TOLERANCE OF COLD AND BERGMANN'S RULE[1]

S. CHARLES KENDEIGH

As size is well known to affect the energy relations between an endotherm and its environment, one would expect that size may also influence or be related to geographic distribution. Bergmann's Rule postulates that geographic races of small size are generally found in the warmer parts of a species' range and races of larger size in the cooler parts. This rule has been attacked by Scholander (1955, 1956) and Irving (1957) on the grounds that the differences in size involved are too small to provide significant heat conservation and that adaptation to cold depends mainly on improved insulation (Scholander et al., 1950a). The rule has been defended by Mayr (1956) and Hamilton (1961) on empirical grounds, and recently from a theoretical basis by LeFebvre and Raveling (1967).

Good comparative data on the weights of different races of a species are difficult to find, but variations of the order of 10 to 100+ per cent exist between extreme northern and southern forms. If we assume that *standard metabolism* in the zone of thermal neutrality, or the energy requirements of the bird at complete rest and in a post absorptive condition, increases with weight (W) as $W^{0.724}$ (Lasiewski and Dawson, 1967) and surface area as $W^{0.667}$, then a 50 per cent increase in weight would reduce the rate of heat loss per unit area body surface only 2.4 per cent. This advantage might well be offset by the 34 per cent increase in the birds' standard metabolism and hence energy requirements.

The importance of size on a bird's tolerance of cold may be analyzed in a more significant manner by comparing the standard metabolism for species in the zone of thermal neutrality with their standard metabolism at 0°C. The lower limit of temperature tolerance for several small tropical resident and migrant passerine species and temperate zone permanent residents in the summer is 0°C or slightly below (Table 2). Winter residents in temperate regions and migrants to the Arctics, however, are able to tolerate much lower temperatures. Equations for the regression of standard metabolism (M = kcal/bird-day) on ambient temperature below the zone of thermal neutrality have been compiled for a number of species from data available in the literature (Table 1). These equations make possible the drawing of regression lines for standard metabolism in relation to weight (W = grams) both for the zone of thermal neutrality and for 0°C (Figure 1). The equations for these lines are as follows:

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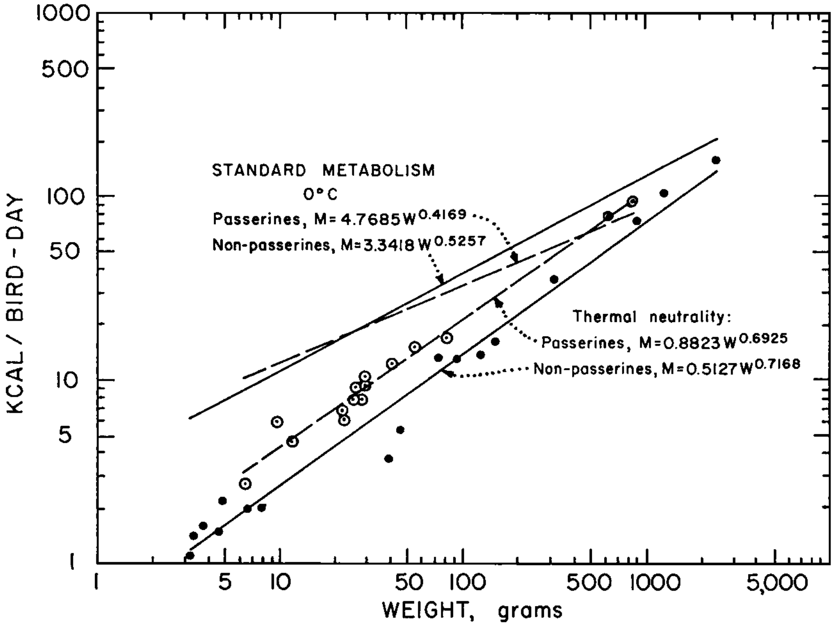

Figure 1. Standard metabolism correlated with size of passerine and nonpasserine species in the zone of thermal neutrality and at 0°C.

