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BROOD SIZE AND THE USE OF TIME AND ENERGY BY THE PHAINOPEPLA¹

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Abstract. Time and energy budgets were calculated for 16 Phainopeplas (*Phainopepla nitens*) nesting in the coastal woodlands of southern California. Brood size differed 50%: 4 pairs raised 3 young and 4 pairs raised 2 young. Compared to pairs feeding 2 nestlings, pairs feeding 3 nestlings spent an average of 42% more time flycatching, 16% more time foraging at fruiting shrubs, and 22% more of their active day in flight. Daily energy expenditure of pairs feeding 3 nestlings was increased a surprisingly small amount compared to that of pairs feeding only 2 young—a mean of 7%, or 12 kJ. Over the entire period from egg synthesis to fledging, total parental energy expenditure is estimated to increase only 4.7% associated with a 50% increase in brood size.

The Phainopepla may exhibit a unique annual cycle; it apparently breeds twice annually, once in its summer range (where the present study was conducted) and once in its winter range in the Sonoran Desert. Using data from this study plus those from a previous one, the 2 breedings were compared in terms of parental energy expenditure from egg-laying until fledging and parental harvesting requirements during the incubation and nestling periods. (Harvesting requirements = parental energy expenditure + the energy requirements of any young being fed.) Remarkable convergences are seen in the reproductive energetics of Phainopeplas breeding in the 2 habitats. Regardless of the striking differences between the 2 seasonal ranges in parental energy expenditure, habitat, daylength, and social system used, a Phainopepla incubating or feeding 2 nestlings in the coastal woodlands has a mean harvesting rate (kilojoules/hour active) virtually identical to that of a bird in a comparable stage of breeding in the desert. Similarly, total parental energy expenditure from egg synthesis until fledging averages only 2.6% different between populations breeding in the 2 areas, when calculated on an energy expended per young fledged basis.

Key words: Brood size; California; energetics; *Phainopepla nitens*; *Ptilonotidae*; reproductive energetics; resource allocation; time and energy budgets.

INTRODUCTION

A general, and often unstated, assumption in ecology is that differing brood sizes are associated with substantially different patterns of parental time and energy expenditure. Though this seems likely, empirical data on this evolutionarily important question are scarce. Models that allow estimation of the energetic cost of egg production and gonadal growth in birds are now available (King 1973, Ricklefs 1974), but data describing the time and energy expenditure of parents in later stages of the reproductive cycle are sparse. This study was designed to quantify and compare the use of time and energy by Phainopeplas (*Phainopepla nitens*) raising broods that differ 50% in size (2 vs. 3 young). *Phainopepla nitens* was chosen for this study because comparative data are already available describing its use of time and energy in various portions of the annual cycle and in 2 different habitats (Walsberg 1977).

The annual cycle of the Phainopepla is perhaps unique in that it apparently breeds twice annually, once in both its winter and summer ranges (Walsberg 1977). In the United States, Phainopeplas winter primarily in the Sonoran Desert, where they breed in March and April. They then move to semiarid woodlands east, west, and north of that desert, where they breed from May through July. My previous studies

(Walsberg 1975, 1977) dealt primarily with the biology of Phainopeplas in 2 portions of these seasonal ranges, the Colorado Desert (that portion of the Sonoran Desert in California) and the riparian woodlands of the Santa Monica Mountains in coastal southern California. Sharp contrasts in territoriality and foraging behavior are seen between these 2 seasonal habitats. Large (\bar{x} = 0.40 ha) feeding and nesting territories are defended along washes in the Colorado Desert, whereas territories are much smaller (\bar{x} = 0.03 ha) and restricted to courtship and nesting in the Santa Monica Mountains. In this latter area, coloniality is common and is associated with socially facilitated foraging. Distinct differences also occur between the 2 habitats in breeding behavior, breeding success, and clutch size. Associated with the use of the 2 contrasting social systems, the Phainopepla's use of time differs greatly between habitats. Woodland birds spend much more time in foraging flights and social behavior than do desert birds. This increased time spent in flight is primarily responsible for the increased rates of energy expenditure occurring in the coastal woodlands as compared to the desert. In the woodlands, Phainopeplas expend 20–30% more energy per day than do desert birds of comparable breeding status. Within either habitat, the daily energy expenditure of nonbreeding and incubating birds is similar, and equal to ≈ 75 –80% of that of adults feeding nestlings. Sample sizes in my previous study (Walsberg 1977)

