

SOCIAL DISPLAYS IN RED-WINGED BLACKBIRDS (*AGELAIUS PHOENICEUS*): SENSITIVITY TO THERMOREGULATORY COSTS

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ABSTRACT.—Breeding male Red-winged Blackbirds (*Agelaius phoeniceus*) engage in territorial advertisement and agonistic displays that have ordered benefits. We studied the frequency of these behaviors in relation to thermoregulatory cost by comparing plots of activity vs. microclimate with plots of energy and water cost vs. microclimate, using standard operative temperature, T_{es} , to quantify microclimate. We used a multiple regression model to control for nonthermal environmental factors covariant with T_{es} to clarify the behavior-thermoregulation relationship. We found that male Red-winged Blackbirds shifted from display to shelter seeking and foraging in proportion to increasing thermoregulatory energy cost. Water costs appeared unimportant. Higher-value agonistic display appeared less sensitive to thermoregulatory cost than did lower-value territorial advertisement. Received 5 June 1986, accepted 18 January 1987.

ENDOTHERMY incurs food and water costs that can be minimized by appropriate behavior (Bartholomew 1964, Morse 1980). King and Murphy (1985) questioned whether food availability is a major limiting factor driving behavior and population dynamics, citing compensating mechanisms and apparent periods of idleness. Maintenance (basal plus thermoregulatory) metabolism, however, accounts for 40–60% of the total avian energy budget (Walsberg 1983a, Weathers et al. 1984). Most small birds probably regulate their food energy budget over periods of, at most, one or a few days because the rate of energy use is large compared with storage capacity (Walsberg 1983b). The time allocated to foraging and shelter seeking vs. other activities thus should respond to thermoregulatory energy and water demands on a short time scale (hours to days). Higher costs do appear to reduce activity (Morton 1967, Morse 1970, Grubb 1975, Evans 1976, Searcy 1979, Grubb and Greenwald 1982). Temperate Zone breeding display presents a paradox, however, as it is concentrated early in the day and early in the year, when temperatures are low and thermoregulatory costs high.

We used male Red-winged Blackbirds (*Agelaius phoeniceus*) breeding in a cattail marsh in

west-central Indiana to test the hypothesis that the allocation of time to two general classes of breeding behavior, territorial advertisement and agonistic display, should be sensitive to thermoregulatory cost and to the potential consequences of the behavior for reproductive success. The null hypothesis was that there is no sensitivity to thermoregulatory cost, possibly because periods of idleness are reduced to support increased foraging effort (Ettinger and King 1980) or because the heat increments of social display activity may substitute for thermoregulatory heat production (Walsberg 1983b, Paladino and King 1984), or both.

MATERIALS AND METHODS

Experimental design.—The experimental design used a reverse optimality approach (McFarland 1977; but see Maynard Smith 1978). Briefly, an optimally adapted animal will have an “objective function” (the animal’s internal representation of costs and benefits, measurable by the resources allocated to the activity) identical to a “cost function” (the actual energetic or reproductive costs and benefits of the activity in that environment). Reverse optimality assumes optimization, and seeks the function being optimized by comparing behavior patterns with possible cost functions. We assumed that time resource allocation inversely proportional to a thermoregulatory cost function indicates that the cost function may enter into the time allocation decision. Similarly, time allocation directly proportional to a benefit suggests that the benefit enters the decision.

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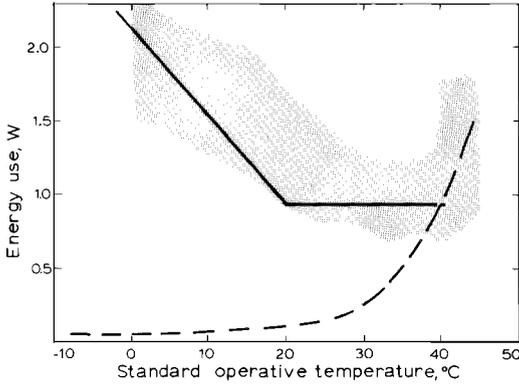


Fig. 1. Thermoregulatory cost function for male Red-winged Blackbirds. The solid line represents the idealized relation between energy use and standard operative temperature given by regression equations for 60-g passerine birds (Calder and King 1974). Below the lower critical temperature near 20°C, energy use increases to maintain body temperature. Laboratory data for male Red-winged Blackbirds (shaded area; Lewies and Dyer 1969) shows a gradual rather than a sharp change in slope around the lower critical temperature. The broken line represents evaporative water loss (Weathers 1981).

