

## SIZE DIMORPHISM: A FACTOR IN ENERGY SAVINGS FOR BROAD-WINGED HAWKS

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SEXUAL size dimorphism exists in many species of birds. Usually the male is larger than the female. Darwin (1922) explained this phenomenon on the basis of intrasexual competition among the males for the possession of mates. The larger males secure more mates and therefore pass on the genetic factors for larger size to more offspring. Although this explanation is generally accepted today (Amadon 1959), it does not explain the reversed size dimorphism (i.e. male smaller than the female) manifest in several groups of birds, including the raptors. Several hypotheses have been previously offered to explain size dimorphism in raptors. Reynolds (1972) reviewed the literature dealing with sexual dimorphism in raptors and offered the hypothesis that the reduced size of the male accipiters gives them a greater foraging efficiency. In summary, he reports (p. 196):

"Since there are greater numbers of species and individuals of smaller avian prey (Eltonian pyramid of numbers), a decrease in size would result in an increase of encounters of optimal, accessible prey. If a smaller male encounters more optimal, accessible prey, and has reduced metabolic needs, then his efficiency at procuring excess food more frequently and at more regular intervals is enhanced."

The question of "reduced metabolic needs" raised by Reynolds is pertinent to this study and the crux of our hypothesis.

In this paper we demonstrate the relationship between size dimorphism and the energy requirements of nesting pairs of Broad-winged Hawks (*Buteo platypterus*) and present a model that predicts the total daily energy saved by a pair of nesting Broad-wings from the magnitude of their size dimorphism.

The hypothesis tested was that the daily energy needs of a dimorphic pair of Broad-wings are reduced from that for a hypothetical monomorphic pair as a direct result of the male's smaller size. That is, as the male becomes smaller than the female the total energy requirements of the pair are reduced.

In order to test this hypothesis, the specific objectives of this study were: (1) to determine the mean metabolic rate of captive male and female Broad-winged Hawks, (2) to estimate the daily energy requirements of free-ranging female Broad-wings during the nesting season from food habits data, and (3) to relate energy savings of nesting pairs of Broad-wings to size dimorphism.

TABLE 1  
WEIGHTS AND MEASUREMENTS OF BROAD-WINGED HAWKS FROM THE  
CENTRAL ADIRONDACKS

Females				Males			
Weight (g)	Wing chord (mm)	Tail (mm)	Sexing method <sup>1</sup>	Weight (g)	Wing chord (mm)	Tail (mm)	Sexing method
389	274	164	3	400	266	146	2
454	286	161	2	360	268	151	3
455	292	178	3	350	272	156	3
420	291	174	3	310	262	152	3
410	—	—	1	345	266	151	3
460	282	163	3	—	275	156	1
447	289	171	3	355	273	142	3
448	286	166	3	375	266	146	3
447	286	162	1	369	278	156	4
459	289	165	1	347	268	151	4
417	279	155	4				
$\bar{X} = 437$	285	166		357	269	161	
SD = 23.8	5.6	6.7		24.6	4.9	4.8	

<sup>1</sup> Numbers designate the method of sexing as follows: 1, internal examination of sex organs; 2, based on courtship behavior at the time of capture; 3, based on behavior of marked nesting pairs; 4, comparison of weight, wing chord, and tail measurements against birds sexed by methods 1, 2, and 3.

#### METHODS

*Capture and care of experimental birds.*—We trapped seven experimental birds used in this study in the general vicinity of the Archer and Anna Huntington Wildlife Forest Station at Newcomb, New York, circa 44° N and 74°, 10' W, between 26 April and 4 May 1972. We caught six birds with a Bal-chatri trap (Berger and Mueller 1959) and the seventh in a bow net trap (Tordoff 1954). All traps were baited with mice, either *Mus* sp. or *Peromyscus* sp.

Captured birds were weighed, and weights adjusted according to crop contents, 30 g being deducted for a full crop. All body weights in this study were taken using a spring scale (0–500 g) accurate to within 5 g. Wing chord and tail were measured in the manner of Mueller and Berger (1968).

We marked captive birds with colored leg bands made of vinyl-coated nylon. They were then tethered to ring or block perches in a chicken-wire enclosure, covered with black plastic sheeting. The enclosure was out-of-doors and shaded by the forest canopy.

We fed the birds each morning a diet of lean venison with occasional parts of snowshoe hare (*Lepus americanus*) and Ruffed Grouse (*Bonasa umbellus*).