¹ Manuscript received 22 November 1976; accepted 29 July 1977.

were too small to allow comparison of the time and energy budgets of adults raising different numbers of young. This relates only to the coastal woodlands, where clutches of either 2 or 3 eggs are laid ($\bar{x} = 2.46$), since clutch size in the Colorado Desert is virtually always 2 (Walsberg 1977).

It is the breeding of Phainopeplas from late May through July in the coastal woodlands of California which this study will consider. In this area, territories usually consist simply of a tree used for nesting, generally an oak or sycamore, plus a small marginal area. Loose colonies of 4–15 pairs are often formed. Food, which is usually obtained outside of the defended territory, consists primarily of small berries, though the young are also fed large amounts of insects. The buckthorn, *Rhamnus crocea*, is the major fruit source during the breeding period in the Santa Monica Mountains, where this study was conducted. Fruiting shrubs which Phainopeplas feed upon in this area are largely restricted to chaparral-covered hillsides and are isolated (usually at least 100 m) from the riparian woodlands in the canyon bottoms. Thus, Phainopeplas make periodic foraging flights throughout the day from their nest tree to the hillside chaparral. Insects are caught during sallying flights from a perch.

METHODS

Study site

All Phainopeplas studied nested in the same colony and foraged in the same areas of hillside chaparral, although data were gathered in 2 different yr (1974 and 1976). This colony was located in Decker Canyon, Ventura County, California, ≈ 1 km south of Westlake Village. The canyon bottom is dominated by valley oak (*Quercus lobata*) and sycamore (*Platanus racemosa*), with a ground cover of grass and a few scattered shrubs—mostly poison oak (*Rhus diversiloba*) and laurel sumac (*Rhus laurina*). Hillsides are dominated by grass, intermixed with patchy, low chaparral, consisting mainly of chamise (*Adenostoma fasciculatum*) with a scattering of other shrubs, primarily buckthorn, laurel sumac, and poison oak.

Time budgets

For each time budget, an individual color-banded Phainopepla was timed with stop watches 30 consecutive min during every hour, from the time it first became active until it roosted for the night. I always remained at such a distance (usually at least 30 m) that the bird's behavior was not noticeably affected. Time budgets were calculated for parent birds 5 to 6 days after their eggs hatched, when the young reached ≈ 50 –60% adult weight (Crouch 1939). Sixteen birds were timed for 1 day each, representing 8 mated pairs. Budgets 1, 2, 9, 5, 6, and 13 were reported previously as budgets 27–32, respectively, in Walsberg (1977). Activity was divided into 7 categories, all except flight

being mutually exclusive: (1) flight; (2) perching; (3) transit, including all locomotion when social behavior or flycatching were not involved; (4) foraging at a fruiting shrub; (5) flycatching, including only the time actually spent in flight; (6) nest attentiveness, the time spent at the nest; and (7) social activity, including aggression and territorial displays. Not included in this category was territorial advertisement by calls, unless obviously stimulated by an intruder. Knowing the time spent in flight and the total time active per day allows calculation of time spent at 3 activity levels: (1) flight; (2) nonflight activity, equal to the bird's active day minus the time spent in flight; and (3) inactive, presumably asleep.

Estimates of energy expenditure

Two general assumptions were made for estimates of energy expenditure. All adult Phainopeplas were assumed to weigh 24.0 g, the average of 33 wild-caught birds (Walsberg 1977). The energy equivalent of consumed O_2 is assumed to be 20.1 kJ/litre O_2 (1 kilojoule = 0.239 kilocalorie).