Zone of thermal neutrality

$$\log M \text{ (passerines, } N = 15) = -0.0544 + 0.6925 \log W \pm 0.0619$$
$$\log M \text{ (nonpasserines, } N = 17) = -0.2901 + 0.7168 \log W \pm 0.1105$$

0°C

$$\log M \text{ (passerines)} = 0.6784 + 0.4169 \log W \pm 0.0764$$
$$\log M \text{ (nonpasserines)} = 0.5240 + 0.5257 \log W \pm 0.0845$$

The slopes of the regression lines for passerine and nonpasserine species in the zone of thermal neutrality are not statistically distinguishable, but the elevations of the two lines are different ($P = < 0.01$). This agrees with Lasiewski and Dawson (1967) who found that nonpasserine species have a lower rate of standard metabolism than do passerine species. These equations are not significantly different from theirs, as recalculated by Zar (1968), either in slope or elevation.

Both equations at 0°C are significantly different from the ones for the zone of thermal neutrality and their slopes are different from each other. The less steep slopes of the regression lines at 0°C indicate that smaller species are more affected by cold than are large species ($P = < 0.5$). The proximity of the regression lines for passerine and nonpasserine species at 0°C means that nonpasserine species are affected more by a drop in temperature than are passerine species.

The analysis of the effect of cold on standard metabolism in birds of different size is complicated by a difference in the extent of the zone of thermal neutrality in which body temperature is controlled by regulating heat loss while heat production remains constant. The zone extends downward to a critical ambient temperature below which heat production must be raised to compensate for the increased rate of heat loss. It is often difficult to determine precisely the lower critical temperature, and in some species no real zone of thermal neutrality exists. It appears (Table 1) that for those passerine species weighing 22 grams or less, the lower critical temperature is commonly above 28°C; for those weighing between 22 and 29 grams it may be as low as 20°C, and for larger species, even lower. The lower critical temperature in the winter acclimatized Snow Bunting, *Plectrophenax nivalis* (33–53 g) (Scholander et al., 1950b), is around 10°C, in the Gray Jay, *Perisoreus canadensis* (71 g) about 7°C except possibly in the summer (Veghte, 1964), and in ravens below zero (Table 1). In nonpasserine species no clear decrease in the lower critical temperature occurs until weights over 150 g are reached, and even then it is not great. It would be interesting to know how the lower critical temperature varies with birds of different size within the same species.

According to Darlington (1957) birds as a group originated in the tropics and dispersed to temperate and arctic regions only as they became adapted to withstand cold. This may have involved a lowering of the zone of thermal neutrality and a reduction in the need for increased heat production at low ambient temperatures (Scholander, 1955; Hart, 1964). Irving (1964) states that the lower critical temperature is low for large arctic animals, higher for small arctic animals, and high for tropical animals regardless of size.

Existence metabolism more nearly approximates the rate at which free-living birds require energy than does standard metabolism, although existence metabolism has been measured only in caged birds by determining the amount of energy metabolized from the food intake while the birds maintain a constant weight. Existence metabolism, like standard metabolism, increases progressively at low temperatures, but no true zone of thermal neutrality has been demonstrated in the 18 species so far studied (Kendeigh, 1969). The equations for existence metabolism (M = kcal/bird–day) in relation to weight (W = grams) at 30°C, which is within the zone of thermal neutrality for standard metabolism for many species, are:

$$\log M \text{ (passerines, } N = 15) = 0.1965 + 0.6210 \log W \pm 0.0633$$

$$\log M \text{ (nonpasserines, } N = 9) = -0.2673 + 0.7545 \log W \pm 0.0630$$

TABLE 1

Equations for the Regression of Standard Metabolism on Ambient Temperatures below the Lower Critical Temperature

