ESTIMATING THE EFFECT OF WIND ON AVIAN METABOLIC RATE WITH STANDARD OPERATIVE TEMPERATURE

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ABSTRACT.—I develop a simplified procedure to estimate the effect of wind on avian energy-use rates from published and unpublished studies of 10 passerine and 7 nonpasserine species. Below the lower critical temperature, energy-use rates of passerines resting in the dark can be estimated as that of a bird of the same species in a metabolism chamber set to the standard operative temperature, T_{es} of the habitat, defined as

$$T_{es} = T_b - (1 + 0.26\sqrt{u})(T_b - T_e).$$

Wind speed is u, and T_b is body temperature. Operative temperature (T_e), is ordinarily close to air temperature for birds resting at night, but T_e can include the effects of thermal and solar radiation. The 95% confidence interval for predictions of the average metabolic rate of a passerine is ±9.3% for air speed up to 4 m/s and temperatures below the thermal neutral zone. The procedure also appears valid for some, but not all, nonpasserines. *Received 22 August 1989, accepted 25 February 1990.*

ENERGY flow is a significant factor in studies of community structure, of the distribution and abundance of organisms, and of behavior patterns and habitat selection. Maintenance (basal plus thermoregulatory) metabolism accounts for 40–60% of the total avian energy budget (Walsberg 1983, Weathers et al. 1984). A simulation model of avian communities (Wiens and Innis 1974) found population densities in various age classes and bioenergetic demands to be significantly sensitive to temperature via the thermoregulatory component of maintenance metabolism. The geographical distributions of the wintering ranges of 60% of passerine species have been reported to be associated with particular January isotherms (Root 1988, 1989; but see Castro 1989).

These studies and the majority of similar reports do not include the effects of sun and wind, which may be regarded as effectively increasing or decreasing the temperature of the environment (Bakken 1980). However, it is often important to do so. The inclusion of the effects of sun and wind significantly improved time-budget estimates of energy expenditure (Weathers et al. 1984) and prediction of time allocated to social displays (Santee and Bakken 1987). Shelter from the wind is often a feature of roost-site selection by birds, and shelter can significantly affect total energy demands (Stalmaster and Gessaman 1984, Buttemer 1985, Walsberg 1986, Webb and Rogers 1988, but see Walsberg and

King 1980). This reduction in thermoregulatory energy demand appears ecologically important. Winter survival is improved by supplemental feeding (Jansson et al. 1981, Brittingham and Temple 1988), although the mechanism is complex and may be mediated by predation (Jansson et al. 1981, Lima 1986, Rogers 1987).

Some field studies have been based directly on laboratory measurement of the thermal effects of wind, radiation, or both (Goldstein 1984, Weathers et al. 1984, Buttemer 1985, Walsberg 1986, Santee and Bakken 1987). Considerable technical difficulty is inherent in the laboratory part of such studies. In many cases, the necessary level of effort is difficult to justify, and a simpler means of approximating the influence of sun and wind on heat loss would be valuable.

My objective was to use published data on the effect of wind on the thermal conductance of various birds and the concept of standard operative temperature, T_{es} (Gagge 1940, Bakken 1976), to develop such an approach. The proposed model differs from an allometric model of conductance developed by Goldstein (1983). I use T_{es}, which leads to a relation independent of mass. Although the procedure could be generalized, few data are available on the conductance of birds exposed to wind, sun, or both, during their active phase, when the thermal environment, behavior, and physiological state of the animal differ significantly from those typical of rest phase. Thus, the reliable applicabil-

ity of this model is limited to the effect of wind on birds resting in the dark. Thermal radiation to the night sky with a radiation temperature typically 20–30°C below air temperature has also not been simulated in laboratory studies. However, the use of operative temperature rather than air temperature compensates for most thermal radiation effects, and rest-phase behavior and physiology are probably unaltered by thermal radiation.

THEORY

Standard operative temperature.—Standard operative temperature, T_{es} (Gagge 1940, Bakken 1976), combines sun, wind, and air temperature to give the temperature of a thermally equivalent laboratory enclosure. The response of the animal to the laboratory enclosure temperature should approximate its response to the field conditions. Bakken et al. (1985) and the references therein provide a detailed derivative of T_{es} from heat transfer theory and of methods for computing T_{es} from microclimate and animal data. Only a brief summary is given here.

