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THE METABOLIC RATE OF TROPICAL BIRDS

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ABSTRACT.—Oxygen consumption was measured in order to estimate basal metabolic rate in a variety of Malaysian birds. Oxygen consumption during the active phase of the circadian cycle was greater than during the resting phase. Oxygen consumption was lower than that of temperate species of the same weight by 30% during the active phase and 35% during the resting phase. Species that forage in the sun seemed to consume less oxygen than those that forage in the shade.

The baseline for many studies of comparative avian metabolism is provided by the basal metabolic rate (H_b); the rate of energy turnover that occurs in the thermoneutral zone of resting, post-absorptive animals. Various factors have been shown to have a systematic influence upon H_b in birds (for recent reviews see Aschoff and Pohl 1970b, Calder and King 1974, Kendeigh et al. 1977). In deriving predictive equations for some of these relationships however, the effect of climate has been largely ignored (King and Farner 1961, Lasiewski and Dawson 1967, Aschoff and Pohl 1970a, b).

An early review by Scholander et al. (1950) concluded that climate had no influence upon energy metabolism although later evidence proved contrary (Enger 1957, Hart 1957, Hudson and Kimzey 1966, Kendeigh and Blem 1974). Desert species and subspecies have been shown to have lower metabolic rates than those from more mesic climates (Trost 1972, Dawson and Bennet 1973). Kendeigh et al. (1977) showed that the widely used equations of Aschoff and Pohl (1970a) are not always applicable if summer or winter temperature adaptation occurs, and gave some indication of latitudinal differences in avian metabolism. In a re-examination of the literature, Weathers (1979) showed that H_b for a variety of species could vary from 50–100% of values predicted by the Aschoff and Pohl (1970a) equations, depending upon the latitude of origin. This being the case, current predictive equations have limited use outside temperate regions. Since data from tropical birds are few, and often conflicting, the aim of this study was to make further measurements, which would allow prediction of H_b for energetics studies in the tropics.

METHODS

All the birds used in this study were mist-netted in Malaysia, within a 25-km radius of Kuala Lumpur (3°7′N, 101°42′E). All the insectivores, and most of the other species were measured on the day of capture. Occasionally some of the bulbuls, estrildids and finches were maintained in an outdoor aviary and given unlimited fruit and seed; the period of captivity did not exceed 48 h for a bulbul or five days for the others. Captive birds were the same weight as freshly caught specimens. The birds were netted between 16:00 and 19:00 and transferred to the laboratory where they were weighed and placed in the respirometer. They remained in the respirometer overnight and were removed, weighed and released at about 09:00 the following morning. Of the two owls measured, one was caught at night, held in a cloth bag and placed in the respirometer the next morning, the other was netted at dawn and placed in the respirometer immediately.

The respirometer chamber was a 5-l glass vacuum desiccator with a porcelain divider below which a trough of 20% KOH acted as a CO_2 absorber. Humidity in the chamber was monitored with a dial hygrometer and was always around 90%, similar to natural conditions in the humid tropics. The chamber was connected to a spirometer of oxygen of 1.8 l capacity (Warren E. Collins Inc.). The pivot wheel drove a continuously rotatable variable potentiometer, which in turn was connected to a pen recorder. As the spirometer float dropped during the course of a run, the pen recorder trace altered accordingly. The apparatus was calibrated and repeatable measurements could be made to an accuracy of 0.3 ml in any hour—equivalent to 1% of the lowest uptake rate recorded during the study. The chamber was immersed in a water bath at 33.0 ± 0.5°C, and the whole apparatus housed in a constant temperature room. Barometric pressure was measured at the start and end of each run and all volumes were corrected to STP.

The trace for each night was measured off at hourly intervals and the oxygen consumption during each hour calculated. The smallest volume of oxygen consumed in one hour was taken to be H_b during the resting phase. The oxygen consumed between 07:00–08:00 (1–2

TABLE 1. Basal metabolic rate in various birds from the Malay Peninsula.

