ENERGETICS OF TWO WINTERING RAPTORS

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Abstract.—We present a deterministic model for predicting daily energy expenditure of two raptors—female American Kestrels (*Falco sparverius*) and White-tailed Kites (*Elanus leucurus*)—wintering in coastal northwestern California. Inputs to the model include body mass, air temperature, photoperiod, energy expenditure of flight, and relative portions of the daytime spent in flight and nonflight activities. A simplified version of the model applicable to birds spending less than 20% of the day in flight and inflating daily energy expenditure by 6% or less is also presented. Inputs to the simplified version include body mass, air temperature, energy expenditure of flight, and relative portions of the 24-h day spent in flight and nonflight activities.

Input data were estimated directly and indirectly. The validity of the model was tested by comparing predicted energy expenditure with energy expenditure estimated by observed food consumption of wild birds. The model predicted that individual female kestrels would expend 42.0–61.0 kcal (2.04 to 2.96 W) daily and that individual kites would expend 105.6–118.3 kcal (5.12 to 5.74 W) daily. Daily energy expenditure estimated by food consumption averaged 42.9 and 113.1 kcal (2.08 and 5.49 W) per individual kestrel and kite, respectively. The degree of correspondence between model prediction and field estimation of energy expenditure of kites was considered adequate for model validation. Even though the model predictions bracketed the field estimation of energy expenditure of kestrels, however, the model predictions were considered to be too high because of an erroneous temperature input, and the field estimation was considered to be too low because of an erroneous estimate of the biomass of an important group of prey. Correcting these errors indicated that the daily energy expenditure of kestrels should average 48.7 kcal (2.36 W) per individual. Using the corrected energy expenditure as a standard for female kestrels and the field estimate of energy expenditure as a standard for kites, the predictive accuracy of the versions of the model was evaluated relative to the predictive accuracy of 11 other models. Three of these models, including the two versions presented here, produced estimates that were within 5% of the mean standard value. Eight of the models under-approximated the mean standard value by 10.3–49.5%; the other two over-approximated the mean standard value by 14.8 and 36.9%. *Received 13 August 1979, accepted 21 April 1980.*

Efforts to approximate the energetics of free-living birds ideally should include consideration of variations in energy expenditures associated with biological and ecological influences (King 1974). A corollary to this proposition is that the approximations attempted should include information on all the influences involved. Approximations made on wintering birds therefore should include information on variations in energy expenditure associated with variations in air temperature, thermal radiation, wind, and humidity (the "climate space" of birds: Porter and Gates 1969); location and use of environmental resources; social and competitive interactions; and antipredator activities.

This is a report of the derivation and field test of a deterministic model developed to predict energy expenditures of two species of falconiform birds, the American Kestrel (*Falco sparverius*) and the White-tailed Kite (*Elanus leucurus*), wintering

in coastal northwestern California. The model makes use of the methodology and research of Kendeigh and his coworkers (Kendeigh et al. 1977) on existence metabolism (EM); the research of Lasiewski (1963), LeFebvre (1964), Tucker (1968, 1972), and Gessaman (pers. comm.) on energetics of avian flight; and the research of many avian physiologists on standard and basal metabolism (SM and BM) (recently reviewed by Calder and King 1974 and Kendeigh et al. 1977).

Inputs to the model include: (1) body mass, (2) amounts of time birds are engaged in flight and nonflight activities, (3) air temperature, (4) photoperiod, and (5) the multiple of basal metabolism expressing energy expenditure of flight. Output from the model is "daily energy expenditure" (*DEE sensu* King 1974) or "daily energy budget" (*DEB sensu* Grodzinski et al. 1975, Kendeigh et al. 1977) per bird. The model may be summarized and symbolized by equation 1:

$$DEB = NFA[(EM_{T_a}) - (1 - P)(SM_{T_{na}})] + FA[(BM)(P)(FC)] + (1 - P)(SM_{T_{na}}) \tag{1}$$

where: NFA = duration of diurnal nonflight activities as a proportion of the photoperiod (daylength) ($NFA = 1 - FA$),

FA = duration of flight activities as a proportion of the photoperiod ($FA = 1 - NFA$),