Heat flow between the animal and its environment can be described by

$$M - E - C \cdot dT_b/dt = K_e(T_b - T_e), \quad (1)$$

where M is total metabolic heat production (W/animal), E is total evaporative cooling (W/animal), C is heat capacitance (W·°C^{-1}·animal^{-1}), and T_b is body temperature (K = °C + 273.16). The overall thermal conductance between the core of the animal and its environment is K_e. Operative temperature, T_e (Winslow et al. 1937, Bakken and Gates 1975), is most easily measured with a suitable taxidermic mount or model of the animal of interest (Bakken and Gates 1975, Bakken et al. 1981, Bakken et al. 1985, Walsberg and Weathers 1986). Equation 1 shows that when $(M - E) = 0$, and T_{bm} is in steady-state $(dT_{bm}/dt = 0)$, $T_{bm} = T_e$. (The subscript m indicates a parameter of a model or mount.) The mount or model should have low heat capacitance to keep T_{bm} near the steady-state.

The T_{es} of a general environment is the temperature in a reference environment (e.g. a typical metabolism chamber) at which the animal would have the same $(M - E)$ as it does in the natural environment. Applying Eq. 1 to this definition, assuming constant T_b,

$$T_{es} = T_b - (K_e/K_{es})(T_b - T_e), \quad (2a)$$

or

$$T_{es} = T_b - (M - E)/K_{es}. \quad (2b)$$

Here, K_e is the overall thermal conductance of the animal in the field and K_{es} is the value in the standard environment. Their ratio, K_e/K_{es}, is a dimensionless measure of the extent to which wind enhances heat flow. Note that, while T_e is an index of thermal potential and requires K_e to specify heat flow (Eq. 1), T_{es} incorporates K_e and specifies heat flow directly. This is because the fixed convection condition sets up a unique relation between the temperature of the standard environment and the sensible heat flow to or from a specific animal. If the reference environment for T_{es} is a typical metabolism chamber and if T_{es} can be determined in the field, metabolic energy expenditure may be estimated directly from published data that relates M to temperature.

Direct measurement of T_{es}.—Chappell and Bartholomew (1981) used an unheated mount to measure T_e as described above, while a nearby anemometer measured wind speed. Laboratory data on heated mounts and live animals were then used to relate K_e/K_{es} to wind speed and temperature. This relation was then used (Eq. 5a) to calculate T_{es}. A recursive calculation is usually needed to determine T_{es}, particularly above the lower critical temperature, as K_{es} varies with T_{es} (Bakken 1980, Chappell and Bartholomew 1981). This procedure is necessary to estimate evaporative water loss, which increases rapidly above the lower critical temperature. However, it is probably valid to assume a standard metabolic rate (with any activity increments) whenever T_{es} exceeds the lower critical temperature. Birds normally avoid conditions above the upper critical temperature (cf. Wiens and Innis 1974).

Simplified determination of T_{es}.—A number of studies have examined the overall conductance of small animals below the lower critical temperature at various wind speeds. The results are fitted by a linear regression:

$$K_e = a + b\sqrt{u}. \quad (3)$$

If the reference environment used to define T_{es} is a typical metabolism chamber with $u \doteq 0$, then $K_{es} = a$, and

$$K_e/K_{es} = 1 + (b/a)\sqrt{u}, \quad (4)$$

so that

$$T_{es} = T_b - (1 + (b/a)\sqrt{u})(T_b - T_e). \quad (5)$$

The wind speed dependence of T_{es} thus may be derived from b/a, and these coefficients or the data needed to derive them are available in the literature for some species. The value of b depends on the units used for wind speeds, and the use of thermal resistance (reciprocal of thermal conductance) gives different b/a ratios than does the use of thermal conductance.

Below the thermal neutral zone, the b/a ratio can be based on the regression of either K_e or M against $\sqrt{u}$. Conductance is computed as $(M - E)/(T_b - T_e)$. In the absence of severe thermal stress, birds normally maintain a fairly constant T_b. Calder and King (1974: eq. 56) found that, at a given experimental temperature, E was a constant fraction, c, of M. Thus, for a series of measurements at a given T_e, K_{es} is a simple multiple of M; i.e. $K_e = M(1 - c)/(T_b - T_e)$. Thus, the regression coefficients for K_e vs. $\sqrt{u}$ and for M vs. $\sqrt{u}$ are also constant multiples of one another, and the b/a ratio is the same for both.