Species		Foraging location[a]	n	Weight (g)	Active phase			Resting phase		
					kJ day^{-1}	SD	% of predicted[b]	kJ day^{-1}	SD	% of predicted[b]
Resident passerines										
Chestnut Munia	*Lonchura malacca*	O	3	11.8	19.09	1.3	73.5	12.18	1.13	63.5
White-headed Munia	*Lonchura maja*	O	3	12.8	23.45	1.4	85.1	13.15	0.17	64.2
Tree Sparrow	*Passer montanus*	O	10	17.5	28.55	7.5	83.4	17.08	2.05	66.9
Yellow-vented Bulbul	*Pycnonotus goiavier*	O	9	28.6	29.27	1.9	60.5	21.14	3.01	57.5
Little Spiderhunter	*Arachnothera longirostra*	S	2	13.0	20.97	0.2	75.5	16.29	2.68	78.8
Magpie Robin	*Copsychus saularis*	O	4	33.5	28.97	7.2	53.6	19.97	5.65	47.6
Stripe-throated Bulbul	*Pycnonotus finlaysoni*	O	3	26.3	27.05	4.3	59.3	19.43	3.09	56.3
Scaley-crowned Babbler	*Malacopteron cinereum*	S	1	15.8	27.13	—	85.0	18.25	—	76.9
Grey-cheeked Bulbul	*Criniger bres*	S	2	35.0	40.07	1.3	71.8	30.69	0.80	72.7
Spectacled Spiderhunter	*Arachnothera flavigaster*	S	2	36.3	35.25	8.0	61.6	25.80	2.70	59.5
Black-naped Monarch	*Hypothymis azurea*	S	1	10.8	15.30	—	63.0	12.00	—	67.2
Greater Green Leafbird	*Chloropsis sonnerati*	S	1	39.7	—	—	—	32.70	—	70.9
Resident non-passerine										
Brush Cuckoo	*Cacomantis variolosus*	S	1	23.8	16.4	—	65.8	10.5	—	52.9
Migrant passerines										
Brown Shrike	*Lanius cristatus*	O	1	26.9	26.3	—	56.9	21.8	—	62.6
Great Reed-Warbler	*Acrocephalus arundinaceus*	O	4	21.9	26.0	5.8	64.9	22.1	4.1	72.5
Black-browed Reed-Warbler	*Acrocephalus bistrigiceps*	O	1	7.9	—	—	—	11.1	—	77.2
Siberian Blue Robin	*Erithacus cyane*	S	3	13.4	22.9	7.0	80.8	15.0	0.4	71.2
Migrant non-passerine										
Common Scops Owl	*Otus scops*	S	2	63.9	—	—	—	30.6	1.7	75.0

[a] S = shade, O = open.
[b] Predicted from Aschoff and Pohl (1970a) % = observ./pred. × 100.

