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BEHAVIOR AND ENERGY BUDGETS OF BELTED KINGFISHERS IN WINTER

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Abstract.—I recorded behaviors and estimated energy intake and expenditures of 16 Belted Kingfishers (*Ceryle alcyon*) during January and February 1994. Each bird was watched for an entire day to examine the relationships among temperature, time of day, and foraging behavior. Estimates of total daily energy intake and expenditure differed by only 2.8 ± 42.9KJ/d (1% of total). The relatively large amount of variation in this difference may indicate that kingfishers are balancing their energy budgets on time scales longer than a single day or may simply reflect the coarseness of the methods used to derive these estimates. There was a significant decline in energy expenditure through the day, due largely to a decrease in the cost of thermoregulation. There was, however, no significant variation in energy intake among times of day. Mean daily temperature was not correlated with the total daily energy balance (intake minus expenditure) of individuals. Perching, flying, and foraging behaviors of Belted Kingfishers varied by time of day. In general, Belted Kingfishers were more active in the afternoon than in the morning. In summary, these observations indicate that there are predictable diel patterns in the foraging behaviors of Belted Kingfishers, that the energy intake resulting from these behaviors is variable, and this variability in energy intake is not correlated with daily temperature.

COMPORTAMIENTO Y PRESUPUESTO ENERGÉTICO INVERNAL DE *CERYLE ALCYON*

Sinopsis—Anoté las conductas y estimé las ingestiones energéticas de 16 individuos de *Ceryle alcyon* entre enero y febrero del 1994. Se observó cada ave durante un día completo para examinar las relaciones entre temperatura, hora del día y conducta alimenticia. Los estimados de ingestión energética total y de desembolso energético difieren por solo 2.8 ± 42.9KJ/d (1% del total). La variación relativamente grande en esta diferencia puede indicar que los individuos de la especie equilibran su presupuesto energético en escalas temporales que exceden un día completo o puede solamente reflejar la crudeza de los métodos para ilegar a estos estimados. Se detectó una reducción significativa en el gasto energético a través del día debido mayormente a una reducción en el costo de la termorregulación. Sin embargo, no hubo variación significativa en la ingestión energética entre horas del día. No se correlacionó la temperatura promedio diaria con el balance energético diario (ingestión menos gastos) de los individuos. El posarse, el volar y las conductas de *Ceryle alcyon* para alimentarse variaron entre horas del día. En general, las aves fueron más activas en las tardes que en las mañanas. En resumen, estas observaciones que hay patrones diarios predecibles en las conductas de alimentación de *Ceryle alcyon* que la ingestión energética que resulta de estas conductas es variable, y que esta variación en ingestión energética no está correlacionada con la temperatura diaria.

Most of the 87 species of kingfishers (Family Alcedinidae) have primarily tropical distributions and forage on terrestrial prey (Fry et al. 1992). Thus, the Belted Kingfisher's (*Ceryle alcyon*) primarily northern-temperate distribution and dependence on aquatic prey are unusual among kingfishers. Specialization on aquatic prey creates unique foraging

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problems at the northern extent of the Belted Kingfisher's range during winter, when individuals may have difficulty catching enough prey to meet their energy requirements.

During winter, avian foraging patterns are related to both time of day and weather conditions. For instance, Hutto (1981) found that foraging patterns of wood warblers reflected diel variation in availability of prey. Further, daily variation in foraging behavior has been demonstrated in birds that have access to unlimited food (e.g., Kessel 1976), which suggests that the cost of foraging in harsh climatic conditions also affects activity patterns. Among species like the Belted Kingfisher, whose winter range limits are strongly affected by climate (Kelly and Van Horne 1997; Root 1988a, b), the link between temperature variation and activity patterns is probably strongest in the northern portion of their winter ranges. Moreover, this relationship should be intensified if both the cost of foraging and availability of prey are affected by climatic conditions.

Northern Colorado is near the northern limit of the Belted Kingfisher's winter distribution, which is associated with a minimum-January-temperature isotherm (Root 1988a). Because of their plunge-diving foraging behavior, it may be energetically expensive for kingfishers to forage at cold temperatures. If so, temperature may be an important contributor to foraging patterns of Belted Kingfishers during winter. In addition, the distribution and extent of ice cover are important determinants of kingfisher distribution during cold periods (Kelly and Van Horne 1997). Thus, daily time and energy budgets of Belted Kingfishers might provide insight into how this species copes with seemingly adverse environmental conditions. There is little information available on the time budgets of Belted Kingfishers (Hamas 1994). Because of the potential relationship between temperature and foraging behavior, I investigated the relationships among temperature, foraging patterns, and energy budgets of Belted Kingfishers during winter in northern Colorado.