*Sex determination.*—Sexing Broad-winged Hawks is difficult because the sexes show no apparent plumage differences, nor is size entirely reliable as a sex character. We sexed 21 birds, including all of the experimental birds, by one or more of the following methods: (1) internal examination of sex organs, (2) behavior of marked individuals at active nests, (3) behavior of paired birds at the time of capture, or (4) comparison of weights and measurements with birds sexed by the other three methods. Marked nesting birds can be sexed by determining the total time each member of the pair spends incubating and/or the presence of a brood patch (Matray MS). Courtship feeding is common in raptors, wherein the male presents a captured prey item to the female (Olendorff 1971). Two of the

TABLE 2  
WEIGHTS OF RECAPTURED BROAD-WINGED HAWKS IN THE CENTRAL ADIRONDACKS

Earliest capture date <sup>1</sup>	Weight (g)	Latest capture date <sup>1</sup>	Weight (g)	Sex
25 April 1972	389	13 May 1971	460	♀
29 April 1972	398	3 May 1971	425	?
6 May 1971	375	13 July 1972	360	♂
2 May 1971	380	27 July 1972	310	♂

<sup>1</sup> Earliest and latest refer to the point during the nesting season that the individual was weighed irrespective of the year.

experimental birds were sexed by noting this behavior, two were sexed internally, and the other three were sexed by comparing weights, wing chord, and tail measurements with the 18 other birds sexed by various means (Table 1).

When body weights were used to determine sex, the mean weights of unsexed birds over periods of 30 to 60 days were compared to the capture weights of the sexed birds to increase the reliability of decisions. Although body weight is usually a satisfactory measure for separating the sexes, several factors causing weight variability, such as crop, stomach, and cloacal contents, must be considered. We estimated crop contents and subtracted these from body weights. The stomach contents of a fully developed juvenile, which was autopsied, weighed 42 g. The maximum weight change over 24 hours for any captive bird was 49 g. Variability in weight for individuals is also shown by data for four recaptured birds (Table 2).

*Conversion factors.*—We oven-dried five samples of fresh lean venison, 42 samples of wasted venison (i.e. venison that was offered but not consumed, and therefore exposed to drying for about 24 hours), and 12 samples of excreta to constant weight to determine wet to dry weight conversion factors (Table 3).

One batch of fresh venison, noticeably drier than the others, was not included in the mean for fresh venison in Table 3. It had a measured conversion factor of 27.1% for a single sample, and this value was used in the calculations for those days when the birds were fed from this batch.

*Metabolic rate determination.*—We measured the daily metabolic energy requirement for each experimental bird over a period of 20 to 28 days employing food balance calorimetry. During this period the birds were housed in 51 cm × 61 cm × 61 cm metal metabolism cages (Figure 1) within the enclosure. Birds were weighed and fed a measured amount of food daily. We collected and weighed wasted food and cleaned cages daily. We lined the cages with weighed

TABLE 3  
WET TO DRY WEIGHT CONVERSION FACTORS FOR VENISON AND  
BROAD-WINGED HAWK EXCRETA

Item	Dry weight/wet weight in %		
	Mean	Range	Sample size (n)
Fresh venison <sup>1</sup>	23.1	22.7–23.4	4
Wasted venison <sup>2</sup>	27.0	21.8–33.6	42
Excreta	19.3	17.2–24.3	12

<sup>1</sup> Lean venison from road-killed white-tailed deer (*Odocoileus virginianus*).

<sup>2</sup> Fresh venison that had been exposed to drying for about 24 hours.

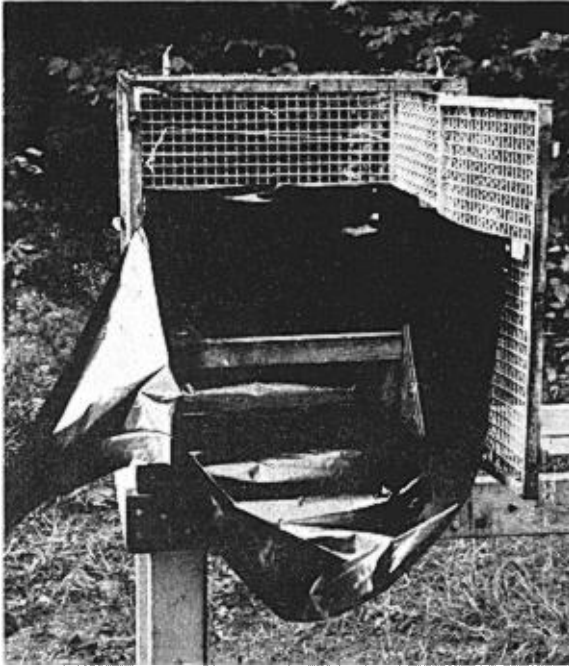


Figure 1. Metabolism test cage. Note plastic liner, perch and line connected to reed switches in top of cage to measure activity (51 cm  $\times$  61 cm  $\times$  61 cm).

plastic sheet linings for 11 days during the metabolism tests in order to collect and weigh the excreta produced.

We recorded activity by placing a trigger wire around the upper perimeter of the inside of each cage (Figure 1). The wire was connected to two reed switches fastened in opposite corners of the cage. The switches were wired to an Esterline-Angus event recorder. Each time the trigger wire was depressed, usually by the bird hitting it with its wing, a single event was recorded. These events were tabulated daily and an hourly average calculated. We converted these daily averages, expressed in events or counts per hour, to an activity index by dividing each daily average for each bird by the overall lowest daily average of any individual (excluding daily records of zero activity). Thus an individual with an activity index of 100 for one day struck the trigger wire 100 times more frequently than did the individual bird that recorded the lowest daily average for the experiment's duration.