Energy expenditure during flight (\dot{E}_f).— \dot{E}_f was estimated using the least-squares regression line that Hart and Berger (1972) fitted to measured \dot{E}_f in 9 bird species. This equation predicts 12.51 kJ/h as the cost of flight for a 24-g bird. Exercise metabolism at the high work levels of flight is assumed to include maintenance energy expenditure and to be temperature independent (i.e., the waste heat of flight activity substitutes for cold-induced thermogenesis), as indicated by the work of Lasiewski (1963), Tucker (1968), and Berger and Hart (1972).

Nonflight energy expenditure.—Nonflight energy expenditure is assumed to incorporate 2 independent quantities, temperature-dependent maintenance metabolism (\dot{E}_m , calculated for the entire day minus time spent in flight), plus an activity increment during nonflight portions of the active day (\dot{E}_{nf}). Thus, exercise metabolism at the low work levels of nonflight activity is considered additive to maintenance metabolism at or below thermal-neutral temperatures (i.e., the waste heat of nonflight activity does not substitute for cold-induced thermogenesis), as indicated by the work of West and Hart (1966), Kontogiannis (1968), Pohl (1969), and Pohl and West (1973). Increased energy expenditure associated with heat stress was not considered in this study, because ambient temperatures never exceeded the Phainopepla's upper critical temperature (43°C, Walsberg 1977) and panting was rarely observed.

\dot{E}_m is assumed to equal the minimal metabolic rate of a fasting bird resting at a specified ambient temperature and is estimated using a regression line fitted to O_2 consumption data measured below the thermal-neutral zone in Phainopeplas (Walsberg 1977). Shade air temperatures (measured 2 m above ground) probably

adequately reflect the average thermoregulatory demand experienced by the bird over a 24-h period, as indicated by the work of Mahoney (1976) and Walsberg (1977). Air temperature was measured hourly at the initiation of each time-budget period and was recorded continuously throughout the night using a mechanical thermograph.

An average daily temperature can be used to predict an average maintenance metabolic rate after correction for 2 sources of error. First, such an average temperature includes periods when ambient temperature exceeds the lower critical temperature (T_{lc}). During these periods, \dot{E}_m is not predicted by the equation of the line below thermal neutrality. This involved only the bird's active period, since nocturnal temperatures never exceeded the T_{lc} (29°C, Walsberg 1977). To correct for this error, all hourly temperatures during the active period that exceeded the T_{lc} were set equal to it.

The second error relates to the inclusion in a simple average daily temperature of the temperatures of periods when the bird is in flight and energy expenditure is not temperature-dependent. This was corrected by weighting temperatures taken hourly at the initiation of each time-budget period (T) by the proportion of time not spent in flight during that period (P).

The corrected mean daily temperature (T_m) was based upon (1) the average of these weighted temperatures, and (2) the average nocturnal temperature (T_n), calculated by integrating with a planimeter the temperature curve produced by the mechanical thermograph. Thus,

$$T_m = \frac{\left[\sum_{i=1}^n (T_i P_i) \right] + (T_n h_n)}{h_{nr}},$$

where h_n is the length (in hours) of the bird's inactive period and h_{nr} is the total hours per day not spent in flight.

Previously (Walsberg 1977), I calculated energy budgets alternatively using shade air temperatures or a temperature model that incorporated a crude estimate of the effect of direct solar radiation. Whenever reference is made to data from Walsberg (1977), only calculations based upon shade air temperatures will be used, in order that the data be comparable to those of the present study.

The average increment of energy expenditure over maintenance levels that is due to nonflight activity was previously estimated, based upon laboratory measurements as 0.636 kJ/h for a 24-g *Phainopepla* (Walsberg 1977). This equals 54% of the basal metabolic rate (BMR), so that a bird in nonflight activity in thermal neutrality has an energy expenditure equal to $1.54 \times \text{BMR}$. This value is close to those derived independently by a number of authors, which range from 1.5 to $2.0 \times \text{BMR}$ (Gessaman 1973). Estimates of daily energy expenditure are relatively insensitive to this assumption. A 50% increase in the estimate of 0.636 kJ/h would

increase estimated daily energy expenditure a mean of only 3.9%.

