

The effects of temperature and artificial rain on the metabolism of American kestrels (*Falco sparverius*)

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Abstract

The effect of rainfall on the metabolism of birds is poorly understood. We measured the metabolism as rate of oxygen consumption ($\dot{V}O_2$) of four male and four female American kestrels (*Falco sparverius*) using open-circuit respirometry. We measured $\dot{V}O_2$ during the spring at ambient temperatures (T_a) of 5, 10, 15, and 25 °C in air without rainfall and with simulated rainfall of 2.5 (low rainfall) and 6.1 cm h⁻¹ (high rainfall). Kestrel metabolism was significantly higher when exposed to the two rainfall levels compared to no rainfall. However, kestrel metabolism was not significantly different at the two rainfall levels. Body temperature (T_b) was significantly lower under high rainfall compared to low rainfall. In addition, under both rainfall levels T_b decreased with decreasing T_a . Calculated thermal conductance was significantly higher in kestrels exposed to rain compared to no rainfall. Kestrels may use sleeking behavior at high rainfall levels to decrease water penetration of the plumage. Daily energy expenditure (DEE) of kestrels exposed to rain may increase markedly, and kestrel energetics may be further exacerbated by wind that often accompanies natural rainstorms.

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1. Introduction

Field observations of mortality due to severe storms have been reported for several species of birds. Odum and Pitelka (1939) reported more than 700 deaths of European starlings (*Sturnus vulgaris*), brown-headed cowbirds (*Molothrus ater*), and common grackles (*Quiscalus quiscula*) in an Illinois roost site totaling over 25,000 individuals after a storm in early February. The storm was characterized by high winds, rain, and a 15 °C drop in ambient temperature in a 5-h period. Kessler et al. (1967) recorded over 8% mortality of cowbirds, grackles, and starlings after heavy rains (19.4 cm) and low minimum ambient temperatures (2 °C) over a 6-day period in early March in a roost of 100,000 individuals in Ohio. Inclement weather may affect

individual species differently. For example, American robins (*Turdus migratorius*) died in a storm with high winds and rains, while house sparrows (*Passer domesticus*) were relatively unaffected (Childs, 1913). The robins were blown out of their roosts and were wetted by water in puddles.

Although these field observations suggest that cold coupled with rain leads to hypothermia resulting to death in these birds, relatively few laboratory studies have examined the direct physiological impacts of plumage wetting. Lustick and Adams (1977) wetted 100 summer and 35 winter-acclimatized European starlings with a 0.5% detergent solution for 1 min. Rates of oxygen consumption ($\dot{V}O_2$), mortality, mass and body temperature (T_b) were then measured at ambient temperatures (T_a s) ranging from 5 to 40 °C for summer birds and between 5 and 15 °C for winter birds during 1-h test periods. The lower critical temperature (T_{lc}) of the summer-acclimatized birds increased from 22.5 °C when dry to 40 °C when wetted with detergent. Winter

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birds, which were significantly heavier than the summer birds, survived a higher percentage of the wetting tests. Starlings that retained more than 20% body mass of water in their plumage had lower survival than those that retained less than 20% body mass of water.

The specific heat of water is high enough to conduct heat away from an animal at 20–30 times the rate of air (Bartholomew, 1977). Consequently, when air within the plumage is displaced with water, heat is lost very quickly. Thus, plumage wetting due to rain, coupled with cold temperature, could significantly affect the energetics and thermoregulation of birds. Only one study has directly measured the metabolism of birds while exposed to artificial rainfall. Stalmaster and Gessaman (1984) measured the $\dot{V}O_2$ of four bald eagles (*Haliaeetus leucocephalus*) at T_a s of 0, 5, 10, 15, and 20 °C and rainfall levels of 6.1 and 22.2 cm h⁻¹. $\dot{V}O_2$ increased by 9% and 21% over resting rates when the birds were exposed to 6.1 and 22.2 cm h⁻¹ rainfall levels, respectively. T_b fell an average of 1.4 °C during the 4-h rainfall trials at all T_a s and both rain intensities. We hypothesized that the effect of rain on the energy metabolism of a smaller bird would be larger than that measured by Stalmaster and Gessaman (1984) due to their larger surface area to volume ratios. We further hypothesized that a smaller bird would be more affected by higher rainfall levels compared to lower rainfall levels. We tested these hypotheses using American kestrels (*Falco sparverius*). We measured the effects of temperature and rainfall on kestrels during spring and early summer in northern Utah, which is the time of year they are most likely to encounter rainfall in their normal habitats (Utah Climate Center, Utah State University). American kestrels are the smallest, most numerous, and most widespread North American falcon. American kestrels inhabit open areas where they hunt primarily from perches (Smallwood and Bird, 2002). Kestrels have been observed to sit out in the open on power lines and fence posts during light rain showers (Chris Shultz, personal communication).