We compared plots of male activity vs. microclimate with the plot of thermoregulatory energy and water cost vs. microclimate derived from the Scholander model of thermoregulation (Scholander et al. 1950) shown in Fig. 1. The thermal environment was quantified by standard operative temperature, T_{es} , as described by Bakken (1976, 1980) and Bakken et al. (1985).

Microclimate is covariant with phenology and circadian rhythms known to influence nonthermoregulatory (e.g. social and reproductive) cost functions. Such covariance may obscure true, or produce coincidental, patterns related to microclimate, and confound the comparison of cost and time allocation functions. Therefore, we used a stepwise multiple regression model (Draper and Smith 1981) to control for some nonthermal factors known to influence singing (Pettingill 1985): date (seasonal phenology), time (circadian activity patterns), global irradiance (light intensity effects that may modify circadian rhythms; see Gwinner 1975, Enright 1980, Pohl 1980), and the square of wind speed (mechanical force interfering with flight and perching). We limited the parameters in the model to a small number of known significance to facilitate interpretation.

The use of T_{es} combines the thermal effects of air temperature, wind, sun, and thermal radiation in the correct nonlinear manner, and so predicts thermoregulatory cost more accurately than using primary variables in the linear regression model (Hayes and Gessaman 1982). Further, in a stepwise regression

model, each variable added accounts only for the effect remaining after removing the effects of variables entered earlier. Thus, by incorporating the purely thermal effects of sun and wind into T_{es} , the thermal and circadian modifier effects of light, and the thermal and mechanical effects of wind are separated as they are entered on different steps.

Behavioral observations.—Observations were conducted in a 100 × 200 m area covered by cattails (*Typha latifolia* and *T. angustifolia*) at the north end of a marsh in section 1, Pierson Township, Vigo Co., Indiana. We used fixed-length interval scan sampling (4 scans within 5 min at 15-min intervals) of a defined area encompassing 6–8 (varied during study) male territories. This method is adequate for quantifying common behaviors (Tacha et al. 1985). Observations were made from a 3-m-high platform by WRS from 0530 to 1200, usually for three consecutive days each week. Observations were grouped into two broad categories: *Territorial advertisement* counted all birds perching conspicuously in the marsh at or above cattail top height. Conspicuous perching appears to constitute territorial advertisement (Walsberg 1977), and males on such perches generally gave undirected medium-intensity song-spread displays at regular intervals. Display terminology follows Orians and Christman (1968) and Peek (1972). *Agonistic displays* counted males giving reciprocal territorial-boundary, high-intensity song-spread and head-forward displays, or fighting. The remaining activity time was spent singing with a low-intensity song-spread display in the trees fringing the marsh, resting, preening, foraging, and out of contact.

Physical observations.—A digital data logger with internal calendar-clock recorded data on magnetic tape at 15-min intervals. Microclimate data included: integrated global irradiance; integrated diffuse sky irradiance; wind speed at 2.0 and 3.5 m above the water surface; air temperatures at, and 0.5, 1, 1.5, 2, 3, and 3.5 m above, the water surface; and vegetation and water temperatures. Reflected solar irradiance was computed by multiplying global irradiance by an estimated albedo of 0.18. Thermal irradiance from the surface was computed using near-surface water temperature in the Stefan-Boltzmann law, and thermal irradiance from the sky was estimated using Swinbank's formula (Swinbank 1963). The T_{es} computed from this data was validated by comparison with simultaneous direct measurements of T_{es} made with taxidermic mounts of male Red-winged Blackbirds as described by Bakken et al. (1985).