Species: Passerine	Weight g	Time of day[1]	Season	Lower critical temperature (°C)	Metabolism M[2] =	Authority
Black-rumped Waxbill, *Estrilda troglodytes*	6.4	?	?	38	13.5–0.284t	Cade et al., 1965
Black-rumped Waxbill, *Estrilda troglodytes*	6.5	D	spring	28	11.1–0.300t	Lasiewski et al., 1964
House Wren, *Troglodytes aedon*	9.7	D	summer	38±	14.6–0.227t	Kendeigh, 1939
Zebra Finch, *Taeniopygia castanotis*	11.5	?	?	29.5	16.3–0.391t	Calder, 1964
Zebra Finch, *Taeniopygia castanotis*	11.7	?	?	36	19.7–0.415t	Cade et al., 1965
Ortolan Bunting, *Emberiza hortulana*	22.0	N	winter	32	18.2–0.354t	Wallgren, 1954
White-throated Sparrow, *Zonotrichia albicollis*	22.5	N	?	20	14.8–0.435t	Hudson & Kimzey, 1964
House Sparrow, *Passer domesticus*	25.1	D	winter	37	22.5–0.356t	Kendeigh, 1944
House Sparrow, *Passer domesticus* (Houston, Texas)	25.5	N	?	20	15.5–0.424t	Hudson & Kimzey, 1964
House Sparrow, *Passer domesticus* (average three other localities)	25.3	N	?	21	20.7–0.568t	Hudson & Kimzey, 1966
Yellow Bunting, *Emberiza citrinella*	26.4	N	winter	25	16.4–0.293t	Wallgren, 1954
White-crowned Sparrow, *Zonotrichia leucophrys*	28.6	N	winter	23	17.4–0.412t	King, 1964
Red Crossbill, *Loxia curvirostra*	29.4	N	winter	15	16.6–0.406t	Dawson & Tordoff, 1964
White-winged Crossbill, *Loxia leucoptera*	29.8	N	winter	14	14.9–0.378t	Dawson & Tordoff, 1964
Cardinal, *Richmondena cardinalis*	41±	?	winter	18	20.7–0.463t	Dawson, 1958
Evening Grosbeak, *Hesperiphona vespertina*	54.5	N	year round	25	28.3–0.535t[4]	West & Hart, 1966
Evening Grosbeak, *Hesperiphona vespertina*	55.3	N	winter	16	25.6–0.624t	Dawson & Tordoff, 1959
Blue Jay, *Cyanocitta cristata*	80.8	N	?	18	24.6–0.410t	Misch, 1960
White-necked Raven, *Corvus cryptoleucus*	640	?	?	< 0°[3]	79.0	Lasiewski & Dawson, 1967
Common Raven, *Corvus corax*	850	?	?	< 0°	92.0	Irving et al., 1955
Common Raven, *Corvus corax*	866	?	?	< 0°	94.9	Lasiewski & Dawson, 1967

TABLE 1 (Continued)

Species: Nonpasserine	Weight g	Time of day[1]	Season	Lower critical tempera- ture (°C)	Metabolism M[2] =	Authority
Costa's Hummingbird, *Calypte costae*	3.2	N,D	autumn	28.5±	6.9–0.203t	Lasiewski, 1963
Black-chinned Hummingbird, *Archilochus alexandrii*	3.3	N,D	autumn	28.5±	5.4–0.142t	Lasiewski, 1963
Allen's Hummingbird, *Selasphorus sasin*	3.7	N,D	autumn	28.5±	8.5–0.243t	Lasiewski, 1963
Rufous Hummingbird, *Selasphorus rufus*	3.8	N,D	autumn	28.5±	7.2–0.201t	Lasiewski, 1963
Anna's Hummingbird, *Calypte anna*	4.8	N,D	autumn	28.5±	9.1–0.243t	Lasiewski, 1963
Rivoli Hummingbird, *Eugenes fulgens*	6.6	?	?	31	9.1–0.228t	Lasiewski & Lasiewski, 1967
Blue-throated Hummingbird, *Lampornis clemenciae*	7.9	?	?	31	8.5–0.209t	Lasiewski & Lasiewski, 1967
Poor-will, *Phalaenoptilus nuttallii*	40.0	?	?	35	18.7–0.429t	Bartholomew et al., 1962
Elf Owl, *Micrathene whitneyi*	45.9	D	winter	33	15.3–0.317t	J. D. Ligon (pers. comm.)
Common Nighthawk, *Chordeiles minor*	72±	D	winter	22	31.5–0.829t	Lasiewski & Dawson, 1964
Mourning Dove, *Zenaidura macroura*	91.4	N	?	30.0	45.2–1.060t	Hudson & Brush, 1964
California Quail, *Lophortyx californicus*	(♀)127	D	?	27.3	40.8–0.989t	Brush, 1965
California Quail, *Lophortyx californicus*	(♂)150	D	?	27.3	47.9–1.16t	Brush, 1965
Pigeon, *Columba*	314	D	winter	19	64.1–1.52t	Kayser, 1940
Black Duck, *Anas rubripes*	904	D	winter	19	124.8–2.69t	Hartung, 1967
Mallard, *Anas platyrhynchos*	1263	D	winter	22	183.1–3.57t	Hartung, 1967
Domestic fowl, *Galus domesticus*	2430	D	?	18.3	193.8–1.95t	Barott & Pringle, 1946