Two questions related to the accuracy of various methods for determining T_{es} below the lower critical temperature can now be stated precisely in terms of the b/a ratio. First, it is unknown whether or not, for a given set of geometrically similar animals (e.g. Passeriformes, or perhaps birds generally), the ratio b/a is sufficiently well-behaved that a standard value—or some allometrically predicted value—can be used in the method of Chappell and Bartholomew (1981) when data on the species of interest are not available. Second, the probable error associated with using a standard b/a ratio to estimate energy use rates is undefined.

MATERIALS AND METHODS

I obtained data from a number of studies that have examined the effect of wind on metaboic rate of birds. These included the Snowy Owl (*Nyctea scandiaca*; Gessaman 1972), White-crowned Sparrow (*Zonotrichia leucophrys*; Robinson et al. 1976), American Goldfinch (*Carduelis tristis*; Bakken et al. 1981), Gambel's Quail (*Callipepla gambelii*; Goldstein 1984), Phainopepla (*Phainopepla nitens*; Walsberg 1986), Little Penguin (*Eudyptula minor*; Stahel et al. 1987), Ruffed Grouse (*Bonasa umbellus*; Thompson and Fritzell 1988), and Verdin (*Auriparus flaviceps*; Webster and Weathers 1988). Data on the Common Grackle (*Quiscalus quiscula*), Brown-headed Cowbird (*Molothrus ater*), and Red-winged Blackbird (*Agelaius phoeniceus*) were taken from Lustick (1983). Data on the Kestrel (*Falco*

sparverius), Red-tailed Hawk (*Buteo jamaicensis*), and the Golden Eagle (*Aquila chrysaetos*) were taken from Hayes and Gessaman (1980), as analyzed by Goldstein (1983). I added my own unpublished data on Dark-eyed Juncos (*Junco hyemalis*).

RESULTS

For analysis, the morphologically homogenous passerines were considered separately from the more diverse nonpasserines.

Wind speed dependence of b/a *for passerine birds.*—The b/a ratio showed no trend with air temperature among 10 groups (species, or sex of a dimorphic species) of passerines (Table 1). The ratio increased with temperature for Brown-headed Cowbirds and American Goldfinches, decreased for male Common Grackles, and varied irregularly for the other groups. I therefore treated the variation among temperatures as replication error for purposes of further analysis. The high and low extremes were excluded from the analysis. These values also appeared unusual when compared with the values for the same species at other temperatures.

Evidence for intergroup differences in b/a is equivocal. There was a marginally significant difference among groups by ANOVA ($P = 0.04$, $df = 8, 32$, Phainopepla excluded). The more conservative Tukey-Kramer HSD test found no significant pairwise differences (smallest $P = 0.16$). To test for a trend with mass, I averaged the b/a values for each group (Table 1) over T_a and, as exact masses were not always available, I then computed the rank correlation. No trend was evident (range 7–160 g, $r = 0.32$, $P > 0.2$, $n = 10$).

For the purposes of developing an approximate general expression, it appeared reasonable to compute a "typical passerine" value that could be used to compute T_{es}. There is a possibility that b/a varies among species or sexes of a dimorphic species, so I weighted groups equally and averaged the 10 mean b/a values. The grand mean was $b/a = 0.26 \pm 0.03$ (± 1 SD). This can be used (Eq. 5) to obtain a general relation to compute T_{es} for resting passerines by the method of Chappell and Bartholomew (1981):

$$T_{es} = T_b - (1 + 0.26\sqrt{u})(T_b - T_e). \quad (6)$$

Here, T_b is the normal body temperature, T_e is measured with an unheated mount, and u is measured with a nearby anemometer.

TABLE 1. Coefficients b/a used in the relation $K_e/K_{es} = (1 + b/a)\sqrt{u}$ for various passerines. The ratio K_e/K_{es} can then be used to estimate T_{es} with Equation 2a. The a and b coefficients are defined by regressions to total net metabolic heat production measured at one air temperature and different wind speeds (Eq. 3). For all species, data from several birds has been averaged at each combination of wind speed and air temperature. Thus, the sample size n is equal to the number of different wind speeds used in the study. Except where indicated, all data were taken in darkened enclosures on unrestrained birds at rest in their rest phase.