2. Materials and methods

2.1. Birds and study site

Four female and four male adult American kestrels were captured using bal-chatri traps during spring near Logan, Cache County, UT (41°45' N, 111°49' W). Mass at capture was measured to the nearest 0.1 g with an Ohaus model CT-1200 portable electronic balance. Following capture, birds were transported to the Utah State University where they were housed individually in wooden cages (32×32×32 cm) equipped with a block perch. The block perch was 6 cm high to maintain the structural integrity of tail feathers. Plumage quality was monitored, and all birds maintained good feather quality except for several broken tail feathers. The cages were kept in a temperature-controlled environ-

mental chamber (3×3×2.5 m) maintained at 18±0.5 °C. While in captivity, each bird was fed fresh or freeze/thawed gerbil, laboratory rat, or pigeon tissue until satiated once daily. All kestrels maintained body mass while in captivity. After metabolic tests were completed, all kestrels were banded with a United States Fish and Wildlife Service band and released at the site of capture.

2.2. Measurement of metabolic rates

The rate of oxygen consumption ($\dot{V}O_2$) of kestrels was measured at ambient temperatures (T_a) of 5, 10, 15, and 25 °C without rain and with stimulated rainfall levels of 2.5 and 6.1 cm h⁻¹ using open-circuit respirometry. The kestrels sat on a block perch within a 20-L effective volume plexiglass and wood metabolic chamber. The wood was sealed to make it water resistant. Metabolic chamber temperature was regulated within ±0.5 °C by placing it in a temperature-controlled environmental chamber. Metabolic chamber temperature was monitored continuously throughout each test with an Omega thermocouple thermometer (Model Omni IIB, previously calibrated to a thermometer traceable to the U.S. Bureau of Standards) attached to a 24-gauge copper-constantan thermocouple inserted into the inlet port of the metabolic chamber. $\dot{V}O_2$ was measured from 0800 to 1700 h MST. Birds were fasted for at least 14 h prior to metabolic tests to insure postabsorptive conditions. Individuals were weighed before and after completion of the metabolic trials to determine mass gain from plumage water retention. $\dot{V}O_2$ was measured using with an Ametek Model S-3A oxygen analyzer (Pittsburgh, PA). Dry, CO₂-free air was drawn through the metabolic chamber using a diaphragm pump. Outlet flow rates of dry, CO₂-free air were maintained at 1096–1118 mL/min by a Matheson precision rotameter (Model 604) calibrated to ±1.0% volumetrically (Brooks vol-u-meter) and located downstream from the metabolic chamber. These flow rates yielded changes in oxygen content between influx and efflux gas of 0.3% to 0.6% and maintained oxygen content of efflux gas above 20.3%. Fractional concentration of oxygen in efflux gas was determined from a 100 mL/min subsample passed through the oxygen analyzer. This subsample of efflux gas was recorded every 15 s using Datacan 5.0 data acquisition and analysis program (Sable Systems, Las Vegas, NV). Oxygen consumption was calculated as steady-state $\dot{V}O_2$ using Eq. 4a of Withers (1977).

$\dot{V}O_2$ was measured on individual birds before and during rainfall at each T_a . Birds were exposed either to low or high rainfall during a single trial. Birds were given at least 2 days between trials. $\dot{V}O_2$ without rain was calculated over a 15-min period after a 1-h equilibration period. Rain was then started and continued for 2-h. $\dot{V}O_2$ in rain was determined during the last 15-min of the 2-h trial. Artificial rain was produced by a metal rainmaker with 144 droplet formers situated in the roof of the metabolic chamber 30 cm above the kestrel (Fig. 1). In rain experiments with bald eagles, the