RESULTS AND DISCUSSION

Time expenditure

Time budgets are presented in Table 1, and mean values for *Phainopeplas* raising 2 or 3 young are compared in Table 2. Per pair, the greatest difference observed is the 42% mean increase in time spent flycatching associated with raising a third nestling. Because adult *Phainopeplas* in this area are primarily frugivorous while breeding and insects are eaten extensively only by the nestlings (Walsberg 1977), one would expect flycatching to increase directly with brood size. This should produce a 50% increase in flycatching for a 50% increase in brood size—very close to the observed value. Average time per pair spent foraging at fruiting shrubs increased much less than did flycatching, being only 16% higher in pairs raising 3 young instead of 2. I estimate (see below) that the addition of a third nestling to the brood should increase the total energy requirements of the parents and young $\approx 18\%$, closely approaching the increase in time spent foraging for fruit. Pairs raising 3 nestlings spent an average of 22% more of their active day in flight than did adults with only 2 nestlings. This resulted in an average increase of $1.22 \text{ h} \cdot \text{day}^{-1} \cdot \text{bird}^{-1}$ in flight.

Energy expenditure

Energy budgets are presented in Table 3 and average values for birds raising 2 or 3 young are compared in Table 4. Neither total energy expenditure nor any of its components described in Tables 3 and 4 differ more than a mean of 2% between males and females with the same brood size. Per pair, the largest change is the 18% average increase in flight costs for adults feeding 3 nestlings instead of 2. Total daily energy expenditure for *Phainopeplas* raising a third nestling is increased a surprisingly small amount—a mean of only 7%, or 12.0 kJ/pair. Males are affected slightly more (\bar{x} increase = 8%) than females (\bar{x} increase = 6%), but the difference is not statistically significant (Student's *t*-test, $P > 0.20$).

The total energetic cost to the parents over the breeding period associated with raising a third young can be estimated assuming that the 7% difference at days 5 and 6 (midway through nestling growth) reflects the average increment over the entire nestling period, and by estimating the energetic cost of egg synthesis and incubation. Previously, I estimated that the synthesis of 1 *Phainopepla* egg requires 16.0 kJ and that incubating *Phainopeplas* in the Santa Monica Mountains expend a mean of $142.2 \text{ kJ} \cdot \text{day}^{-1} \cdot \text{pair}^{-1}$ (Walsberg 1977). I assume that there is no substantial difference in incubation costs associated with the 2 different clutch sizes. Errors due to this assumption should be minor. Even if incubating a third egg entailed a 20% increase in main-