We fed birds only lean venison during the metabolism tests so that their food intake was of uniform and known caloric value, and devoid of indigestible parts that are normally formed into pellets and regurgitated.

Gross caloric content of all materials in this study was determined using a Parr Adiabatic Bomb Calorimeter following standard procedures as described in the Book of ASTM Standards (Amer. Soc. for Testing and Materials 1967). No correction was made for sulphur content, as that of lean beef (assumed similar

to lean venison) may be estimated from the known percentage of sulphur-containing amino acids, at less than 0.03% of dry weight. Samples were oven-dried to constant weight at  $50^{\circ}\text{C} \pm 2^{\circ}$ .

We determined daily caloric intake by subtracting the dry weight of wasted venison from the dry weight of venison provided and multiplied this net intake by the caloric value of dry venison. Metabolized energy was determined by subtracting the caloric value of excreta produced each day from the daily caloric intake.

We calculated digestive efficiency (metabolized energy divided by daily caloric intake) for a period of 13 days and applied this to the days for which intake was known, but excreta produced was not known. In this way it was possible to estimate the metabolic rate for these latter days.

The relationship between activity and metabolic rate was examined via regression analysis using a computer program written by Martin (1969).

No adjustment for the effect of temperature on metabolic rate was necessary because all the captive birds were under the same temperature regime. Ambient temperature was recorded at the enclosure and for one week at an active Broad-wing nest with the temperature sensor in another tree about 50 m away and at about the same height as the nest.

*Food habits.*—We acquired food habits data during the 1971 and 1972 nesting seasons by direct observation at four active Broad-wing nests, and by tethering fledglings (Errington 1932) at two other nest sites.

Upon locating an active nest, we set up a blind either on the ground or in a nearby tree, from which a variable power spotting scope (20 $\times$  to 45 $\times$ ) enabled an observer to identify the species of nearly all prey items brought to the nest. In 1971 nests were watched for short periods each day at varying times with only a few full days of observation. In 1972 nearly all observations each day were made continuously from dawn to dusk (Matray MS).

The weights of prey items used to determine biomass were taken from recorded weights of study specimens at the Adirondack Ecological Center, from captured prey items, and from published information (Burt and Grossenheider 1952, Conner 1966).

## RESULTS

*Food habits.*—In this study, mammals and amphibians collectively comprised the greatest portion of the Broad-winged Hawk's diet (Table 4) both in frequency of prey items (74.0%) and in biomass (70.7%). The frequency of avian prey items (21%) was greater than the reptilian (5.7%), but reptiles made up a larger percent of the total biomass (23.4%) than did birds (6.1%). No invertebrate prey items were detected in this study.

Apparently the high percentage of mammals and amphibians in the Broad-wing's diet reflects the greater availability of these prey items in the Adirondacks, judging from a similar study by Rusch and Doerr (1972) in Alberta, Canada. These authors determined food preferences by analyzing pellets and prey remains of tethered Broad-wings. They found that the composition of prey items was 89% avian and mam-

TABLE 4  
FOOD HABITS OF BROAD-WINGED HAWKS IN THE CENTRAL ADIRONDACKS  
DURING THE 1971 AND 1972 NESTING SEASONS

Prey species	% frequency			% biomass			% kcal	
	1971	1972	Total	1971	1972	Total	Total	
Amphibians								
<i>Bufo americanus</i>	10.8	5.5	9.0					
<i>Rana clamatans</i>	0.5	} 7.3	3.9					
<i>Rana sylvatica</i>	1.3							
<i>Rana pipiens</i>	0.5							
Salamander	0.5	0.9	0.6					
Unidentified toad or frog	21.1	0.9	14.4					
TOTAL AMPHIBIANS	34.5	14.6	27.9	36.8	14.1	28.8	26.7	
Reptiles								
<i>Thamnophis sirtalis</i>	3.1	5.5	3.9					
Unidentified snake	2.7	—	1.8					
TOTAL REPTILES	5.8	5.5	5.7	24.6	21.0	23.4	24.9	
Birds								
Nestlings and fledglings	17.0							
Adults	5.4							
Unidentified birds	4.0							
TOTAL BIRDS	26.4	10.0	21.0	7.6	2.6	6.1	7.7	
Mammals								
<i>Sorex fumeus</i>	0.5	—	T <sup>2</sup>	T	—	T		
<i>Blarina brevicauda</i>	2.7	4.6	3.3	1.0	1.5	1.4		
<i>Condylura cristata</i>	1.3	2.7	1.8	1.9	3.4	2.4		
<i>Parascalops breweri</i>	0.9	—	0.6	1.4	—	0.9		
<i>Tamias striatus</i>	3.6	17.3	8.1	7.3	31.9	15.8		
<i>Tamiasciurus hudsonicus</i>	2.2	0.9	1.8	7.1	2.6	5.6		
<i>Glaucomys sabrinus</i>	—	0.9	T	—	1.6	1.1		
<i>Clethrionomys gapperi</i>	4.5	26.4	11.7	2.5	13.3	6.2		
<i>Peromyscus maniculatus</i>	0.5	2.7	1.2	T	1.2	0.6		
<i>Microtus pennsylvanicus</i>	0.5	—	T	T	T	T		
<i>Lepus americanus</i>	0.5	—	T	1.1	—	T		
Unidentified shrew, mouse or vole	16.1	14.6	15.6	8.0	6.6	9.4		
TOTAL MAMMALS	33.3	69.1	46.1	31.0	62.2	41.9	40.7	

<sup>1</sup> Sample size of 333 prey items brought to three nests in 1971 and one in 1972.