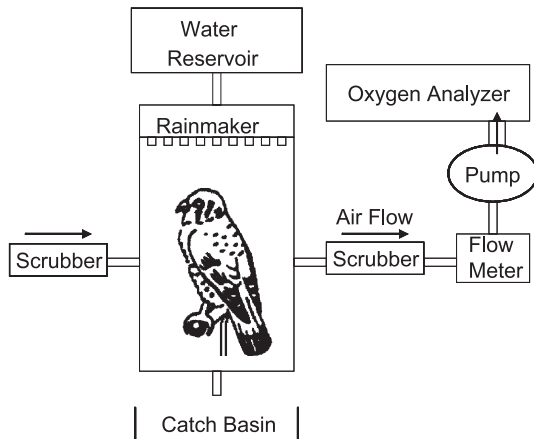


Fig. 1. Schematic diagram of the apparatus used to measure oxygen consumption rates at various ambient temperatures and artificial rainfall levels. Arrows indicate direction of airflow.

rainmaker panel was 1 m above the bird, and the eagles wore masks for collection of $\dot{V}O_2$ data. This increased height would increase the velocity of raindrops compared to 30 cm (Laws and Parsons, 1943) and may increase the plumage penetration of water. However, kestrels in this study did not tolerate masks well and we used the nonrestrictive metabolic chamber to minimize stress on the birds. The two levels of rainfall were controlled by a valve between a 2-L water reservoir and the rainmaker. Tap water was used for rain. The tap water sat in the reservoir for 75 min before rainfall was started. Tap water temperature and dissolved oxygen content were periodically checked to insure that the rainwater temperature was similar to chamber T_a and that the rainwater was nearly saturated with dissolved oxygen. The floor of the metabolic chamber was tilted so that rainwater drained out of the chamber and into the catch basin. Rainwater volume was measured at the end of each rain trial with a graduated cylinder.

At the termination of each metabolic test, birds were removed from the chamber, and body temperature (T_b ; ± 0.1 °C) was recorded with a 30-gauge copper-constantan thermocouple attached to an Omega Model HH25-TC thermometer (previously calibrated to a thermometer traceable to the U.S. Bureau of Standards). The thermocouple was inserted into the cloaca to a depth where further insertion did not alter temperature reading. Thermal conductance was calculated for individuals after exposure to rainfall as $C = \dot{V}O_2 / (T_b - T_a)$ (Scholander et al., 1950). T_b was assumed to be 40.5 °C for kestrels not exposed to rainfall (Bartholomew and Cade, 1957).

2.3. Statistics

Data are reported as means $\pm$ S.D. Body mass data were compared using Student's *t*-tests because variances were equal (*F*-tests for equality of variances). $\dot{V}O_2$, T_b , C , and mass gain data were analyzed by repeated measures ANOVA and Bonferroni post hoc tests for multiple

Table 1

Metabolic rates in the thermoneutral zone for American kestrels from this study compared with other published values

Reference	Metabolic rate	Phase ^a	Captivity ^b
This study	1.94 (8)	Active	Short-term
Hayes and Gessaman (1980)	2.78 (5)	Active	Short-term
Shapiro and Weathers (1981)	2.53 (11)	Resting	Long-term
Wasser (1986)	1.98 (3)	Resting	Long-term

Note: whole-organism metabolic rates are measured in milliliters $\dot{V}O_2$ per minute. Parenthetical values following body mass are sample size.

^a Active phase values are typically 24% higher than resting phase values (Aschoff and Pohl, 1970).

^b Long-term captives are approximately 15% higher than short-term captives (Warkentin and West, 1990).

comparisons. Gender was the between-subject factor, and T_a and rainfall levels were within-subject factors (Zar, 1996). Regression lines were fit by the method of least squares. Statistical significance was accepted at $P < 0.05$. All statistics were computed using SPSS 8.0 (SPSS, Chicago, IL). All data are presented and were analyzed on a whole-organism basis as this avoids confounding effects of ratios (Packard and Boardman, 1999).

3. Results

Mean body mass during metabolic tests was 107.8 ± 6.0 g for males which was not significantly different ($t_{1,6} = 2.39$, $P = 0.06$) than 119.0 ± 7.1 g body mass of females. $\dot{V}O_2$ at 25 °C, which is within the thermoneutral zone for American Kestrels (Shapiro and Weathers, 1981), is compared to published metabolic rates for kestrels in Table 1.