TABLE 1. Time budgets of *Phainopepla* and associated temperature data

No.	Sex	Brood size	Date ¹	Mate ²	Percent of active day spent:						Length of active day (h)	T _m (°C)
					Flying	Perching	In transit	Eating fruit	Fly-catching	At nest	In social activity	
1	♂	2	21 Jun	5	21.1	63.0	13.0	3.9	8.7	7.9	3.5	14.61
2	♂	2	28 Jun	6	23.0	65.1	11.9	3.6	9.9	7.4	2.1	14.68
3	♂	2	17 Jun	7	24.2	62.1	10.0	3.0	9.6	9.0	6.3	14.49
4	♂	2	18 Jun	8	19.6	68.4	11.0	4.0	7.7	8.3	0.5	14.62
5	♀	2	22 Jun	1	21.5	54.5	15.7	4.1	7.6	8.0	10.1	14.67
6	♀	2	29 Jun	2	27.1	54.0	16.1	4.7	10.1	8.9	8.9	14.36
7	♀	2	17 Jun	3	16.0	59.4	12.2	3.8	12.1	10.5	2.0	14.60
8	♀	2	18 Jun	4	20.1	64.6	11.6	3.2	8.3	8.6	3.7	14.58
9	♂	3	3 Jul	13	28.9	58.0	14.1	5.0	11.5	7.8	3.6	14.52
10	♂	3	15 Jun	14	28.5	57.4	15.3	5.0	12.0	7.6	2.7	14.59
11	♂	3	21 Jun	15	25.4	58.1	12.3	3.7	12.2	10.7	3.0	14.68
12	♂	3	26 Jun	16	28.4	51.8	14.6	4.1	15.0	9.4	5.1	14.51
13	♀	3	4 Jul	9	24.2	48.7	16.7	4.8	12.2	8.2	9.4	14.53
14	♀	3	15 Jun	10	30.3	54.8	14.3	4.6	13.4	8.3	4.6	14.51
15	♀	3	21 Jun	11	25.8	60.7	12.5	3.3	13.0	9.5	1.0	14.34
16	♀	3	26 Jun	12	30.3	50.6	16.2	4.7	15.6	9.8	3.1	14.68

¹ Budgets 1, 2, 9, 5, 6, and 13 were calculated in 1974 and were reported previously as budgets 27–32, respectively, in Walsberg (1977). All other data were collected in 1976.

² Identifies time budget of individual's mate.

tenance metabolism (\dot{E}_m) while the parent is on the nest, total parental energy expenditure from egg synthesis to fledging would be increased a mean of only 2%. Assuming the incubation period is 14 days and the nestling period is 20 days (Crouch 1939), total parental energy expenditure per pair from egg synthesis to fledging is 5,465 kJ for pairs raising 2 young ($= [2 \times 16.0] + [14 \times 142.2] + [20 \times 172.1]$) and 5,721 kJ for pairs raising 3 young ($= [3 \times 16.0] + [14 \times 142.2] + [20 \times 184.1]$). Thus, total parental energy expenditure is increased only 4.7% for a 50% increase in brood size.

A value possibly approaching a type of cost:benefit ratio in breeding is the quantity of energy expended per young produced. The above estimates of a pair's expenditure from egg synthesis to fledging are equal to a mean of 2,732 kJ/young for pairs producing 2 young and only 1,907 kJ/young for pairs producing 3 young, or 30% less. Of the clutches laid in the coastal woodlands of California, 54% consist of 2 eggs and 46% consist of 3 eggs (Walsberg 1977); thus, the mean energy expenditure per pair of this population is 2,253 kJ/young. A comparable value can be calculated from data in

TABLE 2. A comparison of mean time budgets for adults with different brood sizes¹

	Flight	Perching	In transit	Eating fruit	Fly-catching	At nest	Social activity
♂♂							
Percent of day spent in activity,							
♂♂ with 3 nestlings:	27.8	56.3	14.1	4.5	12.7	8.9	3.6
♂♂ with 2 nestlings:	22.0	64.7	11.5	3.6	9.0	8.2	3.1
Ratio of values ² :	1.26	0.87	1.23	1.25	1.41	1.09	1.16
Statistically significant differences ³ :	X	X	X		X		
♀♀							
Percent of day spent in activity,							
♀♀ with 3 nestlings:	27.7	53.7	14.9	4.4	13.6	9.0	4.5
♀♀ with 2 nestlings:	23.7	58.1	13.9	4.0	9.5	9.0	6.2
Ratio of values ² :	1.17	0.92	1.07	1.10	1.43	1.00	0.73
Statistically significant differences ³ :	X	X			X		
̄ value per pair.							
Percent of day spent in activity,							
pairs with 3 nestlings:	27.9	55.7	14.6	4.4	13.1	8.9	4.1
pairs with 2 nestlings:	22.9	61.4	13.0	3.8	9.2	8.6	4.3
Ratio of values ² :	1.22	0.91	1.12	1.16	1.42	1.03	0.95
Statistically significant differences ³ :	X	X			X		

¹ Within each brood size category, sample size is 4 for ♂♂, ♀♀, and mated pairs.