METHODS

Between 18 Jan. and 27 Feb. 1994 I located the territories of 16 Belted Kingfishers (14 males and 2 females) along a 20-km long stretch of the Cache la Poudre River in Fort Collins, Colorado (40°35′N, 105°05′W). I observed more males than females because the winter population in my study area had a male-biased sex ratio. I watched each of these birds for 1 d, beginning between 0630 and 0700 h MST and ending when birds went to roost (ca. 1645–1715 h). I recorded behavior continuously until the focal bird left its territory. However, there were blocks of time when I lost contact with the focal individual. The behaviors that I recorded were combinations of perching, calling, flying, preening, and foraging. I also recorded foraging success, handling time, prey species (when possible), and prey size. I recorded the duration of behaviors involving perching and flying, whereas I recorded foraging dives as instantaneous events.

I estimated the length of fish captured in 0.25-bill-length increments. I used length measurements of 21 Belted Kingfisher bills (commissure to tip length) taken in my study area to convert these observations into cm. Prey length was estimated by multiplying average bill length (7.2 ± 0.3 cm) by the recorded fish length.

An ideal method for estimating the mass of prey from their length would be to identify each prey item to species, to derive mass-length relationships for these species, and then to use these relationships to estimate the mass of each prey item. Practically, the similarity in body form among the primary prey species of Belted Kingfishers often made it impossible to identify individual prey to species. Therefore to estimate the mass of prey, I had to make assumptions about the species composition of the prey items. I assumed that all prey species were white suckers (*Catostomus commersoni*) and calculated a mass-length regression for this species. It is unclear how much error this assumption introduces into the calculation of prey mass. However, white suckers were the most appropriate species to use because they were the most common fish species caught in seine sampling in the Cache La Poudre River, their size range encompassed that of prey eaten by Belted Kingfishers, and they were readily eaten by Belted Kingfishers (Kelly 1996).

I collected white suckers that ranged in size from 3–14 cm standard length and killed them with an overdose of ms-222 (Argent Chemical Laboratory, Redmond, Washington). I recorded their wet mass to the nearest 0.1 g and measured their standard length (cm). I used the best-fit equation to estimate mass from length (mass = 8.99 − 3.45 length + 0.39 length^2; $n = 26$, $r^2 = 0.98$, $P = 0.0001$). The gross energy contained within prey was estimated by multiplying the estimated wet mass of prey by 6.27 KJ/g, which is an estimate of the wet mass-specific caloric content of fish (Cummins and Wuycheck 1977:27).

I then converted gross energy in the diet to metabolizable energy by multiplying the gross energy intake by 0.78, which is an estimate of the apparent metabolizable energy coefficient of fish-eating birds (Robbins 1983:293). This estimate is within the range reported by Karasov (1990) for birds that eat vertebrate prey. There is some evidence that metabolizable energy coefficients for a few granivorous birds vary with temperature (Willson and Harmeson 1973). The majority of studies conducted on this topic, however, have found little or no effect of air temperature on metabolizable energy coefficients (Karasov 1990:396). Further, there are few data on these relationships for non-granivorous birds. For these reasons, I assumed that the metabolizable energy coefficient did not vary with temperature.

I divided the hours of the day into five categories (four daytime and one nighttime). I based the daytime categories on the mean ambient temperatures (T_a) of the 16 days of observation. The first time period ranged from 0700–1000 h, during which the average temperature was <0 C. The second time period ranged from 1000–1300 h, during which temperatures were above 0 C and increasing. During time period 3 (1300–1600 h) the temperature was fairly stable. During the last time period (1600–1800 h) temperatures were declining. The fifth time period lasted from 1800 h on the day of observation to 0700 h on the following day. I used T_a measurements taken at Colorado State University, approximately 5 km from my study area.