$\dot{V}O_2$ varied significantly with temperature ($F_{3,18} = 67.26$, $P < 0.001$; Fig. 2). The outstanding difference revealed by Bonferroni's post hoc test was that $\dot{V}O_2$ at 25 °C was significantly lower than 15, 10, and 5 °C ($P < 0.001$ for each temperature comparison). $\dot{V}O_2$ also varied significantly with

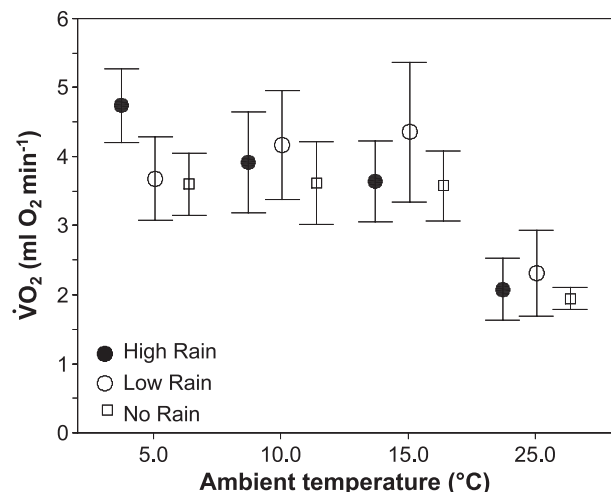


Fig. 2. Metabolic response to varying ambient temperature and levels of artificial rainfall in American kestrels from Utah.

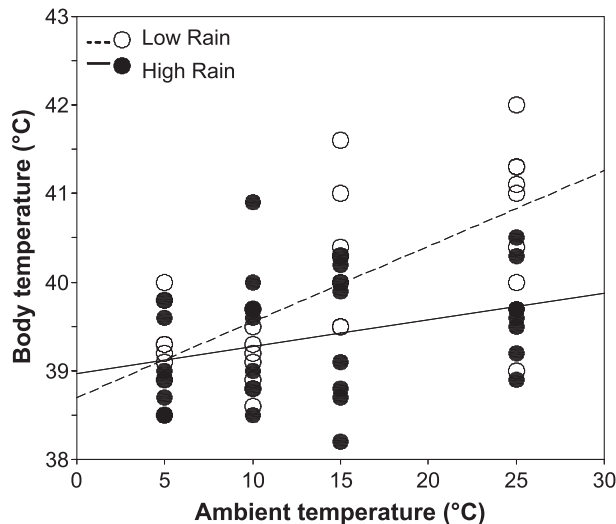


Fig. 3. The relationship between body temperature and ambient temperature for American kestrels exposed to low rainfall and high rainfall. Linear regression equations were, low rainfall kestrels: $T_b = 38.70 + 0.085T_a$ ($n=32$, $r^2=0.45$, $P<0.001$), high rainfall kestrels: $T_b = 38.97 + 0.031T_a$ ($n=32$, $r^2=0.11$, $P=0.05$).

rainfall level ($F_{2,12}=6.38$, $P=0.01$). $\dot{V}O_2$ was significantly higher under low rainfall compared to no rain ($P<0.01$) and was significantly higher under high rainfall compared to no rain ($P<0.001$). However, $\dot{V}O_2$ was not significantly different between low and high rainfall levels ($P=0.9$; Fig. 2). In addition, $\dot{V}O_2$ did not vary significantly due to gender ($F_{1,6}=1.02$, $P=0.35$). There was a significant temperature and rainfall interaction ($F_{6,36}=5.24$, $P<0.01$).

T_b during rainfall trials varied significantly with temperature ($F_{3,18}=30.75$, $P<0.001$; Fig. 3). Bonferroni's post hoc tests showed that T_b was significantly higher at 25 °C compared to 10 ($P<0.01$) and 5 °C ($P<0.001$). T_b was also significantly higher at 15 °C compared to 5 °C ($P<0.01$). T_b also varied significantly with rainfall level ($F_{1,6}=18.66$,

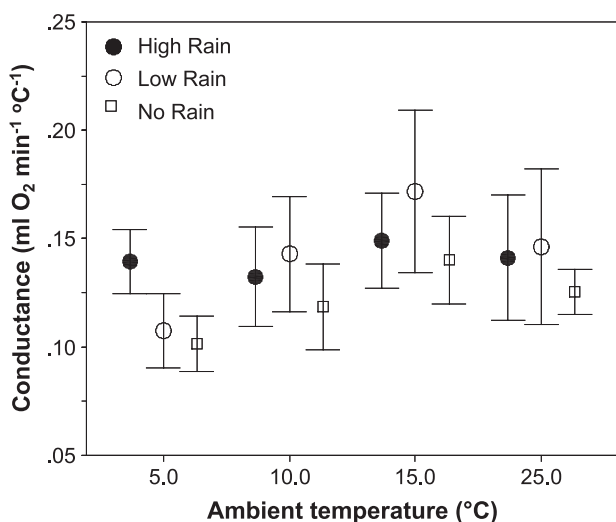


Fig. 4. Response of thermal conductance to varying ambient temperature and levels of artificial rainfall in American kestrels from Utah.