EM_{T_a} = existence metabolism of nonpasserine birds during winter as a function of average daily air temperature (T_a):

$$EM_{T_a} = EM_{0°C} + (T_a)(b) \tag{2}$$

$$\text{where: } b = \frac{EM_{30°C} - EM_{0°C}}{30};$$

$$EM_{30°C} = 1.455 W^{0.6256} \tag{3}$$

$$EM_{0°C} = 4.235 W^{0.5316} \tag{4}$$

$$W = \text{body mass in g}$$

$SM_{T_{na}}$ = standard metabolism of nonpasserine birds during winter at night as a function of average night time air temperature (T_{na}):

$$SM_{T_{na}} = SM_{0°C} - (b)(T_{na}) \tag{5}$$

$$\text{where: } SM_{0°C} = 1.810 W^{0.5944} \tag{6}$$

$$b = 0.0457 W^{0.5886} \tag{7}$$

at the lower critical temperature (T_{lc}), $SM = BM$:

$$T_{lc} = 47.17 W^{-0.1809} \tag{8}$$

BM = basal metabolism

$$BM = 0.4616 W^{0.7340} \tag{9}$$

P = photoperiod as a proportion of the 24-h day.

FC = flight coefficient; the multiple of BM expressing energy expenditure of flight.

DEB, BM, and all expressions of SM and EM are in kcal·bird^{-1}·day^{-1}. Equation (2) is a linear interpolation to T_a of the allometric equations (3) and (4) of Kendeigh et al. (1977) for predicting EM of nonpasserine birds at 0°C and 30°C for 10 ± h photoperiods during winter. Equation (2) is a generalization of an earlier energetics model (Koplin 1972); a modification of the energetics model of Weiner and Glowa-

cinski (1975), derived from allometric equations based on fewer data (Kendeigh 1970); and, except for their use of Kendeigh's (1970) earlier equations, is identical to the energetics model of Wiens and Innis (1973, 1974). Equations (5), (6), (7), and (8) are from Kendeigh et al. (1977) for nonpasserine birds during winter and at night. Equation (9) is Aschoff and Pohl's (1970) allometric equation for resting BM of nonpasserine birds.

There are two components to EM_{T_a}: diurnal nonflight activity and nocturnal rest. Flight of kestrels and kites is a diurnal activity; therefore, the energy expenditure of flight should be prorated with the diurnal nonflight component of EM_{T_a}; equation (1) does this. The component $(EM_{T_a}) - (SM_{T_{na}})(1 - P)$ calculates the total energy expenditure of diurnal nonflight activity by deducting the energy expenditure of nocturnal rest, $(SM_{T_{na}})(1 - P)$, from EM_{T_a}. The coefficient NFA is a correction factor to simulate the portion of DEB attributable to diurnal nonflight activity. The component $FA[(BM)(P)(FC)]$ predicts the portion of DEB attributable to diurnal flight activity. The coefficient P prorates BM, a daily rate, to the photoperiod portion of the 24-h day; FA further prorates BM to that portion of the photoperiod spent in flight. FC is a multiple of BM; the product $(BM)(FC)$ represents the energy expenditure of flight. The portion of DEB attributable to nocturnal rest is predicted by the component $(1 - P)(SM_{T_{na}})$. The coefficient $(1 - P)$ is a correction factor prorating $SM_{T_{na}}$, a daily rate, to the portion of the 24-h day that is dark.

For birds spending 20% or less of the photoperiod in flight activities, as was the case for kestrels and kites wintering in coastal northwestern California (Table 2), a simplified version of equation (1) providing predictions exceeding those of equation (1) by 6% or less is:

$$DEB = NFA'(EM_{T_a}) + FA'[(BM)(FC)] \tag{10}$$

where: NFA' = portion of the 24-h day spent in nonflight activities (nocturnal rest plus diurnal nonflight activities); $(NFA' = 1 - FA')$.
FA' = portion of the 24-h day spent in flight; $(FA' = 1 - NFA')$.
DEB, EM_{T_a}, BM, and FC are as previously defined.