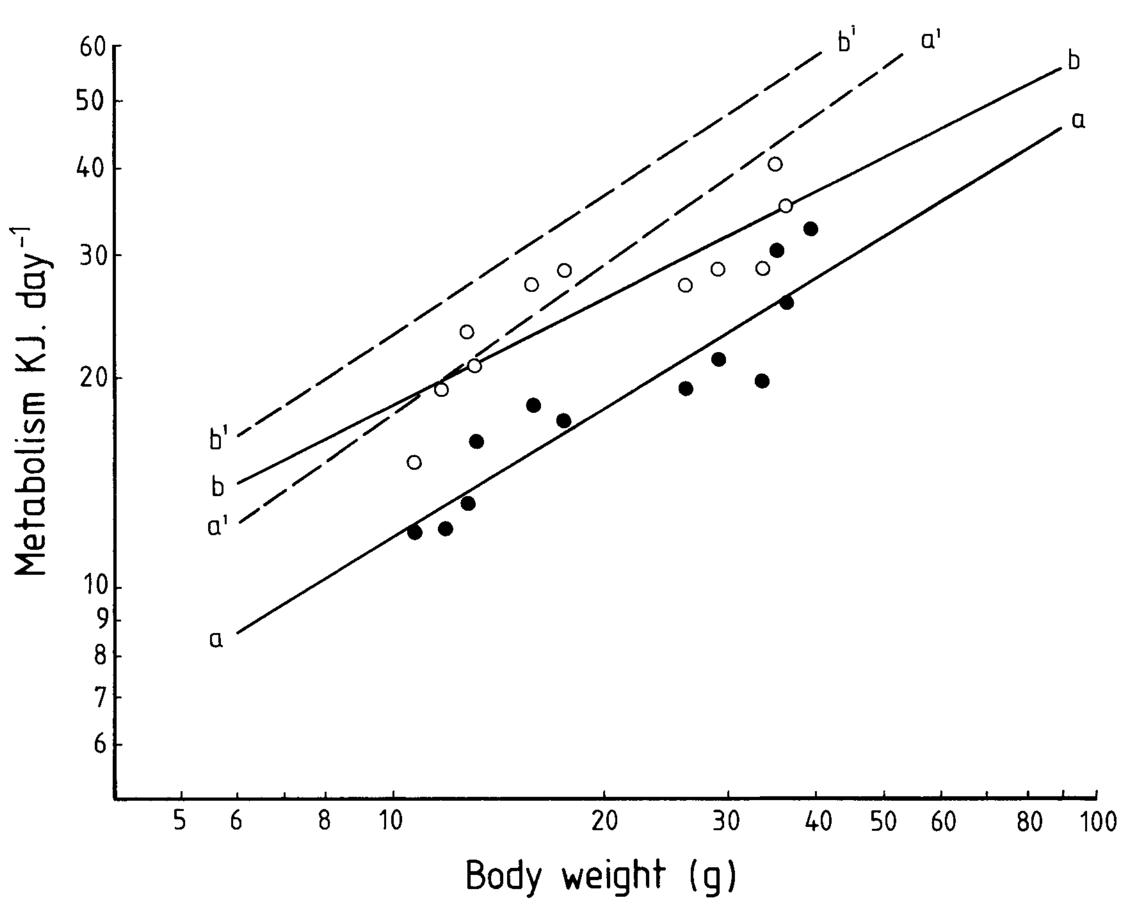

FIGURE 1. Basal metabolic rates of a range of tropical passerines during the active and resting stages of the circadian cycle. Closed circles (a-a) resting phase: $M = 202.15W^{0.615}$. Open circles (b-b) active phase: $M = 188.2\ W^{0.506}$. Lines a'-a' and b'-b' are the regression lines of Aschoff and Pohl (1970a) for temperate passerines during the resting and active phases respectively.

h after the birds' normal dawn) was taken as an estimate of the H_b during the active phase.

RESULTS

Rates of oxygen uptake varied according to normal circadian oscillations (Aschoff and Pohl 1970b); in the diurnal species consumption dropped steadily reaching a low point generally between 24:00 and 04:00. From this low consumption rose steadily until the birds' normal dawn at about 06:00. The low point, which was taken as the resting-phase H_b, occurred at least 7 h after the bird had been captured; thus, all the birds were likely to be post-absorptive. They were therefore assumed to have a respiratory quotient of 0.75; a conversion factor of 20.1 kJl^{-1} O_2 was used to calculate energy expenditure.

Table 1 shows the H_b of all the species in both phases and compares the values obtained with those predicted by the Aschoff and Pohl (1970a) equations. All the species measured had H_b in both phases lower than the predicted value, the active-phase measurements averaged 69.3% of the predicted values and the resting-phase 66.3%. The largest group sampled was the resident passerines (Fig. 1), which averaged 70.2% of predicted values in the active-phase and 65.2% in the resting-phase. In the resting-phase the migrant species were nearer to the predicted values (71.7%) than the residents (64.27%), but the reverse was true in the active-phase (67.5% and 69.8% respectively).

Weathers (1979) suggested that in hot climates H_b of birds that forage in the shade may differ from those which forage in the open. Of the resident species in this study the open foragers averaged 59.3% (resting-phase) and 69.2% (active-phase) of predicted values and the shade foragers 68.4% (resting-phase) and 70.45% (active-phase).

DISCUSSION

Most modern respirometry systems are designed on an open-flow principle incorporating electronic oxygen and/or carbon dioxide analysers. However, lacking such equipment, measuring oxygen uptake from the fall of a small spirometer reservoir is adequate. The apparatus used was thoroughly tested for malfunctions and temperature changes that could have caused changes in gas volumes and hence erroneous results. The commonest fault with this type of system tends to be leaks which give artificially elevated readings rather than the apparently low oxygen consumption rates that were found in this study. My value for the resting-phase metabolism of *Lonchura maja* (1.03 $kJ \cdot g^{-1} \cdot day^{-1}$) compares well with that measured on the same species (1.06 $kJ \cdot g^{-1} \cdot day^{-1}$) by S. F. Chong (unpubl.) using different apparatus, and with that for *L. fuscans* (0.88 $kJ \cdot g^{-1} \cdot day^{-1}$) measured by Weathers (1977).

The data presented support the earlier contentions that H_b is lower in tropical than in temperate species. The extent to which it is reduced appears to depend upon whether a bird is a resident or a migrant and on the phase of the circadian cycle. For a resident passerine, the reduction is approximately 30% during the day and 35% at night. This reduction is greater than that predicted by the Weathers (1979) equation which, at 3°N, predicts a reduction of 23%. However, considering the wide range of studies used by Weathers (1979), which probably induced some of the scatter around his line, this agreement is quite good (his line predicts congruity with Aschoff and Pohl [1970a] at only 26°N). It is possible that the active-phase equations presented here are slightly elevated due to stress and food deprivation effects upon the birds after they had been in the chamber overnight (ca. 14 h). Active-phase H_b is difficult to measure because small movements made by the animal contribute to energy expenditure. Thus the daytime reduction in metabolism might be nearer to the 35% of nighttime if efforts were made to measure only this phase. It is notable that one-third of the tropical studies cited by Weathers (1979) showed reductions of more than 30%.