[1] D, daytime; N, night.

[2] M = kcal/bird-day.

[3] It is assumed that the lower critical temperature of the ravens is 0°C or below as it appears to be in *Corvus caurinus*. Data for this latter species are not included, however, as but one bird was measured, it was not previously fasted, and the metabolic rates were more than double the expected (Irving et al., 1955).

[4] Approximate for range: –10° to +25°C.

TABLE 2

Relation of Tolerance to Cold and Metabolic Potential to Distribution and Migration

Species	Weight in g	Per cent increase in existence metabolism at 0° over 30°	Approximate lower limit of tolerance °C	Maximum metabolism Kcal/day		Authority
				Per bird	Per g($W^{0.5300}$)	
			Tropical residents			
Yellow-bellied Seedeater *Sporophila nigricollis*	9.3	162	–1	16.0	4.9	Cox, 1961
Blue-black Grassquit *Volatinia jacarina*	9.4	137	–1	16.3	5.0	Cox, 1961
Variable Seedeater *Sporophila aurita*	10.7	122	–1	18.0	5.1	Cox, 1961
Zebra Finch *Taeniopygia castanotis*	12.1	172	–1.3	18.5	4.9	El-Wailly, 1966
Green-backed Sparrow *Arremonops conirostris*	37.0	125	–7	30.6	4.5	Cox, 1961
			Migrant between tropics and Illinois			
Dickcissel *Spiza americana*	30.6	143	–2	29.5	4.8	Zimmerman, 1965
			Migrant between Gulf States, Illinois, and Canada			
Field Sparrow *Spizella pusilla*	13.6	116	–14	19.0	4.8	Olson, 1965
White-throated Sparrow *Zonotrichia albicollis*	27.4	98	–26	32.9	5.7	Kontogiannis, 1968

TABLE 2 (Continued)

Species	Weight in g	Per cent increase in existence metabolism at 0° over 30°	Approximate lower limit of tolerance °C	Maximum metabolism Kcal/day		Authority
				Per bird	Per g(W$^{0.5300}$)	
		Resident or migrant within temperate and subarctic regions				
Common Redpoll	14.0	71	–27	21.4	5.3	Brooks, 1965
Acanthis flammea						
Hoary Redpoll	15.0	96	–34	24.3	5.8	Brooks, 1965
Acanthis hornemanni						
Tree Sparrow	19.0	81	–28	32.8	6.9	West, 1960
Spizella arborea						
House Sparrow	25.2	54	$<$–31[1]	$>$ 35.8	$>$ 6.5	Davis, 1955
Passer domesticus						
Evening Grosbeak	55.8	80	$<$–20	$>$ 50.0	$>$ 5.9	Williams (pers. comm.)
Hesperiphona vespertina						
			Large nonpasserine species			
Blue-winged Teal (♀)	309	121	$<$–28	$>$ 169	$>$ 8.1	Owen (1968)
Anas discors (♂)	363	132	$<$–28	$>$ 174	$>$ 7.7	Owen (1968)
Japanese Green Pheasant (♀)	800±	94	$>$–29	$<$ 203	$<$ 5.9	Seibert (pers. comm.)
Phasianus versicolor (♂)	1100±	79	$>$–29	$<$ 252	$<$ 6.2	Seibert (pers. comm.)
Ring-necked Pheasant (♀)	800±	47	$<$–34	$>$ 166	$>$ 4.8	Seibert (pers. comm.)
Phasianus colchicus (♂)	1400±	37	$<$–34	$>$ 200	$>$ 4.3	Seibert (pers. comm.)
Reeves Pheasant (♀)	1000	64	–28±	193	5.0	Seibert, 1963
Syrmaticus reevesii (♂)	1300	58	–32±	287	6.4	Seibert, 1963
Canada Goose (♂)	4300	41	$<$–35	$>$ 695	$>$ 8.2	Williams, 1965
Branta canadensis						