RESULTS

Data were analyzed using the SPSS (Nie 1975) statistical package. All data were used in statistical analysis; for clarity scattergrams show only mean activity levels averaged over 1°C T_{es} in-

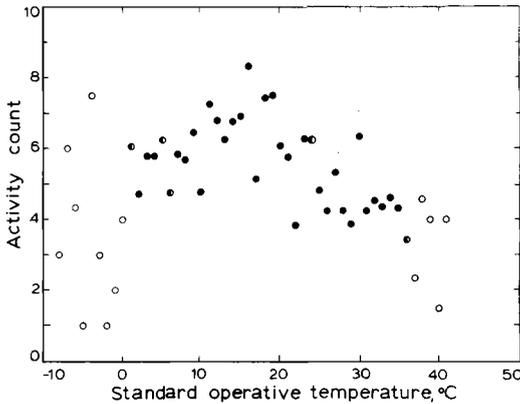


Fig. 2. Territorial advertisement display activity. Activity (total count on 4 scans at 15-min intervals) was averaged over 1°C intervals of T_{es} and the means displayed. The number of data points entering each mean is indicated by the symbol: open, $n = 1-8$; half-solid, $n = 9-16$; solid, $n = 16-32$. Total $n = 811$.

tervals. Territorial advertisement activity had a marked peak in the 15–20°C range (Fig. 2). This peak coincided roughly with the lower critical temperature (LCT), the ambient temperature at which thermoregulatory metabolism begins to increase as T_{es} decreases (Fig. 1). The peak is lower than both published LCT values (Lewies and Dyer 1969) and allometric predictions (Calder and King 1974). The data of Lewies and Dyer (1969) did not show a clear LCT, however, and normal activity probably reduces the effective LCT below that of resting birds in a metabolism chamber. Agonistic display activity (Fig. 3) declined monotonically with increasing T_{es} , with a possible change of slope around 15°C.

Because the dependence of advertisement (and possibly display) activity on T_{es} was non-linear, the data were divided into two sets to allow use of linear statistical analysis. The cold stress zone (CSZ) set included T_{es} from -10° to 20° C, and the thermal neutral zone (TNZ) set included T_{es} from 15° to 40° C. Overlapping data sets were selected because of uncertainty in the location of the peak.

Pairwise correlations (Table 1) between display activity and the physical parameters (date, time, global irradiation, and T_{es}) were relatively low (all $r < 0.29$). Thus, correlations from 0.57 to 0.77 among the physical parameters make it unclear whether a given pairwise correlation between behavior and a physical factor was direct or the result of covariance. The relation-

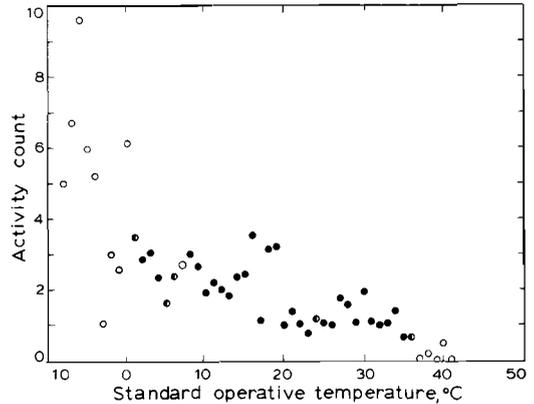


Fig. 3. Agonistic display activity. Symbols and data presentation are defined in Fig. 2.

ships were monotonic and usually linear, however, so that a linear stepwise multiple regression model could be used to control for first-order effects of the nonthermal parameters to clarify the influence of thermoregulatory costs (T_{es}) on behavior.

The stepwise multiple regression models for territorial advertisement and agonistic display, respectively, appear in Tables 2 and 3. All partial regression coefficients, b , included in the model were highly significant ($P < 0.002$). Standardized partial regression coefficients, b' , (regression to the Z-score rather than actual values) are included to show the relative strength of the dependence of activity on each parameter (Nie 1975). Interpretation of b' requires caution. Computed T_{es} values scatter $\pm 5^{\circ}$ C about the T_{es} measured by heated taxidermic mounts (Bakken et al. 1985). Thus, a model II multiple regression would be appropriate, but procedures are not available (Sokal and Rohlf 1981). The slope of a model II regression is always greater than that of the usual regression, however, so the b and b' values for the T_{es} variable are probably too small.