<sup>2</sup> Trace (less than 0.5%).

malian, only 9% amphibian, and 2% invertebrate. No reptiles were brought to the young.

Earlier investigators have reported from stomach analyses only small numbers of avian prey items (less than 10% by frequency) but large numbers of invertebrates (54 to 80%) (Burns 1911, May 1935, Mc-Attee 1935, Mendall 1944). These data were collected throughout the year and from various localities. Errington (1932) felt that stomach

TABLE 5  
DIGESTIVE EFFICIENCY OF CAPTIVE BROAD-WINGED HAWKS<sup>1</sup>

Individual	% efficiency mean ( $\pm$ SD)	Measurements (n)
No. 1	77.2 ( 4.4)	8
2	78.9 (12.6)	11
3	72.3 (12.1)	10
4	79.1 ( 6.1)	11
5	72.4 (13.8)	9
6	75.5 ( 9.7)	11
7	73.1 (10.2)	11
TOTAL	74.1 (10.2)	71

<sup>1</sup> Digestive efficiency equals metabolizable energy divided by energy intake.

analyses do not contribute the best quantitative data. Pellet analysis is similarly considered an unreliable indication of hawk food habits (Glading et al. 1943).

*Bioenergetics.*—Mean values for digestive efficiency ranged from a low of 72.3% to a high of 79.1% (Table 5). Gross caloric values measured in this study for venison and excreta,  $5.35 \pm 0.04$  kcal/g-dry weight ( $n = 7$ ) and  $2.86 \pm 0.07$  kcal/g-dry weight ( $n = 19$ ) respectively, are quite close to the previously published values of 5.6 kcal for venison (Golley et al. 1965) and 2.7 kcal for excreta (Graber 1962). The lower value for venison, compared to that of Golley, is probably due to differences in the condition of the animals. Golley's deer may have had a higher level of fat as they were collected during the fall.

Prey biomass was converted to kilocalories using published energy values for mammals of 4.1 kcal/g-dry weight (from Graber 1962) and for birds (chicken parts) of 5.7 kcal/g-dry weight (from Golley et al. 1965) and from direct measurements in this study for amphibians (4.1 kcal/g,  $n = 3$ ) and reptiles (4.7 kcal/g,  $n = 3$ ). The sample amphibian and reptile were the leopard frog (*Rana pipiens*) and the garter snake (*Thamnophis sirtalis*) respectively, both captured on the Huntington Forest.

*Experimental determination of metabolic rates.*—The results of the metabolic rate determinations are presented in Table 6. The "overall mean rate" is the mean metabolic rate for all days for which it was calculated. Periods varied from 20 to 28 days, as on some days excreta or wasted food could not be weighed, and on other days no food was consumed.

The "constant weight interval" was arbitrarily selected as a period of at least 10 days over which no net change occurred in the individual's weight. The weight selected was the individual's mean weight  $\pm 10$  g.

TABLE 6  
MEAN DAILY METABOLIC RATES FOR CAPTIVE BROAD-WINGED HAWKS

Individual	Sex	Overall mean rate <sup>1</sup>				Rate by constant weight interval <sup>1</sup>			
		Mean M.R.		Mean weight (g)	Sample size (days)	Mean M.R.		Mean weight (g)	Sample size (days)
		Kcal/g	Kcal/bird			Kcal/g	Kcal/bird		
No. 1	♀	0.2294	103.1	450	24	0.2310	106.3	460	13
2	♀	0.1673	69.8	417	28	0.1714	72.0	420	20
3	♂	0.1897	70.0	369	26	0.1907	70.6	370	14
4	♂	0.2162	84.5	391	28	0.2057	79.2	385	14
5	♀	0.1943	93.7	482	20	0.1868	90.6	485	12
6	♀	0.1978	90.8	459	27	0.2007	91.3	455	22
7	♂	0.1893	65.7	347	27	0.1930	66.8	346	18
Means									
Females (n = 4)		0.1967	88.3	450	99	0.1957	88.3	451	67
Males (n = 3)		0.1983	73.6	369	81	0.1964	71.7	365	46
Overall (n = 7)		0.1978	81.7	413	180	0.1962	81.6	416	113

<sup>1</sup> See text for definitions.

This interval estimate should be the more accurate, as it minimizes variation in metabolic rate measurements resulting from weight change. Daily fluctuations in body weight were common among all individuals (see Figure 2).