I used estimates of physiological parameters and allometric equations to estimate the energetic costs of thermoregulation, perching, and flying for Belted Kingfishers (Table 1). I used the sum of the estimates for these three costs as an estimate of energetic costs during the daytime. To estimate nighttime energy costs, I calculated thermoregulatory costs for each bird using the mean temperature for each night (mean across nights; $\bar{x} = -3.7$ C, SE = 1.1 C, $n = 16$ nights) and a body temperature (T_b) of 40 C. My assumption that T_b was maintained at 40 C during the night may slightly exaggerate nighttime energy costs if kingfisher's T_b varies by 1–2 C daily as do those of most birds (Prinzinger et al. 1991, Reinertsen 1996). However, no information specific to variation in kingfisher T_b exists, so to be conservative I assumed a constant T_b. I then assumed that kingfishers spent the entire night perched at a cost of 5.2KJ/h (Table 1) and summed the cost of perching and cost of thermoregulation to derive an estimate of hourly nighttime energetic costs. By using the sum of energetic costs during both daytime and nighttime, I assumed that the energy required for activity (perching and flying) did not substitute for the energy needed for thermoregulation. There is mixed evidence on the validity of this assumption and the degree of substitutability of these costs may depend on ambient temperature (Marsh and Dawson 1989, Walsberg 1983). Also, by using T_a measurements I assumed that the effects of microclimate were negligible. I did not test the validity of this assumption, but it probably generated the largest amount of error at night when kingfishers were at their roost sites, which were generally in protected microclimates such as conifer trees or, less frequently, burrows.

I evaluated the behavior and energy budgets of kingfishers in two ways. First, I averaged behaviors, energy intake, and energy expenditure during each of the daytime categories. Because these daytime estimates were based on the behaviors of the same 16 individuals in four consecutive time periods, I assessed the variation in behavior among time periods using repeated measures ANOVA models. The effect of time period on the response variable was assessed with a univariate test for within-subject effects. For ANOVAs where there was significant variation across time periods, I used the CONTRAST transformation to determine which time periods differed (SAS Institute Inc. 1989). Second, I estimated the total daily energy expenditure and intake for each bird. I then subtracted the total energy expenditure from the total energy intake for each bird to estimate energy balance. To examine the effect of temperature on energy balance, I correlated energy balance with mean daytime temperature. I report all values as means ± SE unless otherwise specified. Significance of all tests was assessed at $P = 0.05$.

RESULTS

I observed Belted Kingfishers for, on average, 76% (± 11%, $n = 16$) of the time between sunrise and sunset. Belted Kingfishers spent nearly

TABLE 1. Estimates of physiological parameters for Belted Kingfishers.

Parameter	Estimate[a]	Equation/Units	Source
Basal metabolic rate(M_b)	3.08 KJ/h	$M_b = 4.0\ W^{-0.27}$; M_b in ml $O_2 \cdot g^{\ 1} \cdot h^{\ 1}$, W in g	Aschoff and Pohl 1970
Thermal conductance (C)			
Active (daytime)	0.25 KJ/h °C	$C = 0.95\ W^{0.48}$; C in ml $O_2 \cdot g^{\ 1} \cdot h^{\ 1} \cdot °C$; W in g	Aschoff 1981
Resting (nighttime)	0.15 KJ/h °C	$C = 0.95\ W^{\ 0.58}$; C in ml $O_2 \cdot g^{\ 1} \cdot h^{\ 1} \cdot °C$; W in g	Aschoff 1981
Body mass (W)	148 g		Dunning 1993:122
Body temperature (T_b)	40.0 °C		Hamas 1981
Lower critical temperature (T_{lc})	27.68 °C	$T_{lc} = T_b - 4.23\ W^{0.21}$; W in g	Weathers and Van Riper 1982
Thermoregulation (M_{tr})	$0.25(27.6 - T_a)$	$M_{tr} = C(T_{lc} - T_a)$; T_a is ambient temperature	Wunder 1975
Perching metabolic rate (M_p)	5.24 KJ/h	$M_p = 1.7(M_b)$	King 1974
Flying metabolic rate (M_f)	44.41 KJ/h	$M_f = 1.01\ W^{0.72}$; M_f in ml $O_2 \cdot min^{-1}$; W in g	Berger and Hart 1974

[a] To convert units, I assumed that the thermal equivalent of one L of O_2 was 20.08 KJ.

TABLE 2. Time budget, energy intake, and energy expenditure of Belted Kingfishers in Colorado during winter days. Sample sizes range from 14–16. Values are means with standard errors in parentheses. Columns that share letters are not significantly different.