The model was tested for robustness by placing alternate data points into two subsets and repeating the analysis (Hofacker 1983). The b coefficients were about the same for both subsets and the whole set, indicating a stable model, although significance and order of entry varied somewhat (Santee 1985). The total variance explained, R^2 , was low (16–26%). This is not surprising, as the small number of males observed introduces sampling error, and latent variables (Box 1966) not in the model (e.g. social

TABLE 1. Pairwise correlation coefficients.

	Agonistic display	Territorial advertisement	Date	Time	Global irradiance	T_{es}
Thermal neutral zone, $T_{es} \geq 15^\circ\text{C}$ ($n = 472^a$)						
Territorial advertisement	0.515					
Date	-0.264	-0.268				
Time	-0.226	-0.195	-0.149			
Global irradiance	-0.235	-0.287	-0.224	0.770		
T_{es}	-0.177	-0.247	0.021 ^b	0.606	0.670	
Wind force	0.018 ^b	-0.019 ^b	-0.338	0.346	0.395	-0.032 ^b
Cold stress zone, $T_{es} \leq 20^\circ\text{C}$ ($n = 460^a$)						
Territorial advertisement	0.554					
Date	-0.275	-0.068 ^b				
Time	-0.219	-0.239	-0.157			
Global irradiance	-0.189	-0.207	-0.267	0.574		
T_{es}	-0.157	0.177	0.448	0.271	0.291	
Wind force	-0.019 ^b	-0.144	-0.401	0.409	0.652	0.177

^a Overlapping ranges; total $n = 811$.

^b Not significant ($P > 0.05$), two-tailed test; all other values significant.

interactions) may introduce unexplained variance. We assume these factors do not covary with T_{es} .

The data were then controlled for nonthermal effects using the regression model. This was done using the model to compute predicted display activity for each data point, with a fixed T_{es} (20°C) substituted for the actual value. This predicted activity was subtracted from the observed value to give a relative activity value controlled for the effects of all model parameters except T_{es} .

There was a highly significant linear reduc-

tion ($b = 0.376$, $F = 108.9$, $P < 0.001$) in controlled territorial advertisement as T_{es} decreased in the CSZ, while there was no change with T_{es} ($b = 0.000$, $P > 0.94$) in the TNZ (Fig. 4). Controlled agonistic activity had a less marked decline in activity as T_{es} decreased in the CSZ ($b = 0.099$, $F = 9.4$, $P < 0.002$), and again no dependence on T_{es} in the TNZ ($b = 0.04$, $P > 0.13$).

DISCUSSION

Uncontrolled territorial advertisement appears to peak near the lower critical tempera-

TABLE 2. Stepwise multiple regression model of time allocation to territorial advertisement. Variables are listed in order of entry. Symbols are: b , regression coefficient; b' , standardized regression coefficient; F , Fisher's F ; R^2 , coefficient of determination; P , probability of $b = 0$ or chance result.

Variable	b	b'	F	R^2	P
			To enter or remove		
Thermal neutral zone, $T_{es} \geq 15^\circ\text{C}$ ($n = 472^a$)					
Global irradiance	-0.006	-0.366	74.4	0.082	<0.001
Date	-0.062	-0.350	68.2	0.117	<0.001
Constant	18.46	—	186.2	—	<0.001
Overall model			58.3	0.199	<0.001
Cold stress zone, $T_{es} \leq 20^\circ\text{C}$ ($n = 460^a$)					
Time	-0.699	-0.266	28.2	0.057	<0.001
T_{es}	0.376	0.544	108.9	0.063	<0.001
Date	-0.082	-0.442	74.4	0.076	<0.001
Global irradiance	-0.008	-0.331	38.0	0.062	<0.001
Constant	-80.8	—	76.4	—	<0.001
Overall model			39.7	0.259	<0.001

^a Overlapping ranges; total $n = 811$.

TABLE 3. Stepwise multiple regression model of time allocation to agonistic display. Variables are listed in order of entry. Symbols are as in Table 2.