Equation (10) is based on limiting constraints of FA and NFA in equation (1). Thus, as FA goes to 0, NFA goes to 1 and equation (1) simplifies to equation (2). Under these conditions the necessity for an explicit estimate of nocurnal rest is superfluous, because, even though unknown, it is implicitly incorporated into equation (2) and therefore does not need to be known. Alternatively, as FA goes to 1, NFA goes to 0 and equation (1) simplifies to two components, the energy expenditures of flight and nocturnal rest. Under these conditions, an explicit estimate of nocturnal rest is paramount. Consequently, as FA goes from 1 to 0 (or as NFA goes from 0 to 1) the necessity of an explicit estimate of the energy expenditure of nocturnal rest becomes progressively less important.

Equations (1) and (10) thus account for variations in energy expenditure associated with variations in air temperature and with location and use of environmental resources. To the extent that they are associated with flight activities and/or minimal diurnal nonflight activities, equations (1) and (10) also account for energy expenditures of social and competitive interactions and antipredator activities. Equations (1) and (10) do not account for energy expenditures of growth, reproduction, and molt, nor the influences of wind, thermal radiation, and humidity.

TABLE 1. Comparison of predicted and measured EM_{T_a} for seven species of falconiform birds. Paired t-test (13 df) = 0.11; P = 0.91.

Species	W (Body mass g)	T_a (Temperature °C)	EM_{T_a} (kcal/day)[a]	
			Predicted[b]	Measured
Accipiter striatus	99	15.2	37.1	39.1
A. striatus	108	17.2	37.4	37.6
A. striatus	108	15.5	38.7	42.9
A. striatus	108	13.9	40.0	36.2
A. striatus	107	16.5	37.7	33.0
Falco sparverius	126	8.2	48.4	40.8
F. columbarius	174	9.0	57.0	64.5
F. columbarius	173	12.0	54.0	50.6
F. columbarius	172	12.6	53.2	50.0
F. tinnunculus	194	13.1	56.4	58.9
F. tinnunculus	196	13.2	56.6	53.2
F. mexicanus	497	12.0	97.2	84.0
F. cherrug	1,036	11.8	147.0	184.0
Buteo jamaicensis	1,389	12.6	171.6	162.5

[a] S.I. conversion: 1 kcal/day = 4.85 × 10^{-2} watt (W).
[b] Equation (2).

METHODS

Use of equation (2) to predict energy expenditure of nonflight activities was tested by a paired statistical comparison of values of EM_{T_a} predicted by the equation with values of EM_{T_a} measured experimentally (Table 1). Pairs of predicted and measured EM_{T_a} were obtained for individual birds with an average body mass (W) at an average air temperature (T_a). Experimental values of EM_{T_a} were obtained by energy balance measurements on birds housed in rooms 3.3 m long by 2.6 m wide and 2.9 m high. With the exception of room size, temperature, and light control, methodology for measuring EM_{T_a} was similar to that used by Kendeigh (1949), i.e. the difference between energy content of food consumed and energy content of egesta of birds maintained at constant body mass for periods of 3 or more days. Birds were fed ground, eviscerated rat (stomach and intestinal tract removed), eviscerated rabbit, or beef heart. Energy content of food and egesta was measured in an adiabatic bomb calorimeter. All experimental measurements were made during the winter; temperatures in the rooms, ventilated to the outside through screened windows, were monitored continuously by thermographs. Experimental T_a was calculated by summing thermograph records at hourly intervals and dividing the sum by the number of hours in each experiment. Natural light filtering through windows in the rooms was the source of light during the experiments. Thus, temperature and light conditions were as close to natural as experimental conditons allowed.

Inputs to equations (1) and (10) were estimated directly and indirectly. NFA and FA (NFA' and FA') were estimated directly by dawn-to-dusk field observations totalling approximately 300 h of individual kestrels and approximately 400 h of individual kites (Table 2). Field observations were made of birds wintering on agricultural lands in the vicinity of Arcata and Eureka, Humboldt County, California. T_a was estimated directly by averaging daily maximum and minimum temperatures occurring between sunset plus 0.5 h and sunrise minus 0.5 h. P was estimated directly by averaging and adding 1 h to the daily amount of time elapsing between sunrise and sunset. Data on temperatures and photoperiod were obtained from the U.S. Weather Bureau in Eureka; the data were averaged over the 92-day period between mid-November and mid-February, which we considered to be the winter season. Body mass (W) was estimated indirectly from the literature for kestrels, and indirectly from the literature and from unpublished data on live birds and in various museums for kites. FC was estimated indirectly by comparing the ratio of available data on the energy expenditures of flight to BM of nonpasserine birds (Table 3).