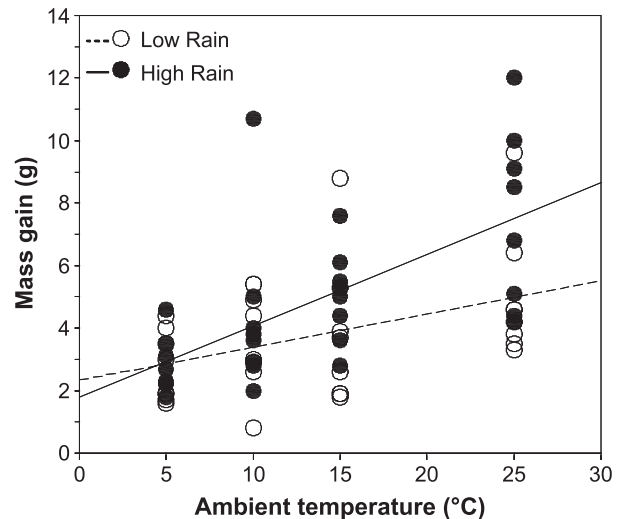


Fig. 5. The relationship between mass gain and ambient temperature for American kestrels exposed to low rainfall and high rainfall. Linear regression equations were, low rainfall kestrels: mass gain = $2.43 + 0.095T_a$ ($n=32$, $r^2=0.13$, $P=0.04$), high rainfall kestrels: mass gain = $1.78 + 0.23T_a$ ($n=32$, $r^2=0.41$, $P<0.001$).

$P=0.01$; Fig. 3). T_b did not vary significantly with gender ($F_{1,6}=0.20$, $P=0.67$). T_b decreased linearly with decreasing T_a for both low and high rainfall treatments (Fig. 3).

Thermal conductance during rainfall trials varied significantly with temperature ($F_{3,18}=11.28$, $P<0.001$; Fig. 4). Bonferroni's post hoc tests showed that C was significantly lower at 5 °C compared to 10 ($P=0.03$), 15 ($P=0.01$), and 25 °C ($P=0.05$). C also varied significantly with rainfall level ($F_{2,12}=10.96$, $P=0.01$; Fig. 4). C was significantly lower in birds exposed to no rain compared to low rain ($P=0.03$) and high rain ($P<0.001$). C did not vary significantly with gender ($F_{1,6}=0.85$, $P=0.39$). There was a significant temperature and rainfall interaction ($F_{6,36}=2.83$, $P=0.02$).

Mass gain during rainfall trials varied significantly with temperature ($F_{3,18}=10.77$, $P<0.001$; Fig. 5). Bonferroni's post hoc tests showed that mass gain was significantly higher at 25 °C compared to 5 °C ($P<0.01$). Mass gain also varied significantly with rainfall level ($F_{1,6}=10.62$, $P=0.02$; Fig. 5). Mass gain did not vary significantly with gender ($F_{1,6}=0.11$, $P=0.75$). Mass gain increased linearly with increasing T_a for both low and high rainfall treatments (Fig. 5).

4. Discussion

Our metabolic data at 25 °C compare favorably to published values of metabolic rates within the thermoneutral zone for American Kestrels. Kestrels in this study were tested while postabsorptive during the active phase of the daily cycle. Although this may limit our comparisons with published thermoneutral metabolic rates, we believe that measuring metabolism under artificial rainfall conditions during the active phase is more ecologically realistic than at

night. In spite of this limitation, our value of $1.94 \text{ mL } \dot{V}O_2 \text{ min}^{-1}$ at 25°C only varies as little as 2% from other published values (Table 1). In addition, time in captivity has varied markedly for kestrels that have been used for metabolic studies. Our kestrels were short-term captives (less than 1 month) where some kestrels tested have been in captivity for up to 3 years (Shapiro and Weathers, 1981). Warkentin and West (1990) found that merlins (*Falco columbarius*) held for 7 months to 3 years had approximately 15% higher metabolic rates than freshly captured merlins. The greatest difference in kestrel metabolism in Table 1 is the current study compared to Hayes and Gessaman (1980). The kestrels used by Hayes and Gessaman (1980) were captured from the same locations as the current study but were winter-acclimatized individuals. American kestrels may show significant seasonal changes in metabolism to tolerate severe winter conditions encountered in northern Utah.