Bird name/air temp. (°C)	Wind speeds (m/s)	b/a	n	Source
Verdin				
30	0.05–3.00	0.265[a]	5	Webster and Weathers 1988: table 1.
20		0.212[a]	5	
10		0.288[a]	5	
5		0.367[a]	5	
$\bar{x}$		0.283		
Phainopepla				
10	0.00–4.00	0.230	6	Walsberg 1986.
White-crowned Sparrow				
20	0.06–1.68	0.252	5	Robinson et al. 1976: table 1.
10		0.302	5	
1		0.235	5	
$\bar{x}$		0.263		
Common Grackle (male)				
10	0.00–4.19	0.264	4	Lustick 1983.
5		0.274	4	
0		0.274	4	
−5		0.343	4	
−10		0.350	4	
$\bar{x}$		0.301		
Common Grackle (female)				
10	0.00–4.19	0.284	4	Lustick 1983.
5		0.341	4	
0		0.428[b]	4	
−5		0.242	4	
−10		0.314	4	
$\bar{x}$		0.295		
Brown-headed Cowbird				
10	0.00–4.19	0.393	4	Lustick 1983.
5		0.327	4	
0		0.302	4	
−5		0.204	4	
−10		0.206	4	
$\bar{x}$		0.286		
Red-winged Blackbird (male)				
10	0.00–4.19	0.227	4	Lustick 1983.
5		0.170	4	
0		0.248	4	
−5		0.220	4	
−10		0.267	4	
$\bar{x}$		0.226		
Red-winged Blackbird (female)				
10	0.00–4.19	0.216	4	Lustick 1983.
5		0.211	4	
0		0.206	4	
−5		0.139[b]	4	
−10		0.239	4	
$\bar{x}$		0.218		

TABLE 1. Continued.

Bird name/air temp. (°C)	Wind speeds (m/s)	b/a	n	Source
Dark-eyed Junco				
20	0.10–3.00	0.208	4	G. S. Bakken, M. T. Murphy, and D. J. Erskine, MS.
15		0.264	4	
10		0.240	4	
5		0.234	4	
0		0.212	4	
−5		0.304	4	
−10		0.260	4	
x̄		0.246		
American Goldfinch				
15	0.15–1.52	0.304	4	Bakken et al. 1981.
5		0.289	4	
−5		0.264	4	
−15		0.258	4	
x̄		0.278		
Mean of all spp.[c] (± SD)		0.263 (± 0.030)		

[a] Animal in dark during active phase.
[b] Extreme value; excluded from averages.
[c] Each species or sex of a dimorphic species is weighted equally in the final average. Error limits are ±1 standard deviation.

Wind speed dependence of b/a *for nonpasserine birds.* —The results for Sphenisciformes and Falconiformes also conformed to Eq. 6, as mean b/a values ranged from 0.228 to 0.306 (Table 2). This is somewhat surprising, as these animals were studied in the active phase, when metabolism is elevated and the thinly insulated head exposed, whereas the passerines were all studied in rest phase. The heads of birds were covered by the mask used for respiratory measurements. The mask may have approximated the effect of tucking the head back in the scapulars in a nocturnal resting position. The b/a ratios for the Ruffed Grouse, Gambel's Quail, and Snowy Owl clearly fell outside the range for the other species.

Nevertheless, Eq. 6 appears potentially applicable to many species over a size range from Verdins to Golden Eagles (7 g to 3.8 kg, nearly 3 log orders). This result is surprising, given the strong size dependence of convective heat transfer (Kreith 1965) and the allometric scaling of most thermal properties of live birds (Calder and King 1974, Goldstein 1983).

DISCUSSION

Estimating energy-use rates. —The ratio K_e/K_{es} responded similarly to wind in all passerine

species (Table 1), even though the values of a and b are mass-dependent (Calder and King 1974, Goldstein 1983). If so, T_{es} can be estimated for resting passerines from Equation 6. Standard plus thermoregulatory metabolic energy-use rate can be estimated as the value measured in the laboratory with chamber temperature equal to T_{es} if it is below the lower critical temperature, and as the standard metabolic rate if T_{es} is above the lower critical temperature. If Equation 6 or a similar relation applies to active birds, total daily energy expenditure could be computed from an estimate of standard plus thermoregulatory energy, time-energy budget data, and metabolic increments of activity, digestion, and reproduction. The TB-1 method described by Weathers et al. (1984) provides an appropriate model.

The statistical uncertainties in standard plus thermoregulatory energy-use rates below the lower critical temperature can be estimated by assuming that 95% of the true values of b/a are in the range 0.18–0.32 (0.25 ± 2.26 [SD]). The corresponding 95% confidence limits on $(M - E)$ are ±9.3%, assuming $T_b = 40°C$ and $u = 4$ m/s. This uncertainty is acceptable for many purposes. The uncertainty will often be reduced, as birds that roost overnight in cold conditions commonly have $T_b < 40°C$, and also often

TABLE 2. Coefficients b/a used in the relation $K_e/K_{es} = (1 + b/a)\sqrt{u}$ for various nonpasserine species. Procedures and interpretation are as in Table 1, except as indicated.