The validity of the model was tested by comparing DEB predicted by equation (1) with DEB estimated on the basis of observed food consumption by free-living birds (Tables 4 and 5). Information on types and amounts of prey eaten by free-living birds was obtained in connection with observations of daily flight and nonflight activities (Table 5 and Appendix).

The predictive accuracy of the two versions of our energetics model relative to the predictive accuracy of other energetics models was evaluated by comparing DEB predictions of the models to standard DEB

TABLE 2. Flight (*FA*) and nonflight (*NFA*) activities of female American Kestrels and White-tailed Kites wintering on agricultural lands in coastal northwestern California during the average 11-h photoperiod.

Activities	Percent of photoperiod	
	American Kestrels[a]	White-tailed Kites[b]
Perched (*NFA*)		
Searching	74.7	60.1
Inactive	8.6	16.6
Eating	3.6	3.0
Other	6.5	0.8
Subtotal	93.4	80.5
Flying (*FA*)		
Directional	2.5	9.1[c]
Hovering	3.4	8.9
Other	0.7	1.5
Subtotal	6.6	19.5
TOTAL	100.0	100.0

[a] Based on a total of 316.7 h of continuous observation of 7 birds, 4 during the winter of 1972–73 and 3 during the winter of 1973–74.
[b] Based on a total of 441.2 h of continuous observation of four birds during the winter of 1973–74.
[c] Flight to and from the nocturnal roost, which was not found; daily duration estimated to average 1 h.

values (Table 6). Fortunately, our studies provided estimates of all information needed as inputs by the full complement of energetics models evaluated. Information needed in addition to that required for our model included energy-balance data on captive animals (Table 1) and detailed data on time and activity budgets (Table 2). All allometric equations for predicting *BM, SM,* and *EM* were expressed in terms of mean body mass (Table 4). *BM* was increased by a factor of 1.091 for kestrels and 1.078 for kites in models predicting *BM* with the allometric equation of Lasiewski and Dawson (1967) for nonpasserine birds. Where possible, only those behavioral and physiological aspects pertinent to kestrels and kites wintering in coastal northwestern California were considered in predictions by other models. That is, only behavioral acts such as flight, eating, preening, etc. and physiological processes such as temperature regulation were included in predictions by other models. Behavioral acts such as hopping, singing, etc. and physiological processes such as reproduction were omitted from predictions by other models.

RESULTS AND DISCUSSION

Fourteen measurements of EM_{T_a} were obtained from seven species of falconiforms ranging in size from a Sharp-shinned Hawk (*Accipiter striatus*) (about 100 g) to a Red-tailed Hawk (*Buteo jamaicensis*) (about 1,400 g) (Table 1). T_a ranged from 8.2°C to 17.2°C during the measurements; hourly temperatures differed from T_a by a maximum of ± 5.0°C. Photoperiod ranged from 10 to 12 h. The null hypothesis that no differences existed between pairs of predicted and measured values of EM_{T_a} was accepted at the 0.05 level of significance. Thus, it was concluded that, under conditions similar to those in the laboratory, linear interpolation of equations (3) and (4) for predicting EM_{T_a} between 0°C and 30°C for wintering falconiforms is a realistic approximation of the birds' total nonflight energy expenditure.

Kestrels and kites averaged 10.3 h and 8.9 h, respectively, in nonflight activities and 0.7 h and 2.1 h, respectively, in flight activities during the daily photoperiod (Table 2). Birds were assumed to be at rest during the dark, which averaged 13 h daily.

FC, the ratio of energy expenditure of flight to *BM*, ranged from 12.0 to 14.5 and averaged 13.7 for five species of nonpasserine birds ranging in mass from 3 g to approximately 400 g (Table 3). Flight energy calculated by the empirical equation

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TABLE 3. Relationship between BM and flight energy (FE) of five species of nonpasserine birds as an estimate of FC.