Variable	<i>b</i>	<i>b'</i>	<i>F</i>	<i>R</i> ²	<i>P</i>
			To enter or remove		
Thermal neutral zone, $T_{es} \geq 15^{\circ}\text{C}$ ($n = 472^a$)					
Date	-0.040	-0.333	59.0	0.070	<0.001
Global irradiance	-0.003	-0.310	51.0	0.091	<0.001
Constant	9.80	—	106.6	—	<0.001
Overall model			44.9	0.161	<0.001
Cold stress zone, $T_{es} \leq 20^{\circ}\text{C}$ ($n = 460^a$)					
Date	-0.070	-0.446	69.0	0.076	<0.001
Global irradiance	-0.005	-0.246	19.1	0.074	<0.001
Time	-0.433	-0.193	13.6	0.019	0.001
T_{es}	0.099	0.167	9.4	0.017	0.002
Constant	-10.1	—	1.5	—	0.22
Overall model			25.88	0.185	<0.001

^a Overlapping ranges; total $n = 811$.

ture (Fig. 2). Similar results were reported in rodents (Kenagy 1973) and White-crowned Sparrows (*Zonotrichia leucophrys*; Mahoney and King 1977). Because the LCT is the joint minimum for energy and water use (cf. Fig. 1), it has been suggested (e.g. Mahoney and King 1977) that animals free of other demands seek a joint minimization of energy and water. Because free water was readily available at the Indiana study site, it seemed more likely that activity declined as T_{es} increased above the LCT because of covariance of T_{es} with the decline in territorial display activity as the breeding season progressed. Indeed, once the effects of date and irradiance were removed, there was no change of activity level as T_{es} increased above the LCT (Fig. 4).

Territorial advertisement display activity had a precise inverse relationship to thermoregulatory energy cost (cf. Figs. 1 and 4). We interpret this to mean that energy costs entered the decision to engage in display activity, but water costs did not. Comparison of Figs. 1 and 5 suggest a similar dependence of agonistic display on thermoregulatory energy cost. The apparent importance of thermoregulatory energy cost for territorial behavior is supported further by Searcy's (1979) finding that display activity was increased by supplemental feeding.

The visual impression that agonistic display was less sensitive to T_{es} than advertisement was supported by comparing the standardized partial regression coefficients, b' . In the CSZ, b' was 0.544 for advertisement and 0.167 for agonistic

display ($P < 0.01$, analysis of covariance; a model II regression probably would reduce the difference in slopes). This differential sensitivity to thermoregulatory cost of territorial advertisement and agonistic display may result from ordered potential consequences for reproduc-

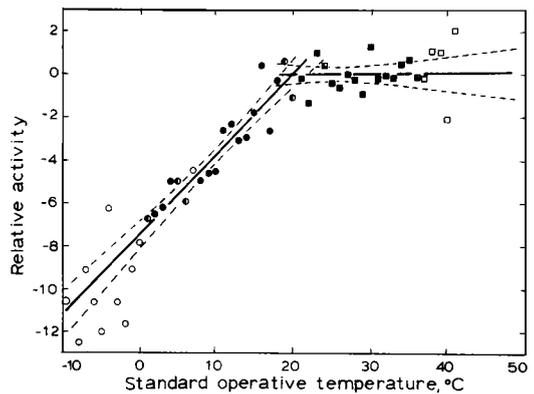


Fig. 4. Relative territorial advertisement display activity, controlled for date, time, and global radiation by a piecewise-linear multiple regression model. Data are the residuals of the regression with T_{es} held constant at 20°C . As in Figs. 2 and 3, data are averaged for 1°C intervals and the means displayed, with symbols indicating n as in Fig. 2. Circles are residuals of the -10° to 20°C submodel, squares of the 15° to 42°C submodel. Solid lines are partial regression lines, broken lines are 95% confidence intervals. The plot resembles an inversion of Fig. 1, implying that increasing thermoregulatory energy needs inhibit advertisement behavior below 20°C . Above 20°C there is no dependence on T_{es} .