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[1] Approximately 0°C during the summer, $<$–31°C during the winter.

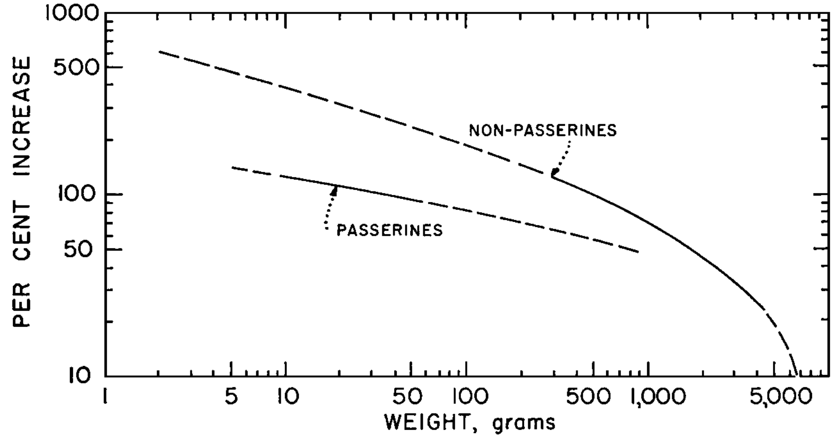

Figure 2. Per cent increase in existence energy at 0°C over what it is at 30°C in passerine and nonpasserine species.

The equations for existence metabolism against weight at 0°C are not significantly different for passerines and nonpasserines and have been combined:

$$\log M \text{ (all species, N = 24)} = 0.6372 + 0.5300 \log W \pm 0.0613$$

The slope of the regression line for existence metabolism at 0°C (0.5300 log W) is also less steep than those at 30°C (0.7545 and 0.6210 log W). For instance a drop in temperature from 30° to 0°C would increase the existence metabolism of a 500-gram nonpasserine bird 99 per cent, of a 550-gram bird 95 per cent (4 per cent less), a 750-gram bird 82 per cent (17 per cent less), and a 1,000-gram bird 70 per cent (29 per cent less). For a 20-gram passerine species an increase of 10 per cent in weight would reduce the increase in metabolism at 0°C about 2 per cent, a 50 per cent increase about 8 per cent, and a 100 per cent increase about 13 per cent. In addition to the advantages accruing from a smaller surface area for heat loss relative to the body mass for heat production, larger birds also have relatively heavier plumage and more effective heat insulation than small birds (Herreid and Kessel, 1967; Kendeigh, 1969). The regression line for nonpasserine species is lower at 30°C than for passerine species and the same at 0°C—another indication that nonpasserine species are affected by cold more than passerine species. These relations are shown in Figure 2.

The effect of cold on existence metabolism varies much independent of size. Six of the temperate and subarctic passerine species in Table 2 are smaller than two of the six tropical species, yet are less affected by cold. The subarctic Common Redpoll has a percentage increase in metabolism only one-half that for the migrant tropical Dickcissel weighing more than twice as much. It would be interesting to know the relative efficiencies of the plumage in reducing heat loss in these different species. One would expect that small species would require considerably increased insulation to inhabit cold climates. Of interest in this connection are observations by Pitelka (see West 1962: 329–330) that the apteria of northern finches are densely covered with down feathers while in southern finches the apteria are bare.