Species	W (Body mass g)	BM (kcal/ h)[a]	FE (kcal/ h)[a]	FC (FE: BMR)	Reference
Calypte costae	3	0.05	0.60	12.0	Lasiewski (1963)
Melopsittacus undulatus	35	0.26	3.68	14.2	Tucker (1968)
Falco sparverius	126	0.67	9.12	13.6	J. A. Gessaman (pers. comm.)
Larus ridibundus	350	1.42	20.13	14.2	Tucker (1972)
Columba livia	384	1.52	22.00	14.5	LeFebvre (1964)

[a] S.I. conversion: 1 kcal/h = 1.163 W.

of Hart and Berger (1972) is 14.9-fold higher than BM for nonpasserine birds. Flight energy calculated by Tucker's (1974) equation 2 for a 119-g bird, the average body mass of female American Kestrels (Table 4), is 14.1-fold higher than BM and is 18.3-fold higher than BM for a 331-g bird, the average body mass of White-tailed Kites (Table 4). Thus, even though the ratios of flight energy to BM in Table 3 average slightly less than those predicted from a larger sample of empirical data (Hart and Berger 1972) or are comparable to or moderately less than those predicted theoretically (Tucker 1974), we prefer the ratio 13.7 for the following reasons. First, Hart and Berger's (1972) empirically derived equation includes data on three species of birds for which measurements were obtained during flights lasting only 7–15 s (Berger et al. 1970: 202); metabolic rates during the first few minutes of flight may be 15-20% higher than later (Tucker 1974: 302). Second, Tucker's (1974) theoretical equation predicts (as seen for kestrels and kites) an increasing ratio of flight energy to BM with increasing body mass, predictions conforming poorly with empirical observations, especially by predicting unreasonably high ratios for large birds (King 1974: 32).

It should be noted that a FC of 13.7 represents the predicted energy expenditure of birds ". . . flying near the maximal steady-state power output . . ." (King 1974: 32). We assumed that maximal steady-state energy output was the best overall predictor of the types of flights kestrels and kites performed, reasoning that there was probably as much flight activity in which energy expenditure exceeded maximal steady-state output as there was in which energy expenditure was less than required

TABLE 4. Inputs to and DEB predicted by equation (1) for female Kestrels and White-tailed Kites wintering on agricultural lands in coastal northwestern California.

		Kestrels	Kites
Body mass (g)	W	119 (86–165)[a]	331 (310–372)[a]
Average air temperature (C)	T_a	8.9	9.1
Average nocturnal air temperature (C)	T_{na}	8.5	8.8
Average photoperiod (% of 24-h day)	P	45.8	45.8
Average duration of darkness (% of 24-h day)	$1 - P$	54.2	54.2
Daily nonflight activities (% of 11-h photoperiod)	NFA	93.4	80.5
Daily flight activities (% of 11-h photoperiod)	FA	6.6	19.5
Daily energy budget (kcal·bird^{-1}·day^{-1})	DEB	50.6 (42.0–61.0)[b]	110.0 (105.6–118.3)[b]

[a] Mean body mass; range in parentheses. Data from Roest (1957), Brown and Amadon (1968), Stendell (1972), and P. M. Bloom (pers. comm.).

[b] DEB predicted on basis of mean body mass; range predicted on basis of range in body mass in parentheses. S.I. conversion: 1 kcal/day = 4.85×10^{-2} W.

TABLE 5. *DEB* calculated on the basis of observed food intake for female American Kestrels and White-tailed Kites wintering in coastal northwestern California. See appendix for details on weights and calorific equivalents of prey.[a]

	Kestrels	Kites
Number prey killed/day		
Vertebrates	2.2	3.1
Invertebrates	46.5	—
Biomass of prey killed/day (g)		
Vertebrates	21.6	76.6
Invertebrates	12.6	—
Energy ingested (kcal/day)		
Vertebrates	30.3	137.9
Invertebrates	20.1	—
Energy assimilated (kcal/day)		
Vertebrates	25.6	113.1
Invertebrates	17.3	—
TOTAL energy assimilated = *DEB* (kcal·bird^{-1}·day^{-1})	42.9 (2.08 W)	113.1 (5.49 W)

