2–5 vs. average of days 6–9 were tested for timed activities, and average of days 0–5 vs. average of days 6–10+ were tested for DEE_{act} and DEE_{tot}.