We used Student's *t*-test to test the significance of differences between male and female mean metabolic rates per gram. Neither the "overall mean rate" nor "rate by constant weight interval" are significantly different for males and females ( $\alpha = 0.05$ ). There is no overlap of the 95% confidence intervals for the mean daily energy requirements (kcal/bird/day) of males and females for either method. Contrary to our findings, other authors have reported data for raptors suggesting that the lighter male may have a higher metabolic rate per gram than the heavier female (Graber 1962; Gatehouse and Markham 1970). For Saw-whet Owls (*Aegolius acadicus*), Graber (1962) reported 0.200 kcal/g/day for one 96 g female and 0.213 kcal/g/day for one 75 g male. Gatehouse and Markham (1970) reported a metabolic rate of 0.189 kcal/g/day for one 96.9 g male American Kestrel (*Falco sparverius*) and of 0.151 and 0.130 kcal/g/day for two females weighing 104.5 g and 113.6 g respectively. The sample sizes in both these studies were small and the reported metabolic rates may not reflect actual differences between the mean rates for the sexes, which is the interpretation that our data support.

Kendeigh (1970) has shown convincingly that, over the broad range of avian weights, as body weight increases the metabolic rate per gram



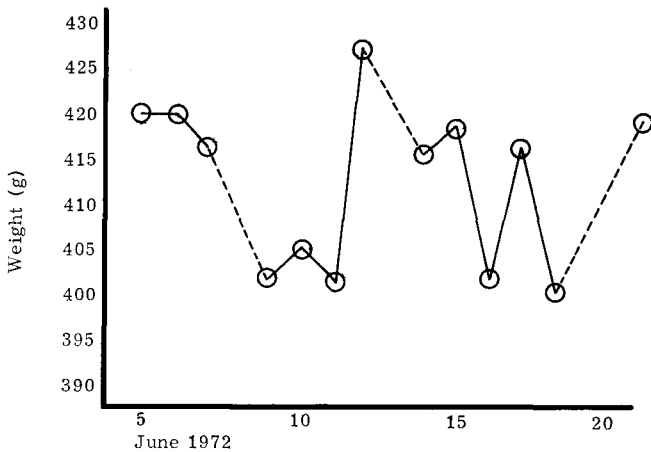


Figure 2. Daily weight variation for a representative captive Broad-winged Hawk; experimental bird number 2.

decreases. However within a species, sexual size dimorphism may not necessarily lead to metabolic rate differences on a per gram basis. Data from Moore (1961) and Seibert (1963) as reported in Kendeigh (1970) show that the lighter of the sexes may even have the lower metabolic rate per gram.

By regressing metabolic rate on the activity index, we generated the equation  $Y = 0.1903 + 0.00013X \pm 0.0446$  ( $r = 0.472$ , significant at  $\alpha = 0.05$ ) which predicts a resting metabolic rate (RMR) of 0.190 kcal/g/day when activity ( $X$ ) equals zero (Figure 3).

Kendeigh's (1970) equation for nonpasserine birds relating existence energy (equivalent to RMR) to body weight at 30°C ambient temperature predicts a metabolic rate of 0.127 kcal/g/day for a bird the size of a Broad-wing. This is 33.4% lower than our estimate predicted from the activity-metabolic rate regression. This is due in part to the fact that our captive birds were under ambient temperature conditions (Figure 4), which were generally lower than Kendeigh's controlled temperature of 30°C. Thus increased metabolic rate caused by thermoregulation could explain the difference between Kendeigh's value and ours.

*Estimate of resting metabolic rates from field data.*—An estimate of the daily metabolic rate for a free-ranging female Broad-wing can be derived from field observations and quantification of food habits data. It has been established that the male Broad-wing does all the hunting and feeds the female during incubation and early brooding (Matray MS). Further, the number of feedings per day by the male can be

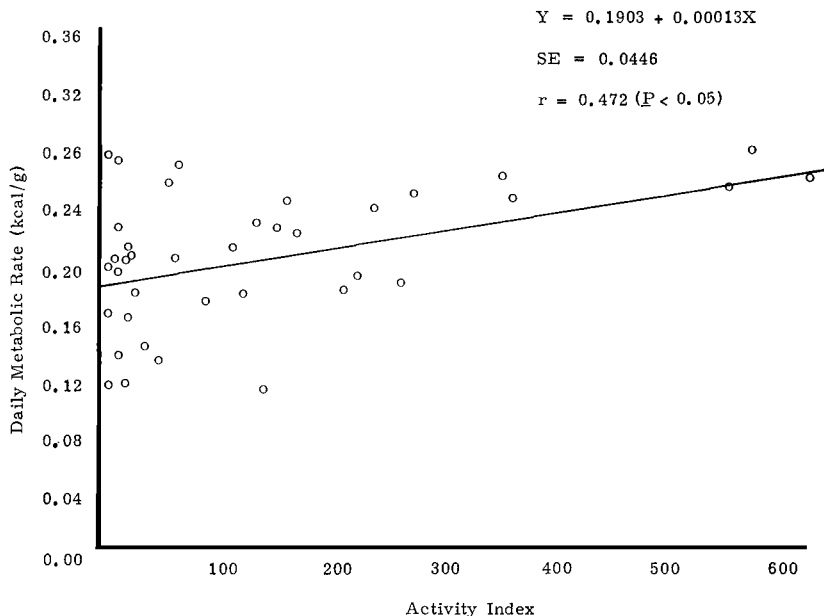


Figure 3. Metabolic rate vs. activity index for captive Broad-winged Hawks. This equation was used to calculate RMR when activity index was zero. Data points represent daily metabolic rates for individual birds.