[a] Kites were observed to consume California voles (*Microtus californicus*) and western harvest mice (*Reithrodontomys megalotis*). Kestrels were observed to consume Lepidoptera larvae and adults, grasshoppers, earthworms, various Coleoptera, California voles, harvest mice, vagrant shrews (*Sorex vagrans*), garter snakes (*Thamnophis sirtalis*), red-legged frogs (*Rana aurora*), and Pacific tree frogs (*Hyla regilla*). Ingested energy corrected to account for the fact that kestrels and kites both usually eviscerated small mammal prey before consumption. Assimilation efficiency assumed to 0.82 for small mammals and 0.86 for other vertebrates and invertebrates, based on efficiencies obtained during feeding experiments.

for maximal steady-state output. Both species averaged 30–50 flights per day. Each flight lasted from a few seconds to about 45 min, and averaged 1–4 min. All flights involved ascending from perches or the ground, many involved hovering, and some involved transporting prey from the ground to elevated perches—types of flight exceeding maximal steady-state energy expenditure (Tucker 1968, 1974). All flights also involved descending from aerial heights or perches, some involved soaring or "kiting," and a few involved long-distance movements between roosts and hunting areas—types of flight requiring less than maximal steady-state energy expenditure (Tucker 1968, 1974; Pennycuick 1971).

Expressed in terms of the range in body mass of the birds, *DEB* approximated by the energetics model (Table 4) bracketed *DEB* estimated by food consumption (Table 5). In terms of mean body mass, however, the model predicted *DEB* 18.0% higher for kestrels and 2.7% lower for kites than *DEB* estimated by food consumption. The discrepancy between *DEB* approximated by the model in terms of mean body mass and *DEB* estimated by food consumption for kites is considered to be inconsequential. Presumably, the discrepancy is attributable to sampling errors in body mass of kites, a total of only four of which were monitored in the field, and/or in weights of prey of kites in the field; a slight energy-expending imbalance among the three elements of the "climate space" unaccounted for in our model; or to some combination of these three phenomena. In any event, the model and existing inputs to the model are considered to provide a realistic approximation of *DEB* for White-tailed Kites living under winter conditions in coastal northwestern California.

The relatively small discrepancy between model prediction and field estimation of *DEB* for kites suggests that the relatively large discrepancy between model prediction and field estimation of *DEB* for kestrels is related to erroneous inputs to the model, a sizable energy-conserving imbalance among the elements of the climate space unaccounted for in our model, erroneous field estimates of food consumption, or to some combination of the three phenomena, but not to any important inade-

quacies of the energetics model. The field estimate of food consumption was based on information from only seven kestrels. Thus, it is possible that body mass of the seven birds averaged less than 119 g, resulting in a realistic but low field estimate of *DEB*. A bias of the magnitude needed to account for the total discrepancy, however, would necessitate body masses of the seven birds involved to cluster at the very lower limit of body mass known for female kestrels, an extremely unlikely possibility. An indication of the prospect of obtaining such an extreme sample mean is provided by the only body masses of local female kestrels we were able to find— two HSU museum specimens (111 g and 116 g) and an injured live bird (130 g)— which averaged exactly 119 g. Nevertheless, it is possible that body mass of the seven birds averaged somewhat less than 119 g, accounting for some of the discrepancy.

A sizable energy-conserving imbalance among elements of the climate space of kestrels in the field is another possibility that may account for the discrepancy between model prediction and field estimation of *DEB*. We consider this possibility unlikely for several reasons. First, and most important, White-tailed Kites and kestrels were exposed to similar climatic conditions; as previously indicated, if there existed a climatically related alteration in *DEB* of kites, it operated to expend, not to conserve, energy. Second, a climatically related conservation of energy would have to have resulted from absorption of solar radiation. During the 184 days of the winters of 1972–73 and 1973–74, there was sunshine an average of only 44% of the time possible, resulting in a mean of 4.8 h of sunshine daily, and there was sunshine during the whole photoperiod on only 19 days (Local Climatic Data, U.S. Weather Bureau, Eureka). Furthermore, even when there was sunshine, the sun was at a low angle; at the latitude of 44°30′N, its warming influence was minimal during the winter. Thus, even though solar radiation may have had a conserving influence on daily energy expenditure of kestrels, we feel that influence could not have accounted for an 18.0% conservation of daily energy expenditure.