² Calculated as: (value for adults with 3 nestlings)/(value for adults with 2 nestlings).

³ Student's *t*-test, *P* < .05.

TABLE 3. Daily energy budgets of Phainopeplas

No. ¹	Energy expenditure (kJ/day) due to:			Total daily expenditure
	Maintenance ²	Nonflight activity ³	Flight ⁴	
1	35.21	6.87	47.56	89.64
2	36.22	7.20	42.29	85.67
3	36.85	6.99	43.92	87.59
4	36.72	7.49	35.80	79.93
5	36.97	7.33	39.57	83.82
6	35.05	6.66	48.69	90.40
7	35.97	6.87	47.44	90.23
8	35.88	7.33	38.06	81.23
9	35.00	6.53	52.55	94.12
10	34.21	6.62	52.04	92.87
11	35.84	6.95	46.69	89.43
12	36.09	6.62	51.54	94.21
13	35.09	6.99	44.05	86.13
14	32.62	6.41	55.06	94.04
15	35.59	6.82	46.69	89.02
16	34.67	6.49	55.69	96.80

¹ See Table 1 for sex, date, and brood size data.² Temperature-dependent maintenance metabolism for nonflight periods (see **Methods** section).³ Does not include maintenance expenditure for nonflight periods (see **Methods** section).⁴ Total energy expenditure for periods spent in flight, including maintenance expenditure (see **Methods** section).

Walsberg (1977) for Phainopeplas breeding in a contrasting habitat, the Colorado Desert. Here, mean energy expenditure from egg synthesis to fledging is 4,588 kJ/pair, or 80% of the value for coastal birds with 2 nestlings. Because average clutch size in the Colorado Desert is 2.0, 2,294 kJ are expended per young

produced—only 2.6% different from the population average in the coastal woodlands. (The proportion of eggs that produce fledged young apparently does not differ significantly between the 2 habitats [Walsberg 1977].) This remarkable coincidence in energy expenditure per young produced is the product of apparently independent parallel increases in clutch size and energy expenditure. Clutch size averages 23% greater in the coastal woodlands than in the Colorado Desert, probably associated with greater insect abundance, and energy expenditure averages $\approx 20\%$ greater in the woodlands than in the desert, associated primarily with qualitative changes in territorial systems and foraging patterns (Walsberg 1977). That these parallel increases are independent is further supported by the weak coupling demonstrated in this study between brood size and parental energy expenditure.

Harvesting requirements

The minimal amount of energy that a Phainopepla must acquire in its daily foraging can be estimated by (1) assuming the bird is in energy balance and acquires energy at a rate equal to its expenditure, and (2) estimating the energy requirements of any nestlings it is feeding, including maintenance and growth metabolism. The assumption of energy balance may be violated if adult Phainopeplas lose weight while feeding young, as do some other species (Ricklefs 1974). However, even a 20% body weight loss in pure fat (40 kJ/g, Kleiber 1961) would reduce parental harvesting requirements a mean of only 7–9%, assuming fat is used at a constant rate

TABLE 4. A comparison of mean energy budgets for adults with different brood sizes¹

	Energy expended for:			
	Maintenance ²	Nonflight activity ³	Flight ⁴	Total daily expenditure
♂ ♂				
Energy expenditure (kJ/day),				
♂ ♂ with 3 nestlings:	35.30	6.70	50.70	92.66
♀ ♀ with 2 nestlings:	35.26	7.16	42.41	85.71
Ratio of values ⁵ :	0.97	0.94	1.20	1.08
Statistically significant differences ⁶ :		X	X	X
♀ ♀				
Energy expenditure (kJ/day),				
♀ ♀ with 3 nestlings:	34.50	6.70	50.37	91.49
♀ ♀ with 2 nestlings:	35.97	7.03	43.46	86.42
Ratio of values ⁵ :	0.96	0.95	1.16	1.06
Statistically significant differences ⁶ :		X	X	X
Total per mated pair.				
Energy expenditure (kJ/day),				
pairs with 3 nestlings:	69.80	13.36	101.1	184.1
pairs with 2 nestlings:	72.22	14.19	85.79	172.1
Ratio of values ⁵ :	0.97	0.94	1.18	1.07
Statistically significant differences ⁶ :		X	X	X