Bird name/air temp. (°C)	Wind speed (m/s)	b/a	n	Source
Sphenisciformes				
Little Penguin				
6	0.00–4.7	0.290[a]	5	Stahel et al. 1987.
Falconiformes				
Red-tailed Hawk				
−5	0.10–13.4	0.306[b]	4	Goldstein 1983; data from Hayes and Gessaman 1980.
Golden Eagle				
−5	0.10–13.4	0.284[b]	4	Goldstein 1983; data from Hayes and Gessaman 1980.
Kestrel				
20	0.10–13.5	0.195[b]	4	Goldstein 1983; data from Hayes and Gessaman 1980.
−7		0.261[b]		
$\bar{x}$		0.228		
Falciform spp. ($\bar{x}$)		0.273		
Galliformes				
Ruffed Grouse				
−5	0.00–3.00	0.091[c]	4	Thompson and Fritzell 1988.
−15		0.128[c]	4	
$\bar{x}$		0.110		
Gambel's Quail				
20	0.06–2.31	0.726[d]	5	Goldstein 1983.
10		0.610[d]		
$\bar{x}$		0.668		
Strigiformes				
Snowy Owl				
−10	0.00–7.47	0.383[c]	3	Gessaman 1972: eqs. 3 and 5.
−20		0.448[c]		
−30		0.494[c]		
$\bar{x}$		0.442		

[a] Data were taken during the active phase using a face mask. The bird faced away from the wind.
[b] Data obtained from birds in the active phase using a face mask.
[c] Data were taken using unrestrained animals in rest phase in a darkened enclosure.
[d] Data were taken using unrestrained animals in active phase.

occupy sheltered sites with $u < 1$ m/s (e.g. Francis 1976, Buttemer 1985, Walsberg 1986, Webb and Rogers 1988, but see Walsberg and King 1980).

Possible systematic errors needing further study.— Equation 6 appears useful for passerines, and perhaps for some nonpasserines, when data on the true dependence of K_e/K_{es} on wind are not available. However, only a few species have been studied, and there is equivocal evidence for interspecific differences. There are uncertainties in the data on which this analysis is based, as few have monitored the behavior, posture, and T_b of the animal during the experiment. Variation during the measurements could obscure true effects or create artifacts. For ex-

ample, the behavior and posture of American Goldfinches respond systematically to wind or the noise produced by the fan or blower (K. Lee and G. S. Bakken unpubl. data). Body temperature may vary, even in well-fed birds in good condition (Paladino 1986). Additional data to test the validity of Equation 6 would be useful.

The applicability of Equation 6 to nonpasserines is unclear. The cause of causes for the unusual b/a ratios of the Ruffed Grouse, Gambel's Quail, and Snowy Owl must be identified. The role of head position needs study. The Gambel's Quail had their heads exposed to convection (Goldstein pers. comm.). The Snowy Owls almost certainly had their heads exposed, as this is their normal behavior (Gessaman pers.

comm.). In contrast, passerines in rest phase normally bury their face under the scapulars, and the penguins and raptors wore face masks during the study. Thermograms of birds show that the head is a major avenue of heat loss (Veghte and Herreid 1965, Hill et al. 1980). Because of its small size and thin insulation, heat loss from the head is probably highly sensitive to wind (cf. Porter and Gates 1969), and may have increased the wind sensitivity of the overall conductance.

Future experimental studies should compare animals with the head exposed to the same animals with the head covered. Various species should be studied when active with the head exposed to assess the validity of Equation 6 for birds under these conditions.

Interspecific comparisons of wind sensitivity.—Inferences about the adaptive nature of measured differences in wind sensitivity of various species should be tempered by the equivocal results of the analysis of variance. There is no clear evidence for or against the proposition that passerine species differ significantly in sensitivity to wind. Further interspecific comparisons would be valuable, and should concentrate on data that can test reliably for adaptive differences in wind sensitivity. Identification of interspecific trends will require careful technique. In addition to the usual precautions in gas-exchange measurements, wind instruments must be calibrated against a reliable primary standard (e.g. pitot tube). A hot-wire anemometer is required to measure turbulence levels and uniformity of wind speed over the test section. Possible blockage effects should be evaluated (Stahel et al. 1987, Bakken 1990). During measurements, posture and behavior should be monitored (e.g. by closed-circuit TV) and recorded along with T_b.

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