We feel that a conservative error in our estimates of T_a and T_{na} accounted for part of the discrepancy between model approximation and field estimates of *DEB* for female kestrels. T_a and T_{na} are based on outside air temperatures; kestrels, however, are known to roost in cavities, crevices, recesses, etc. (Brown and Amadon 1968, personal observation), situations in which air temperatures undoubtedly are warmer than outside. The magnitude of the difference is indicated by studies of incubating kestrels (Gessaman and Findell 1979). Average night-time temperatures in nest boxes of incubating kestrels ranged from 4.5 to 16.0°C and were 4.0–5.0°C warmer than temperatures outside (Gessaman pers. comm.). Daily maximum and minimum air temperatures in California averaged 12.1°C and 5.7°C, respectively, during the two 92-day winters kestrels were studied in the field. If temperature in the nocturnal roosts of the birds averaged 4.5°C warmer than outside, then T_a should be 11.2°C and T_{na} 13.0°C. On the basis of these inputs, the energetics model predicts *DEB* to be 48.7 kcal/day (2.36 W) for a 119-g bird. We consider this approximation to be more realistic for female kestrels than the approximation in Table 4. Nevertheless, the corrected approximation is still 13.5% higher than *DEB* estimated by food consumption (Table 5), indicating the existence of one or more additional errors.

The most likely possibility to account for the remaining discrepancy between model approximation and field estimation of *DEB* for kestrels is a conservative error in our estimate of the weights of prey, especially of unidentified invertebrates (Ap-

TABLE 6. Comparison of accuracy of energetics models for predicting *DEB* for female American Kestrels and White-tailed Kites wintering in coastal northwestern California. Arranged in decreasing order of accuracy.

DEB predicted[a]		DEB/BM				
Kes-trels	Kites	Kes-trels	Kites	Mean	Method of prediction[b]	Source/comment
48.7	113.1	3.16	3.46	3.31	—	Standard values
50.7	110.0	3.29	3.37	3.33	Equation (1)	Present study
46.1	112.0	2.99	3.43	3.21	A	Holmes et al. (1979)
51.4	113.8	3.44	3.49	3.47	Equation (10)	Present study
41.1	106.8	2.67	3.27	2.97	A	Wakely (1978)
56.9	106.6	2.40	3.27	2.84	A	Withers (1977)
52.1	137.5	3.38	4.21	3.80	B	Mosher and Matray (1974)
46.0	85.4	2.99	2.62	2.81	B	West and DeWolfe (1974)
46.4	81.1	3.01	2.48	2.75	Equation (2)	Wiens and Innis (1973, 1974), Wiener and Głowacinski (1975)
38.2	92.1	2.48	2.82	2.65	B	Kushlan (1977)
70.8	145.7	4.60	4.46	4.53	C	King (1974)
23.4	86.5	1.52	2.65	2.09	A	Tarboton (1978)
22.0	67.0	1.43	2.05	1.75	A	Walter (1979)
25.6	54.6	1.66	1.67	1.67	A	Dwyer (1975)

[a] S.I. conversion: 1 kcal/day = 4.85×10^{-2} W.

[b] A, time-activity budget combined with published allometric equations for predicting *BM* and/or *SM*. B, time-activity budget combined with energy-balance studies on captive animals—from Table 1, measured metabolism = $2.2731 W^{0.6055}$; W = body mass in g; "measured metabolism" comparable to Mosher and Matray's (1974) "resting metabolic rate," West and DeWolfe's (1977) "caged existence requirements," and Kushlan's (1977) "aviary existence metabolism." C, daily energy expenditure, $DEE = 2.4345 W^{0.7052}$; W = body mass in g.

pendix), consumed in the field. Thus, an underestimate in the mean live weight of individual unidentified invertebrates of only 0.08 g (i.e. a live weight of 0.20 g rather than 0.12 g per individual—Appendix), a very likely possibility, could account for the remaining 13.5% discrepancy.