Tropical residents and migrants do not tolerate temperatures much below 0°C (Table 2), those migrant between the Gulf states and southern Canada tolerate lower temperatures, while those resident or migrant within northern latitudes are still more tolerant of cold. The House Sparrow's tolerance fluctuates from about 0°C in summer to over –31° in winter. Within each distributional passerine group there is some relation between the lower limits of tolerance and weight, but obviously other factors are involved. Compare for instance the tolerance of –27° to –34°C in the Redpolls weighing 14–15 grams, with that of several of the more southern species that weigh up to twice as much.

Tropical residents and migrants likewise cannot mobilize as much energy to tolerate cold as can northern species. In terms of per gram metabolic weight ($W^{0.5300}$), the maximum potential of tropical species is about 4.9 kcal/day, while for passerine species resident or migrant within temperate and subarctic regions it varies from 5.3 to 6.9 kcal/day. There is no correlation here with the size of the bird. Although the White-throated Sparrow overwinters as far south as the Gulf of Mexico, it seems in several respects to conform better with the metabolic characteristics of northern than with southern species. The Field Sparrow on the other hand agrees closer with tropical species.

DISCUSSION

Increased size appears of obvious physiological advantage for tolerating cold in several ways: 1) reduction in relative amount of energy required for existence, 2) lower metabolic stress per degree drop in temperature, 3) extension of zone of thermal neutrality to a lower critical ambient temperature, and 4) lower extreme limits of tolerance. Although this analysis is based on interspecific differences in metabolism correlated with weight, in all probability it applies also to intraspecific differences (Kleiber, 1961; LeFebvre and Raveling, 1967).

Other factors than size affect the tolerance of birds to cold. Northern species have evolved capacities for higher rates of metabolism. Some small northern species have evolved exceptionally heavy feather insulation (Kendeigh, 1969). Nonpasserine species are affected by cold to a greater extent than are passerine species. The fact that species vary in some of their responses to cold independent of size, and to an extent perhaps greater than differences in insulation might explain, suggests the possibility of differences between species in still other ways, such as in hormone action, enzyme systems, or fatty acids.

The physiological advantages that increase in size gives to birds for tolerating cold may be partially offset in that an increase in size demands a greater total intake of food. Increases of 10, 50, and 100 per cent in weight raise the total existence energy requirements at 0°C by 5, 24, and 44 per cent respectively. Larger birds doubtlessly consume larger quantities of food at a time, but whether this compensates for the greater amount required without increasing the daily period of feeding is uncertain. The shorter photoperiods in the north during the winter may be critical for permanent resident species. Snow (1954) working with the genus *Parus,* makes a point of this "latitude effect," in that at equivalent temperatures larger birds in this genus tend to occur in the mountains at lower latitudes where the photoperiods are longer. On the other hand Barth (1966) suggests that the increased size of some northern birds may be the result of the increased feeding activity the long arctic day allows in the northern summer.

CONCLUSIONS

Although the standard metabolism of passerine species in the zone of thermal neutrality and existence metabolism at 30°C are higher than in nonpasserine species, they are more nearly the same at 0°C. Thus nonpasserine species are affected by cold more than passerine species.

The slopes of the regression lines for both standard and existence metabolism on weight are significantly less steep at 0°C than at 30°C, indicating that small species are affected more by cold than are large species.

Large species tend to have the lower critical temperature of the zone of thermal neutrality come at lower ambient temperatures than do small species.

Northern species tend to be affected less by cold than southern species of similar or even greater weight, to have greater feather insulation, and to have evolved capacities for higher rates of metabolism. This indicates that factors other than size are also involved in adaptation to cold.

Although in general larger birds are favored physiologically for living in cold climates because of less stress on body temperature regulation, they may be at a disadvantage ecologically because they require more from their environment in the way of food. For Bergmann's Rule to become expressed in the distribution of the races of a species, the physiological advantages must outweigh the ecological disadvantages.

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Department of Zoology, University of Illinois, Champaign, Illinois 61820.