

## Response to Ward et al.

J. DAVID LIGON,<sup>1</sup> CYNTHIA CAREY,<sup>2</sup> SANDRA H. LIGON,<sup>1</sup> AND GREG H. FARLEY<sup>1</sup>

Ward et al. (1989) briefly reviewed Ligon et al. (1988), and presented suggestions or observations that they felt cast doubt on the interpretations. Here we respond to each of their points.

1. Ward et al. speculated that the agitation of the woodhoopoes at 19°C resulted from their inability to join other birds in a communal roost, and that this is driven by a circadian rhythm. Two birds were hatched in the U.S. and all three had been maintained on natural photoperiods in the Denver or Albuquerque zoos for many months (i.e. their circadian rhythms, as indicated by roosting behavior, etc., were adjusted to local conditions). Sunset in these locations in early December was 1630–1700 MST. The birds were taken from the zoos on the morning of the tests, and they would be expected to exhibit the hypothetical elevation in activity associated with pre-roosting behavior at about 1630–1700. However, they were quiescent in the chambers from their introduction at 1600 until about 2330, when ambient temperature was lowered to 19°C. A 6-h delay in the expression of behavior associated with roosting seems unlikely. Thus we conclude that a circadian rhythm of activity was not responsible for the occurrence of the agitated behavior.

2. Ward et al. felt that Ligon et al. (1988) ignored the effect of circadian rhythms on metabolic rate. In fact, we timed the measurements to take this into account. The woodhoopoes were placed in the chambers at 1600 and left undisturbed until 2000 to ensure that the measurements were taken in the inactive (dark) phase of the daily cycle. In addition, they had received no food over the previous 8 h. Metabolic rates at 30°C were similar to those reported by Aschoff and Pohl (1970) for nonpasserines in the inactive phase. Circadian rhythms of metabolism result in a decrease in metabolic rate during the inactive phase of diurnally active birds (Aschoff and Pohl 1970). If the results at 19°C had been caused by a circadian rhythm of metabolism, we would expect that metabolic rates of the woodhoopoes would have continued to decrease at 27°C and 19°C as measurements were made progressively later into the inactive phase; however, rates abruptly increased at 19°C. A circadian rhythm that drives metabolism upward in the middle of the inactive phase is improbable. Therefore, we conclude that the increase in metabolic rate at 2330 and at 19°C was not driven by a circadian rhythm of metabolism.

3. Ward et al. suggest that the low cloacal temperatures of woodhoopoes at 2400 also were a function of a circadian rhythm. Circadian rhythms in birds and mammals produce lower body temperatures during the inactive portion of the daily cycle, but this is true only when the animals are quiescent (e.g. Bartholomew and Dawson 1958). Struggling results in substantial increases in body temperatures in birds (e.g. Lasiewski 1964). Since the woodhoopoes were exceptionally active in the chambers just before removal, it is unlikely that the low body temperatures recorded (33–36°C) resulted from a circadian rhythm. We know of no evidence among birds that body temperatures normally fluctuate by 6–7°C during a circadian cycle in the absence of adaptive hypothermia (cf. Ohmart and Lasiewski 1971). Adaptive hypothermia is not accompanied by intense activity. (It appears that locomotor activity may prove to be either a widespread last-ditch mechanism for heat production or an attempt to escape unmanageable environmental conditions. One of us has recently observed that House Finches (*Carpodacus mexicanus*) exposed to –20°C became extremely active just as they became hypothermic [C. Carey unpubl. data]).

Ward et al. seem to have presented a self-contradictory argument. On the one hand, they argued that activity and metabolism increased at 2330 and at 19°C because of a circadian rhythm; on the other hand, they suggested that at the same time body temperatures were lowered, also because of a circadian rhythm. However, under benign conditions, increased metabolic rates and decreased body temperatures do not occur simultaneously in birds. These responses typically occur together only when the bird is exposed to ambient temperatures below the Lower Critical Temperature (LCT). As we mentioned previously, under such conditions the usual avian response is inactivity, which minimizes heat loss.

4. The observation that woodhoopoes were active in the early morning at ambient temperatures below 20°C does not bear on our results or interpretations, for several reasons. First, after dawn the birds were able to move actively and to forage, which in equatorial Kenya they could not have done for the previous 12 h. Second, like many other avian species, woodhoopoes bask in the sun after emerging from their roosts. Third, they leave their roosts later on overcast mornings than on sunny ones. In short, low ambient temperatures for a brief period in the early morning do not pose the same problems for active woodhoopoes that the same temperatures would present to an immobile bird in darkness over a period of many hours.

The closing quote of Ward et al. is taken out of

<sup>1</sup> Department of Biology, University of New Mexico, Albuquerque, New Mexico 87131 USA

<sup>2</sup> Department of EPO Biology, University of Colorado, Boulder, Colorado 80309 USA.

context and thus also requires a comment. The half-sentence quoted refers to a consideration of an adaptive vs. nonadaptive interpretation of the dependence of woodhoopoes on cavities for roosting, given the high rate of predation that occurs at cavities. Our point was that an either/or interpretation was inappropriate.

Finally, although we dispute the suggestions of Ward et al., we recognize that the study was brief (of necessity), and thus incomplete, and that many important, unanswered questions remain concerning the ecological physiology of Green Woodhoopoes. We also acknowledge a weakness in the original discussion, which emphasized standard metabolic rate (SMR) and ignored the issue of Lower Critical Temperature. Although LCT was not determined, it may have been well above 19°C. LCT reflects the degree of insulation (feathers and fat) possessed by a given species, and for the woodhoopoes and at least some other coraciiform birds (e.g. Bryant et al. 1984), a high LCT may be the critical factor leading to dependence on cavities for roosting.

#### LITERATURE CITED

- ASCHOFF, J., & H. POHL. 1970. Rhythmic variations in energy metabolism. *Fed. Proc.* 29: 1541-1552.
- BARTHOLOMEW, G. A., & W. R. DAWSON. 1958. Body temperatures in California and Gambel's quail. *Auk* 75: 150-156.
- BRYANT, D. M., C. J. HAILS, & P. TATNER. 1984. Reproductive energetics of two tropical bird species. *Auk* 101: 25-37.
- LASIEWSKI, R. C. 1964. Body temperatures, heart and breathing rate, and evaporative water loss in hummingbirds. *Physiol. Zool.* 37: 212-223.
- LIGON, J. D., C. CAREY, & S. H. LIGON. 1988. Cavity roosting, philopatry, and cooperative breeding in the Green Woodhoopoe may reflect a physiological trait. *Auk* 105: 123-127.
- OHMART, R. D., & R. C. LASIEWSKI. 1971. Roadrunners: energy conservation by hypothermia and absorption of sunlight. *Science* 172: 67-69.
- WARD, D., B. PINSHAW, D. AFIK, Y. LINDER, & N. WINKLER. 1989. Cavity roosting, philopatry, and cooperative breeding in the Green Woodhoopoe may not reflect a physiological trait. *Auk* 106: 342.

*Received 17 October 1988, accepted 18 October 1988.*