Our results demonstrate that American kestrels have significantly increased metabolic rates when they are exposed to artificial rainfall compared to no rainfall. Metabolic rates of bald eagles increased approximately 10% when exposed to 6.1 cm h^{-1} rainfall compared to no rainfall at 15 and 10°C and increased 16% at 5°C (Stalmaster and Gessaman, 1984). Because kestrels in this study did not have any significant differences in metabolism at low rainfall compared to high rainfall levels, we calculated metabolic increases compared to air by averaging both high and low rainfall metabolic rates. For kestrels, metabolism increased 12% in the rain at 15 and 10°C and increased 17% at 5°C . Thus, overall increases in metabolism under rainfall are nearly identical for American kestrels and bald eagles. We must reject our original hypotheses that the effect of rain on metabolism would be greater for smaller birds and also that a smaller bird would be more affected by high rainfall levels compared to low rainfall levels.

Although kestrels did not have significant differences in metabolism at the different rainfall levels, they did exhibit significant differences in T_b . Average T_b in high rainfall was $0.5\text{--}1.0^\circ\text{C}$ lower than in low rainfall (Fig. 3). This may be indicative of increased thermal stress under high rainfall. Higher rainfall levels may be more likely to penetrate the plumage and conduct heat away from the body. Thermal conductance was significantly higher in rainfall compared to in air. In addition, thermal conductance decreased with decreasing temperatures below the thermoneutral zone which was especially evident in birds in low rainfall compared to high rainfall. This indicates that thermal conductance is modified to increase effective insulation as kestrels were exposed to colder temperatures. In general, birds increase their insulation by increasing ptiloerection (Hohtola et al., 1980). However, when exposed to rain, increased ptiloerection would increase water penetration of the plumage. Instead of increased ptiloerection, birds generally adopt a sleeking behavior in the rain to reduce

plumage wettability (reviews: Kennedy, 1970; Hume, 1986). Sleeking is characterized by a more upright posture, feathers that are flat against the body and retracting the head. Sleeking decreases water penetration and increases run off of water from the feathers. Bald eagles under artificial rain also used sleeking behavior (Stalmaster and Gessaman, 1984). Elkins (1988) suggested that birds may not be affected by light rainfall but may be forced to sleek or find shelter during heavy rainfall. The physiological trade-offs between sleeking to reduce water penetration and the consequent reduction in insulatory space between the skin and the outside layer of the plumage are unknown.

In addition to the metabolic and conductance data, more evidence for sleeking behavior in this study includes mass gain under the different rainfall exposures. Although mass gain due to water penetration into the plumage was higher in kestrels exposed to high rain levels compared to low levels at colder temperatures, the amount of mass gain for the two conditions merged at low ambient temperatures. This suggests that kestrels under high rain used more sleeking behavior than those under low rainfall causing less wetting of their plumage. In addition, as ambient temperatures increased under both rainfall levels, the amount of water retained in the plumage also increased. These data agree with findings of Van Rhijn (1977) who showed that when feathers were immersed in water of various temperatures, feathers weighed more after immersion at higher temperatures.

Metabolism in kestrels under artificial rainfall increases 14% on average below 25°C . We calculated how this increased metabolism would affect the ecological energetics of kestrels in northern Utah. Kestrels are sit-and-wait diurnal predators that locate prey visually from exposed hunting perches, such as power lines (Bildstein and Collopy, 1987). Kestrels may remain vigilant for prey during light rainfalls (Chris Schultz personal communication). If a kestrel perched on a utility pole were exposed to rainfall for 4 h, total metabolism would increase by 10.9 kJ assuming an RQ of 0.80. This would represent an increase in daily energy expenditure (DEE) of 5.6% for kestrels from northern Utah calculated by Gessaman and Haggas (1987). Even with a modest increase of 5.6% in DEE, kestrels would have to increase their food intake to compensate for the higher energetic demands. If a kestrel were in a heavy rainstorm similar to the high artificial rainfall levels, they may adopt a marked sleeking behavior or seek shelter although their DEE may not increase more than 5.6% above normal because prey may become less visible and prey items may also seek shelter under high rainfall conditions.

Artificial rainfall significantly increased metabolism in kestrels in this study. Many naturally occurring rainstorms are also accompanied by wind. Heat loss due to the combined effects of wind and wetting by rainfall may increase metabolism significantly more than rainfall alone. Further study is needed to provide more information about the heat loss of birds in natural rainstorms.

Acknowledgments

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