	Time of day (h)			
Variable	0700–1000	1000–1300	1300–1600	1600–1800
Energy expenditures				
Perching				
Perch bout duration(min)	15.7 (2.1)^{a}	8.5 (1.4)^{b}	7.1 (1.5)^{b}	5.7 (1.4)^{b}
% of time perched	99.2 (0.1)^{a}	98.7 (0.2)^{b}	98.9 (0.1)^{b}	98.2 (0.3)^{c}
Cost of perching (KJ/h)	5.2 (0.0)	5.2 (0.0)	5.2 (0.0)	5.2 (0.0)
Flying				
No. of flights/h	4.1 (0.5)^{a}	6.4 (0.6)^{bc}	7.2 (0.9)^{b}	6.5 (0.9)^{c}
Duration of flights (s)	5.7 (0.5)	5.5 (0.4)	5.0 (0.6)	6.7 (0.6)
% of time flying	0.8 (0.1)	1.2 (0.2)	1.1 (0.2)	1.8 (0.3)
Cost of flight (KJ/h)	0.3 (0.1)^{a}	0.6 (0.1)^{b}	0.5 (0.1)^{b}	0.8 (0.1)^{c}
Cost of thermoregulation (KJ/h)	8.0 (0.4)^{a}	6.5 (0.4)^{b}	5.8 (0.5)^{c}	5.9 (0.5)^{c}
Total energy costs (KJ/h)	13.5 (0.4)^{a}	12.0 (0.5)^{b}	11.5 (0.5)^{c}	11.9 (0.5)^{b}
Energy intake				
Foraging				
No. successful dives/h	0.6 (1.2)^{a}	1.2 (0.3)^{ab}	2.5 (0.4)^{c}	2.5 (0.7)^{bc}
No. failed dives/h	0.1 (0.1)^{a}	0.4 (0.1)^{b}	0.6 (0.2)^{b}	0.1 (0.2)^{a}
Total energy intake (KJ/h)	9.2 (3.2)	33.9 (10.2)	28.5 (5.9)	29.9 (10.4)

all of their time perched (Table 2). The length of perch bouts varied significantly with time period ($F_{3,39}$ = 2.14, P = 0.0003) and percent of time spent perching declined from morning through evening ($F_{3,39}$ = 7.05, P = 0.0007). Energy cost of perching/h was simply percent of time spent perching multiplied by 5.27KJ/h. The number of flights/h increased from morning to midday and decreased again in the evening ($F_{3,39}$ = 7.5, P = 0.0004). Duration of flight bouts did not vary by time period ($F_{3,39}$ = 2.79, P = 0.0533). Because observation time was made up of only two behavioral categories perching and flying, patterns in percent time spent flying and energy costs of flying mirror of those for perching. The cost of thermoregulation decreased through the day ($F_{3,39}$ = 42.65, P = 0.0001) and this decline was responsible for a decline in total energetic costs through the day ($F_{3,39}$ = 26.97, P = 0.0001). Belted Kingfishers made more successful foraging dives in the afternoon than in the morning ($F_{3,42}$ = 4.06, P = 0.01) and the number of failed dives/h also varied by time period ($F_{3,42}$ = 3.63, P = 0.02). However, there was no difference in the rate of energy intake among time periods ($F_{3,39}$ = 2.14, P = 0.11).

I added my estimate of nighttime cost of thermoregulation ($\bar{x}$ = 4.7 ± 0.17 KJ/h; n = 16 birds) to the cost of perching to derive an estimated nighttime energetic cost of ($\bar{x}$ = 9.9 ± 0.17 KJ/h; n = 16) for kingfishers. Thus, I estimated the mean energy spent by kingfishers during a 13-h night to be 128.7 ± 2.2 KJ (n = 16). I added the nighttime total to the estimate derived from the 11-h daytime period ($\bar{x}$ = 135.3 ± 4.6 KJ; n =

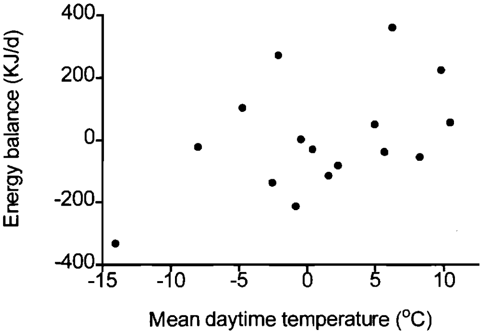

FIGURE 1. Energy balance (total daily energy intake minus total daily energy cost) plotted against mean daily temperature for Belted Kingfishers wintering in Colorado.