determined by daily observation at the nest. When the male brings food to the female she signals the transfer with a recognizable vocalization (Matray MS). Given an energy value of 1.0 kcal/g for whole prey, an average prey weight of 41.5 g (both derived from Table 4), and an average digestive efficiency of 74.1% it can be estimated that the average energy per prey item available to the bird is 30.8 kcal.

An average of 136 kcal/day of prey was delivered per female at two nests in 1971, based on 5 full days of pre-hatch observation. This yields a metabolizable energy consumption rate of 103 kcal/day. Assuming an average female weight of 437 g (Table 1) the per gram metabolic rate is 0.236 kcal/g/day. This rate is comparable to the RMR estimate of 0.1903 kcal/g/day for the captive birds, but is 21% higher. This higher estimate from the field data can be explained by a combination of two factors. First, the digestive efficiency of a free-ranging bird feeding on whole prey should be lower than the 74.1% measured for captive birds on a diet of lean venison; accordingly a reduction of digestive efficiency to 61% would be sufficient to yield a metabolic rate equal to that for the captive birds. Secondly, it is reasonable to assume that the activity level of a free-ranging female would be somewhat higher

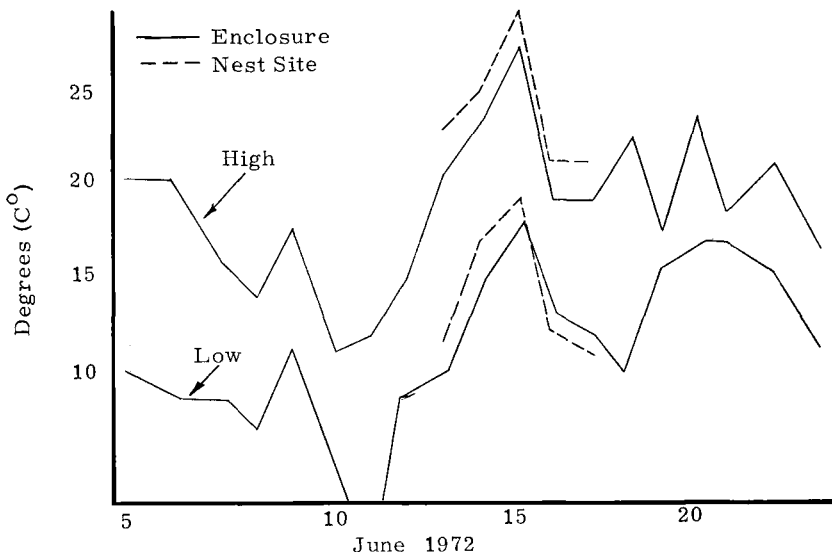


Figure 4. Temperature record for experimental bird enclosure and an active Broad-wing nest site.

than for the captives, which would lead to a higher rate for wild birds. This could be offset by an increased metabolic rate of the captive birds caused by the stress of confinement.

During 19 full days of observation at three nests (post-hatch), the average energy value of prey delivered by the parents to each nestling was 137 kcal/day. For two nests, the average amount per nestling was identical (155 kcal) even though one nest had three nestlings and the other only two. The third nest had three nestlings, each of which received an average of 112 kcal of prey per day.

#### DISCUSSION AND CONCLUSIONS

*Model of energy saving resulting from size dimorphism.*—The working hypothesis of this study was that the daily energy needs of a pair of Broad-winged Hawks are reduced over that for a hypothetical monomorphic pair as a direct result of the male's smaller size. We have shown that the mean metabolic rate per gram is the same for both male and female Broad-wings during the nesting season (Table 6). The smaller size of the male relative to the female has not led to a higher metabolic rate in contrast to the general body size—metabolic rate relationship previously discussed. It follows then that the smaller male Broad-wing requires less total energy per day than the larger female at the same level of activity.