¹ Within each brood size category, sample size is 4 for $\delta\delta$, $\varphi\varphi$, and mated pairs.² Temperature-dependent maintenance metabolism for nonflight periods (see methods section).³ Does not include maintenance metabolism during periods of nonflight activity (see methods section).⁴ Total energy expenditure for periods spent in flight, including maintenance metabolism (see methods section).⁵ Calculated as: (value for adult with 3 nestlings)/(value for adult with 2 nestlings).⁶ Student's *t*-test, $P < .05$.

TABLE 5. A comparison of some energetic parameters between Phainopeplas residing in the Colorado Desert and the coastal woodlands of southern California¹

Parameter and locality	Breeding status:			
	Nonbreeding	Incubating	Feeding 2 nestlings	Feeding 3 nestlings
Daily energy expenditure (kJ/day).				
Coastal woodlands:	76.50 (3)	71.09 (6)	86.06 (8)	92.07 (8)
Colorado Desert:	60.63 (7)	59.02 (4)	72.81 (6)	...
Ratio of values ² :	1.26	1.21	1.18	1.26 ⁴
Statistically significant differences ³ :	X	X	X	X
Daily harvesting requirements (kJ/day).				
Coastal woodlands:	76.50 (3)	71.09 (6)	117.4 (8)	139.1 (8)
Colorado Desert:	60.63 (7)	59.02 (4)	104.2 (6)	...
Ratio of values ² :	1.26	1.21	1.13	1.33 ⁴
Statistically significant differences ³ :	X	X	X	X
Average harvesting rate (kJ/h active).				
Coastal woodlands:	5.23 (3)	4.90 (6)	8.04 (8)	9.46 (8)
Colorado Desert:	5.99 (7)	4.98 (4)	8.08 (6)	...
Ratio of values ² :	0.87	0.98	0.99	1.17 ⁴
Statistically significant differences ³ :				X

¹ Data for woodland birds feeding nestlings from present study, all other data from Walsberg (1977). Values given are on an individual basis, not per mated pair, and assume that the sexes share equally in feeding the young. Data for ♂♂ and ♀♀ are combined, because sexes differed <5% in each category.

² Calculated as: (value for woodland birds)/(value for desert birds).

³ Student's *t*-test, *P* < 0.05.

⁴ Calculated as: (value for woodland birds with 3 nestlings)/(value for desert birds with 2 nestlings).

during the nestling period. Estimation of nestling growth requirements requires knowledge of the growth rate, the energy density of tissues, and the efficiency of growth processes. Though the nestling growth curve for *Phainopeplas* is sigmoidal, growth is virtually linear from day 5 through 14, when it averages 2.3 g/day (Crouch 1939). I will assume that this average rate applies to days 5 and 6. The energy density of the nestling is assumed to be 5.23 kJ/g, the average estimate at 50% adult weight for 7 passerine species reviewed by Ricklefs (1974). Assuming a 75% net efficiency of synthesis (Ricklefs 1974), the energy required for growth is estimated as $16.04 \text{ kJ} \cdot \text{day}^{-1} \cdot \text{nestling}^{-1}$ ($= 2.3 \text{ g} \times 5.23 \text{ kJ/g} \div 0.75$). Nestling maintenance metabolism is estimated as equal to the adult's weight-specific basal metabolic rate (Ricklefs 1974), which is $1.18 \text{ kJ} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ (Walsberg 1977). This equals 15.34 kJ/day, assuming 5- to 6-day-old nestlings weigh 13 g (Crouch 1939). (Estimates of the total energy requirements of the parents and nestlings are relatively insensitive to assumptions regarding this parameter. A 50% increase in the nestlings' maintenance metabolism or an equal increase in energy expenditure due to nestling activity would increase the parents' required harvesting only 6.5% for pairs raising 2 nestlings and 8.3% for pairs raising 3 nestlings.) The total cost per nestling for growth and maintenance is thus estimated as 31.38 kJ/day. Total harvesting requirements for pairs feeding 5- to 6-day-old nestlings are presented in Table 5, and are compared to values calculated using the above assumptions and data from Walsberg (1977) for nonbreeding and incubating birds in the coastal woodlands, as well as nonbreeding and breeding *Phainopeplas* in the Col-