16) to estimate the total daily energy expenditure of kingfishers to be 264.4 ± 6.5 KJ (n = 16 birds). The estimated total daily energy intake was 267.2 ± 38.8KJ (n = 16). The difference between energy intake and energy expenditure ($\bar{x}$ = 2.8 ± 42.9KJ/d; n = 16) was not significantly correlated with mean daytime temperature (Fig. 1; r = 0.48; P = 0.06) and this relationship only approached significance because of the large influence of a single data point (−14.0 C).

DISCUSSION

The estimated mean daily energy expenditure of kingfishers exceeded mean intake by only 1% of the total costs. There was, however, a large amount of daily variation in energy balance, which ranged from −331.2 to 361.6 KJ/d. The close agreement between mean expenditure and intake and the large variation around these means may indicate that kingfishers are balancing their energy budgets on time scales longer than one day. An alternative explanation is that the coarseness of the estimates used to calculate energy intake produced large variation. Because of this possibility, patterns of energy budgets presented here must be interpreted with caution. Despite these concerns the estimates of energy intake and expenditure presented here closely matched the estimate of 267KJ/d predicted for a 148 g bird from an allometric equation of total field metabolic rate (Nagy 1987). Also, these estimates are close to, but greater than the range (230–254 KJ/d) reported from a detailed energetics study on captive Belted Kingfishers (Vessel 1978). Based on these comparisons, it seems that estimates of energetic costs and intake presented here provide a reasonable basis for evaluating variation in energy budgets.

Because I reasoned that it was likely to be more energetically costly for kingfishers to forage at cold temperatures, I expected to find a strong relationship between mean daily temperature and energy balance in Belted Kingfishers, however, there was none (Fig. 1). This lack of pattern may either indicate that the foraging patterns of Belted Kingfishers were relatively insensitive to daily temperature variation or that my sample of daily variation was not sufficient to detect this pattern. For example, the kingfisher that was observed on the coldest day did not capture any fish. If typical, this lack of foraging may indicate that the effects of temperature occur below a threshold rather than in a linear fashion. An additional concern in interpreting this correlation is that Belted Kingfisher foraging patterns may show lag effects from events that occurred on previous days and my sampling technique was inadequate to detect these lags.

During this study I recorded several anecdotal observations that may provide some insight about the relationship between foraging behavior and temperature. When I observed kingfishers forage at temperatures below freezing, it was not uncommon for ice to form on the birds feathers. These observations may indicate that kingfishers are insulated well enough that temperature does not have a substantial effect on foraging during cold periods. This conjecture is contradicted by my estimate of T_{lc} (27.6 C) and by other observations where birds appeared to seek sunlit perches and only began to forage after basking on such a perch. This type of heliothermy has been documented in other birds during winter; such as the Greater Roadrunner (*Geococcyx californianus*, Hughes 1996). The contradiction between these observations may indicate that other variables, such as hunger level of the individual, wind speed, solar radiation, or humidity of the air, interact with temperature to influence foraging behavior.

A significant portion of the variation in duration of perch bouts, number of prey captured and number of flights/h was related to time of day (Table 2). These patterns indicate an increase in the foraging activity of Belted Kingfishers late in the day and may reflect their need to obtain energy for overnight energetic requirements (Wolf and Hainsworth 1977). Alternatively, areas with shallow, still water may warm up in the late afternoon. If warmer water attracts fish, then the availability of prey late in the day may be greater than during the morning. An increase in prey availability could contribute to the diel variation in kingfisher behavior.

In summary, Belted Kingfishers increased their foraging activity through the day. This increased activity was coincident with declining energy cost through the day. Energy intake, however, was not related to time of day. Because energy intake was highly variable, energy balance showed no correlation with mean daily temperature. Thus, the relationship between daily temperature and the energetics of kingfishers was weaker than expected given the northern location of the study area. These patterns may indicate that kingfishers budget energy on a time scale longer than one day, that more precise measurements are necessary to detect variation in energy balance related to temperature, or that energy intake is not strongly affected by temperature except at the extreme.

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