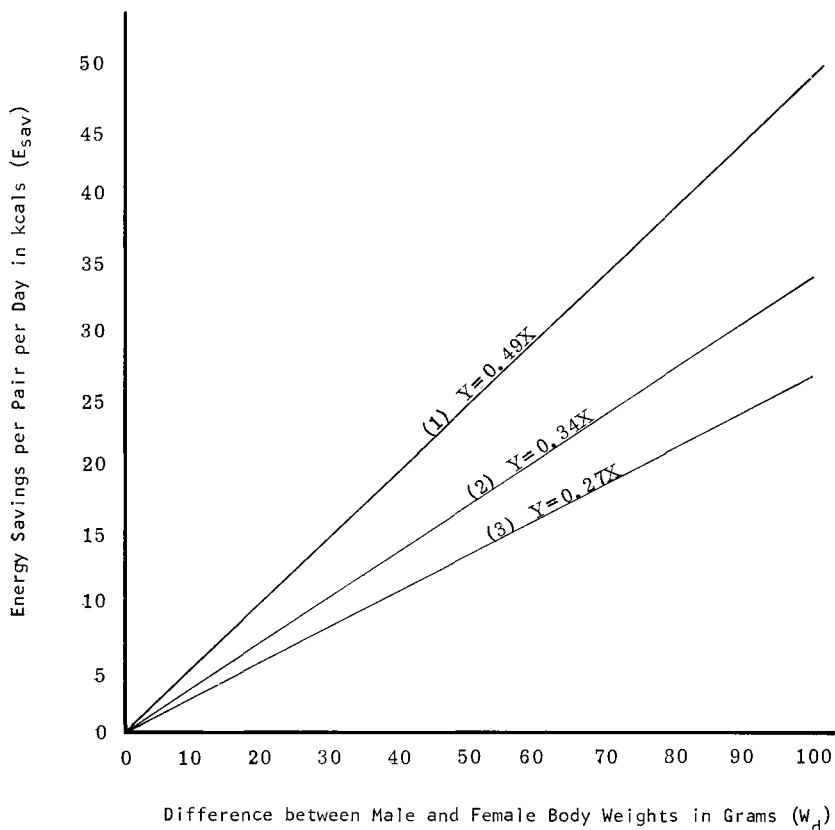


Figure 5. Energy saved per day per pair of Broad-winged Hawks predicted from the degree of size dimorphism. For equations 1, 2, and 3 the activity metabolic rate corresponds to 4, 2, and 1 hours of active flight daily.

We have constructed a model that relates the weight difference between male and female Broad-wings to the energy saved per day for the pair during incubation and early brooding (Figure 5). This model is based on the following assumptions.

First, the male Broad-wing does all the hunting from the time incubation begins until about the second week of brooding (Matray MS).

Second, the female Broad-wing's weight remains fairly constant or at least does not decrease significantly during incubation and early brooding. Weight data taken from captured females during the nesting period lend some support to this assumption (Matray MS).

Third, the male's level of activity is equivalent to from 1 to 4 hours of active flight per day. This assumption represents a subjective judg-

ment based on personal field observations. No data exist that would provide a basis for determining at what level of activity the male functions during the nesting period.

Finally, the energy expenditure for flight is assumed to be about 10 times the resting metabolic rate. This represents an estimate derived from measurements reported by Tucker (1969) for the Laughing Gull (*Larus atricilla*) of 11 to 14 times standard metabolic rate (SMR) and by LeFebvre (1964) for pigeons (*Columba livia*) of 13.4 times SMR. Both of these species have a manner of flying not too dissimilar to the Broad-wing's. The slightly lower multiple of 10 was chosen for this model because, when it is multiplied by Broad-wing RMRs, the calculated values are essentially equivalent to metabolic values for flight derived from SMR by Tucker (1969) and LeFebvre (1964). At any rate, our calculated flight values probably are not overestimates.

*Derivation of model equation.*—The following symbols are used in the derivation of the model equation and subsequent discussion:

- $E_{\text{mon}}$  = Total energy expenditure of a monomorphic pair.  
 $E_{\text{dim}}$  = Total energy expenditure of a dimorphic pair.  
 $E_r$  = RMR (kcal/g/day).  
 $E_a$  = Activity metabolic rate (kcal/g/day), AMR (varies with level of activity, i.e. number of hours flying per day).  
 Note: When activity is zero  $E_a = E_r$ .  
 $W_f$  = Weight of female (g).  
 $W_m$  = Weight of male (g).  
 $W_d = W_f - W_m$ .

Assuming that the daily energy expenditure of the brooding female is given by ( $E_r \times W_f$ ) and the daily energy expenditure of the active male is given by ( $E_a \times W_m$ ), and since  $W_f = W_m$  for a monomorphic pair the total daily energy expenditure of monomorphic and dimorphic pairs are respectively given by:

$$(1) E_{\text{mon}} = E_r W_f + E_a W_f$$

$$(2) E_{\text{dim}} = E_r W_f + E_a W_m$$

The energy savings due to dimorphism is:

$$(3) E_{\text{sav}} = E_{\text{mon}} - E_{\text{dim}}$$

or

$$(4) E_{\text{sav}} = [E_r W_f + E_a W_f] - [E_r W_f + E_a W_m]$$

leaving

$$(5) E_{\text{sav}} = E_a W_f - E_a W_m$$

or

$$(6) E_{\text{sav}} = E_a (W_f - W_m)$$

or

$$(7) E_{\text{sav}} = E_a W_d$$

*Model predictions and implications.*—It is apparent from this model (Figure 5) that the energy advantage for a nesting pair of Broad-winged Hawks increases as both the degree of dimorphism and the activity level of the male increases. For the average condition ( $W_a = 80$  g) from Table 1, with the male active for 2 hours per day, the daily energy savings for a dimorphic pair is 27.2 kcal or about 39 g of whole mammalian prey. Using the capture weights for males and females of four mated pairs, the average weight difference is 100 g. At the same activity level (2 hours) this increases the energy savings to about 35 kcal or about 47 g of whole prey. This savings is about 17% of the pair's daily requirements and is probably a low estimate of the real savings. At the same degree of dimorphism (100 g) and an activity level of 4 hours per day for the male, the savings increases to 49 kcal or about 23% of the pair's daily requirements. We feel that the actual savings lies between these two estimates.