In summary, because of the similarity between model prediction and field estimation of *DEB* for White-tailed Kites and because most of the discrepancy between model prediction and field estimation of *DEB* for female kestrels is likely attributable to an error in our field estimates of weights of an important class of prey consumed, we feel that our energetics model provides a more realistic approximation of *DEB* for kestrels than the estimate based on observed food consumption. Because of errors in temperature inputs to the energetics model, however, we feel the *DEB* in Table 4 for 119-g kestrels is too high. Although we have no means of providing corrected estimates of the temperature inputs other than those previously indicated, we can predict limits. Thus, the value in Table 4 is considered to be the upper limit. The lower limit would occur if kestrels roosted at night under conditions of thermalneutrality.

At thermalneutrality, equation (8) predicts T_{na} for a 119-g nonpasserine to be 19.9°C (at thermalneutrality $T_{na} = T_{lc}$); under these conditions T_a would be 16.0°C and *DEB* 46.0 (2.23 W)/bird. The value we postulated earlier (48.7 kcal [2.36 W]/bird) lies almost midway between these limits, and in the absence of a better prediction is accepted as the most reasonable approximation of *DEB* for female kestrels wintering in coastal northwestern California.

If the *DEB* just approximated for female kestrels is accepted as a standard for birds weighing 119 g and if the *DEB* estimated by food consumption is accepted as a standard for kites weighing 331 g, it is possible to evaluate the predictive accuracy of the two versions of our energetics model relative to the predictive accuracy of other models (Table 6). Accordingly, equations (1) and (10) and the model of Holmes

et al. (1979) are most accurate, predicting values averaging within 5.0% of the mean standard value. The models of Mosher and Matray (1974) and King (1974) over-approximated the mean standard value by 14.8 and 36.9%. The remaining models under-approximated the mean standard value by 10.3–49.5%. Thus, it may be concluded that the two versions of our energetics model approximate the expected energy expenditure of the two falconiforms wintering in coastal northwestern California as accurately as the most accurate of other models evaluated and more accurately than most models evaluated. We wish to emphasize that the foregoing comparisons are offered not as an attempt to affirm or refute the validity of energetics models other than ours, but rather as an indication of the applicability of a group of models to predict energy expenditure of a specific taxon of animals living under a specific set of environmental conditions.

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APPENDIX. Average weight, calorific content, and number of prey consumed by female American Kestrels and White-tailed Kites wintering in northwestern California. Weights of small mammals are for eviscerated individuals; parenthetical values are weights of intact individuals.[a]

Prey	Mean live weight (g/individual)	Mean dry weight (g/individual)	Mean calorific content (kcal/g dry wt.)[b]	Mean number consumed/day	
				Kestrels (number prey = 1,533)	Kites (number prey = 168)
Lepidoptera	0.69	0.21	5.83	0.27	—
Orthoptera	1.10	0.39	5.61	0.31	—
Coleoptera	0.67	0.18	5.72	8.80	—
Lumbricidae	0.40	0.07	4.62	6.00	—
Unidentified invertebrates	0.12	0.05	5.72	31.11	—
Microtus californicus	26.6 (34.0)	9.58 (10.80)	5.00	0.34	2.80
Reithodontomys megalotis	7.1 (9.0)	2.62 (2.95)	5.00	0.09	0.30
Sorex vagrans	3.9 (4.9)	1.39 (1.60)	5.00	0.75	—
Fringillidae	20.0	6.00	6.00	0.05	—
Thamnophis sirtalis	11.7	3.98	4.10	0.12	—
Rana aurora	16.5	3.28	4.10	0.21	—
Hyla regilla	4.6	0.60	4.10	0.68	—

[a] Weights of small mammals were measured: *M. californicus*, n = 177; *R. megalotis*, n = 64; *S. vagrans*, n = 14. All other weights except unidentified invertebrates obtained from the literature (Collopy 1975). Weights of unidentified invertebrates visually estimated relative to size of identifiable invertebrates. Calorific data determined by calorimetry or from the literature (Collopy 1975). Daily consumption rates based on observations totaling 316.7 h for kestrels and 441.2 h for kites. Prey selection by kites verified by analysis of 76 pellets, which contained the skulls of 82 voles and 9 harvest mice.

[b] S.I. conversion: 1 kcal = 4.187 kilojoule (kJ).