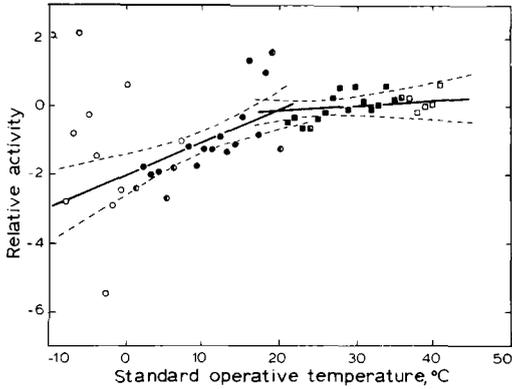


Fig. 5. Relative agonistic display activity, controlled for date, time, and global radiation as in Fig. 4, shows a similar pattern, but with less marked dependence on T_{es} .

tive success (assuming that possession of a territory improves fitness; Orians 1971, Peek 1972). The song-spread display given during advertisement appears to warn away other males and attract females to the territory (Weatherhead and Robertson 1977). Benefits of advertisement are moderate, because territories can be abandoned without immediate loss unless a challenger is present. Benefits of agonistic display are high, as an undefended territory is lost quickly (Nero 1956a, b; Orians 1961). Experimental impairment of agonistic display often results in loss of territory (Peek 1972, Smith 1972). By reverse optimality, the value of an activity for territory retention thus may enter the time-allocation decision.

The differential sensitivity to T_{es} also might result from substitution of the metabolic increment of activity for thermoregulatory metabolism. Agonistic display would then be less sensitive to T_{es} than advertisement display because of its greater metabolic increment (2.3 for hopping and 13.2 for flight, vs. 1.98 for alert perching; Weathers et al. 1984). However, substitution of activity for thermogenic metabolism is controversial (Paladino and King 1984). There may be no dependence of agonistic display on T_{es} . Males are usually present in the cattails before agonistic display is initiated, and the dependence of agonistic display on T_{es} may result indirectly from the dependence of advertisement display on T_{es} .

The common observation that singing and other territorial behavior is most intense early

in the breeding season and early in the morning of each day, when conditions are usually coolest, makes the finding of a decrease in activity at low T_{es} appear paradoxical. Our results indicate only that, at any time on a particular date, activity will be greater at thermoneutral T_{es} than when it is cool. The metabolic cost of thermoregulation evidently acts as a suppressor variable that counteracts the tendency toward territorial activity early in the season or early in the day. Thus, territory establishment appears to incur a significant thermoregulatory energy cost.

The sensitivity of territorial advertisement to thermoregulatory cost, even with mild stress, suggests that it can be profitable to study the effects of thermoregulatory energy costs on behavior and ecology in equable as well as severe climates.

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100 Years Ago in The Auk



From "Individual Variation in the Skeletons of Birds, and other matters" (1887, *Auk* 4: 266-268):

"Speaking now on the individual variation in the skeletons of birds I would like to reproduce here, in illustration of it, a pair of skulls which figured in an article of mine in 'Science' not long ago. As many readers of the 'The Auk,' [sic] both at home and abroad, possibly may not subscribe for that estimable journal, I was led to believe that in bringing these drawings more directly before ornithologists, many of them could not fail to find something of interest in them.

"These each represent a skull ($\times 2$) of the Yellow-headed Blackbird (*X. xanthocephalus*), the specimens having been collected by myself, and are now in my possession. We are very well aware that throughout animate nature, all specific forms vary more or less, and that the corresponding structures of any two species are never quite alike, either in form or size. So far as birds are concerned, I think it would be hard to find a pair of skulls, that would better show, taking this part of their organization into consideration, how great this variation may be sometimes. It is very evident that an *exact* description of one of these skulls would not answer for the other, notwithstanding that they are both from birds of the *same species*,—yet a

general description could be written that would fully cover all their salient features, and sufficiently differentiate them from descriptions of the skulls of other birds.

"With respect to *measurements* and exact descriptions, however, for any structure, for any particular species of bird, we are in the same quandary in our accounts of such structures among the lower vertebrates as the anthropotomists are with respect to descriptive human anatomy. Much might be written about these two skulls here figured which lack of space forbids, but this will not debar the thoughtful ornithotomist from making a careful study of them for himself. One thing it must point out to all, and that is, for our descriptions of such structures to be broad and full we should have before us, whenever it is possible, *abundance of material*,—and, too, with respect to measurements, we should aim to establish reliable *standards* through the calculation of averages computed from carefully taken individual data. . . ."

R. W. SHUFELDT, *Fort Wingate, N. Mexico*,
May 21, 1887.