While it is not possible to generalize from these data concerning the significance of size dimorphism to the energetics of all raptors, it is reasonable to speculate on the possibility of such an energetics advantage acting as a selection factor for size dimorphism. The point at which such selection could occur would be on the male's ability to provide sufficient food for his mate and offspring and on the female in her selection of a male of proper size. The pair with the smaller male should be able to fledge a greater number of young on the average or fledge young more regularly resulting in more young fledged over the reproductive life of the pair. A further possibility is that the fledglings of the more dimorphic pair are better nourished and therefore survive to reproduce more frequently than the young of the less dimorphic pair.

If energy is assumed to be a selection force then we should see a positive correlation between the degree of dimorphism shown by a species and the extent to which the male is the sole food provider during incubation and early brooding. If hunting activity was shared equally the energy savings to the pair would be markedly reduced. Hill (1944) pointed out that this general trend is found between size dimorphism and the distribution of incubation responsibilities for the broad range of raptor species.

Further, species that expend relatively large amounts of energy per prey capture should be subject to the greatest selective pressure, suggesting that raptors that pursue very agile prey should show more dimorphism than those that pursue less agile prey or rely on surprise from a perch as the principal hunting tactic. The general increase in dimorphism from vulturine species to mammal hunting hawks to the bird hawks as noted by many authors (Storer 1966, Earhart and John-

son 1970, Craighead and Craighead 1956) is certainly not inconsistent with energy as a selection factor for size dimorphism.

The ground nesting habit of at least two raptor species, the Marsh Hawk (*Circus cyaneus*) and the Burrowing Owl (*Speotyto cunicularia*) seems to have placed unique selection pressures on them such that they do not fit with most raptor dimorphism trends. The Marsh Hawk is more dimorphic than would be expected from its food and hunting habits and the Burrowing Owl is normally dimorphic (i.e. male is larger than the female). Our energetics hypothesis explains these anomalies no better than any previous hypotheses that have been offered.

Several factors oppose the further evolutionary reduction in the size of the male, not the least of which is the obvious physical incompatibility that would result between males and females if the difference in size became too great. Reynolds (1972) suggested for accipiters that interspecific competition may also be a factor, at least for some species. Relative to our hypothesis, as the male becomes smaller the size of prey he can capture also becomes smaller. Even if the numbers of smaller prey are greater (Eltonian pyramid), the male would reach a point where the energy expended in the capture of these prey items would exceed the energy value that could be derived from them. Also, if the male becomes too much smaller than the female, the point will undoubtedly be reached where the size reduction will result in an increase in his metabolic rate thereby negating any further decrease in size.

In conclusion we suggest that the male Broad-wing has evolved as small as he can "afford" to, considering other pressures, under the selective pressure to reduce his metabolic needs thereby improving his ability to provide sufficient food for mate and offspring during the nesting season. The male's smaller size may have evolved in concert with the segregation of incubation and hunting responsibilities between male and female.

#### ACKNOWLEDGMENTS

We are grateful for the support provided to this study by the Archer and Anna Huntington Wildlife Forest Station and the Department of Forest Zoology, State University of New York College of Environmental Science and Forestry.

Special thanks are due R. Brocke, whose counsel and encouragement throughout this study were of immeasurable value.

We would also like to thank the members of the Huntington Forest staff for their willing and valuable assistance.

For their understanding, encouragement, and sacrifices, we would especially like to thank our wives, Susan and Kam.

#### SUMMARY

We examined the energy requirements of Broad-winged Hawks during the nesting season to test the hypothesis that sexual size dimorphism

results in a decrease in the energy requirements of nesting pairs of Broad-wings over that of a hypothetical monomorphic pair.

Metabolic rates of seven captive Broad-wings were measured using food balance calorimetry and daily metabolic rates of free-ranging female Broad-wings were estimated from food habits data acquired by observation at active nest sites.

We found no significant difference between male and female metabolic rates per gram for the captive birds. Therefore we concluded that males require less energy per day in direct proportion to their reduced weight at the same level of activity. We constructed a model describing this relationship that predicts the energy saved by a pair of dimorphic Broad-wings as a function of the magnitude of the dimorphism.

The proof of our hypothesis rests with the model based on experimental data. The model clearly shows that as dimorphism increases (by the male becoming smaller) the daily energy requirements of the pair during the nesting season decrease.

We discuss the significance of this energy savings and suggest that it could result in an enhancement of the ability of the dimorphic pair to contribute more offspring that reach reproductive maturity to the next generation.

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