Data presented by Weathers (1979) suggested that a reduction in H_b between active and resting phases may occur only in birds that forage in the open. In the present study, both groups showed such a reduction although it was less in those species that forage in the shade. The only other study I know of to survey a variety of tropical species sampled exclusively shade foragers and did not find any consistent reduction in H_b (Vleck and Vleck 1979). Although that study was done in the neotropics it is unlikely that Old World and New World birds differ in this regard. It may be significant that my study was carried out at 3°C higher experimental temperature and that the low point in the circadian cycle was identified.

The migrant species measured in this study also showed a phase reduction in H_b. This is analogous to seasonal adjustments to higher ambient temperatures between winter and summer shown in other studies (see Kendeigh et al. 1977). However, this reduction, coupled with ambient temperatures close to thermoneutral, points out the saving in daily energy requirements a migrant may have in its winter quarters.

Birds in the humid tropics are subjected to hot, humid weather and often intense sunlight at all times of the day, conditions that aggravate the dissipation of excessive heat loads created by muscular exercise. Under these circumstances, a reduced rate of endogenous heat production is advantageous. Furthermore, the birds in this study normally and predictably spend much of the day at temperatures within, or very close to, the thermoneutral zone. A high level of endogenous heat production is therefore unnecessary and its reduction would be adaptive in lowering daily energy demands. Birds foraging in the open are more subject to excessive heat loads, and thus they seem to have a lower H_b than those foraging in the shade. The resting-phase reduction of basal metabolic rate in shade-foragers and the nocturnal *Otus scops* indicates however, that other factors besides direct solar radiation have led to the lower rate in tropical birds.

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Condor 85:65

RECENT PUBLICATIONS

The Country Journal Book of Birding and Bird Attraction.—Alan Pistorius. 1981. W. W. Norton & Company, New York. 274 p. $15.95. A truly fine gift to whet an interest in birds and birding. In the same readable, informative style of *Country Journal* magazine, the book provides a blend of traditional widsom and modern scientific thought, without trying to cover all aspects of all subjects. An introductory chapter puts the seasonal biology of birds in perspective and progresses into the subject of feeders and feeding. The Christmas Count and the Big Day, are highlighted for the lessons they teach about the role of the amateur observer in ornithology, and provide direction for the enthusiastic beginner. Bird distribution is treated through a discussion of avian atlases. Nesting boxes and other ways of attracting birds are treated with humor and sensitivity for the species discussed. Since the book is written with the conditions of an "extended Northeast" in mind, readers who live elsewhere will have to enjoy this very pleasant book while understanding that it may not apply in all matters to their region. Bibliography, index. Pen-and-ink drawings by Don Almquist.—J. Tate.

The Birdwatcher's Dictionary.—Peter Weaver. 1981. T. & A. D. Poyser Ltd., Calton, England. 155 p. $17.50. Source: Buteo Books, P.O. Box 481, Vermillion, SD 57069. If you think that American birders use a language unto themselves, this book will convince you that the British provide more than a different accent to that language. This glossary of more than 1,100 words and their definitions is just what elitist birders need to duly impress and confound their fellows. A great deal of fun can be had, for example, with "twitching" and "ringing," "flows and mosses" (listing, banding and two types of marsh). Ornithological words are well represented and generally well defined so that the book's utility is clear. Appendix A contains abbreviations, including those of the many British conservation organizations. Appendix B is a cross-comparison of British, North American, and scientific names; while Appendix D provides the entire British and Irish list of birds. Appendix C shows the high level of British concern for bird life with the Birdwatcher's Code of Conduct. Pen-and-ink drawings; black-and-white figures and maps.—J. Tate.

Birds at Risk/A Comprehensive World-survey of Threatened Species.—Ralph Whitlock. 1981. Moonraker Press, Great Britain. 159 p. $30.00. Source: Humanities Press, Inc., Atlantic Highlands, NJ 07716. The timing of this book to coincide with the 1982 reauthorization of the Endangered Species Act in the United States is appropriate. Except for the introduction, which presents an emotional, but largely unsupported view that early man was responsible for wholesale extinctions due to his predatory efficiency, the story of thoughtless overexploitation is well told. A chapter on birds with restricted ranges (islands and island-habitats) is confusing, at least in part due to lack of cross-reference to the fine maps. Environmental changes, especially those hastened by man, are discussed in two chapters. The final chapter argues that examination of those species that are doing well will better prepare us for the management and conservation of all species. A fine idea, but, unfortunately, so little specific detail is provided that the argument is not convincing. The attractive photographs and paintings, many of them in color, make this an interesting coffee-table book. Maps, bibliography, index.—J. Tate.