orado Desert. These data suggest that raising a third nestling in the coastal woodlands requires the adults to acquire 18% more energy per day, which is a substantially greater increase than that in the rate of parental energy expenditure (7%).

An alternative way to consider harvesting requirements is in terms of the average harvesting rate per hour active, rather than the total energy acquired over an entire day (Table 5). During their June–July breeding in the coastal woodlands of California, *Phainopeplas* are exposed to substantially longer daylengths than during their March–April breeding in the Colorado Desert. These differences in available foraging time almost exactly compensate for differences in the amount of energy which must be acquired (Table 5). If brood size is held constant at 2 young, total energy requirements during the nestling period average 13% greater in the woodlands than in the desert, but because woodland birds have an active day averaging 12% longer than desert birds, the average harvesting rates (kilojoules/h active) differ <1% between habitats. A similar situation occurs during the nestling period. Parental energy expenditure averages 21% greater in the woodlands than in the desert, but because the active day averages 23% longer in the woodlands, the amount of energy which must be acquired per hour active differs a mean of only 2% between habitats. Thus, regardless of the striking differences in parental energy expenditure, habitat, time of year, and social system used, a *Phainopepla* incubating or feeding 2 young in the coastal woodlands must acquire energy at the same rate as it would in a comparable stage of breeding in the Colorado Desert. *Phainopeplas* raising a third young in the woodlands are

conspicuous exceptions; their average harvesting rates are 18% higher than pairs feeding 2 nestlings in either the desert or the coastal area. Though the ecological significance of these results is not certain, it is tempting to speculate that the values for incubating *Phainopeplas* and those feeding 2 young represent evolutionary optima. If so, feeding a third young requires foraging above the optimum rate during the nestling period; this may be a selective factor favoring broods of 2.

These convergences in average harvesting rates are produced by essentially independent increases in daylength and energy requirements. For example, although daylength is also increased $\approx 23\%$, energy requirements during incubation are increased 23% in the woodlands compared to the desert primarily because woodland birds spend a mean of 4 \times as much of their active day in flight as do desert birds. These differing amounts of flight are associated with contrasting territorial and foraging systems (Walsberg 1977).

Are the convergences that have been described between the 2 breeding habitats in harvesting rates and parental energy expenditure per young produced merely fortuitous events, or do they reflect regulation of energetic variables by the *Phainopepla*? Certainly, such constancy in factors associated with reproduction is intriguing, but constancy in itself does not demonstrate regulation. It is readily possible, however, that *Phainopeplas* do regulate these variables. This could be accomplished, for example, by choice of nest location in relation to foraging sites. During the period between the mid-April entry of *Phainopeplas* into the coastal area and their breeding from late May through July, the local distribution of this species is distinctly unpredictable. *Phainopeplas* frequently establish territories and occupy an area, only to abandon that locality after a number of days. On occasion, established colonies (i.e., after nest construction but prior to egg laying) apparently shift location *en masse* (Walsberg 1977). At least in part, this behavior probably represents an exploration and evaluation of potential breeding sites. Possibly, a more specific function is the locating of sites which will allow the birds to reproduce at the apparently optimal levels which have been described above for harvesting rates or parental energy expenditure per young produced.

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