

ing on mistletoe in their winter range (Walsberg 1975), the much larger gizzards of *Phainopepla* collected in their summer range (August and September samples) all held multiple fruits. This method of fruit processing is similar to that of nonmistletoe-specializing frugivores that typically use the gizzard to mechanically reduce multiple fruits at a time (Walsberg, unpubl. data). This presumably is associated with the easier handling characteristics of fruit without the adhesive qualities of mistletoes.

Major restructuring of body components is characteristic of the annual cycle of many bird species. This restructuring can include alteration in plumage, fat reserves, and locomotor muscles (King and Murphy 1985). The alteration in gizzard size observed in the *Phainopepla* reinforces the view that the avian digestive tract also can exhibit substantial seasonal restructuring (e.g., Davis 1961, Ankney 1977, Al-Dabbagh et al. 1987). Although digestive efficiency and rate during summer months have not been measured, the altered gizzard morphology does suggest that adaptations for seasonal dietary specialization may not entail substantial reduction in the effectiveness of food processing at other times of the year.

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COMMUNAL ROOSTING IN A VERY SMALL BIRD: CONSEQUENCES FOR THE THERMAL AND RESPIRATORY GAS ENVIRONMENTS¹

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Key words: *Auriparus flaviceps*; *Black-tailed Gnatcatcher*; *communal roosting*; *energetics*; *microhabitat selection*; *Poliophtila melanura*; *roost-site selection*; *thermal ecology*; *Verdin*.

Communal roosting within a cavity represents an extreme in microhabitat selection that has been described for several bird species (e.g., Knoop 1957, Frazier and Nolan 1959, White et al. 1975, Pitts 1976). Although such dense and enclosed aggregations of endotherms have the potential to importantly alter their local environment by elevating temperature, depleting oxygen, and generating carbon dioxide, the physiological con-

sequences of such behavior are not well-known (Reinertsen 1988). Such communal roosting can result in individuals being directly warmed through contact with others as well as experiencing indirect warming associated with heating the air within the cavity and reducing convective heat loss through the cavity entrance. I report here observations of the thermal and gaseous environment within the first reported communal roost of Black-tailed Gnatcatchers (*Poliophtila melanura*), a small (about 5 g) Sonoran Desert insectivore.

METHODS AND MATERIALS

The roost was located along a wash in Vekol Valley, Maricopa County, Arizona, at 570 m elevation. The wash is a normally dry watercourse passing through a desert valley dominated by bursage (*Ambrosia dumosa*) and creosote bush (*Larrea tridentata*) with a scat-

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tering of ocotilla (*Fouquieria splendens*) and cactus (e.g., *Ferocactus*, *Opuntia*, *Carnegia*). The wash edges are populated by large shrubs and small trees such as palo verde (*Cercidium floridum*), mesquite (*Prosopis velutina*), ironwood (*Olneya tesota*), and catclaw acacia (*Acacia greggii*).

During December 1989, a group of gnatcatchers roosted most nights inside the oval-shaped, domed nest of a Verdin (*Auriparus flaviceps*) located 2.2 m above ground in a catclaw acacia. The approximately 18-cm nest (outside diameter) had a single entrance hole directed slightly downward and was constructed of thorny twigs with an interior chamber lined with grass and feathers.

Numbers of birds using the roost were determined by arriving at the site prior to dawn and observing the nest entrance from about 15 m with the aid of binoculars and a telescope. The birds were counted at dawn as they emerged from the roost.

Temperature within the roost was determined hourly between 17:00 MST and 08:00 MST using four 24-ga. copper/constantan thermocouples attached at 1-cm intervals along a 3-mm diameter wooden rod. The rod was inserted through the nest walls such that the thermocouples were centered in the nest cavity. The thermocouples were connected in series so that the resulting signal represented the average temperature of the four thermocouples. Air temperature was measured simultaneously using a shielded 24-ga. thermocouple placed at nest height and within 0.5 m of the roost. Temperatures were recorded using a Li-Cor LI1000 data logger. Local apparent sunrise and sunset occurred at approximately 08:15 MST and 17:15 MST. Additionally, heavy vegetation shaded the nest for several hours prior to sunset. Thus, roost temperatures should not be importantly influenced by solar heating.

The gaseous environment within the roost was sampled by connecting a 2-mm diameter polyethylene tube from outside of the nest to the wooden rod in the center of the nest cavity. A syringe was used to withdraw 60 ml of air from within the nest at 06:30 MST, approximately 1 hr before sunrise. The initial 10-ml sample was discarded to avoid contamination by air contained within the tubing. Air from the general atmosphere outside of the nest was simultaneously collected for comparison. The sealed syringes were returned to the laboratory at Arizona State University. Oxygen content was measured within 2 hr of collection by injecting samples through a train of H₂O and CO₂ absorbants (silica gel and Ascarite, respectively) into an Applied Electrochemistry S3a oxygen analyzer. Dry air from the open atmosphere was used as a standard and assumed to contain 20.93% O₂ and 0.04% CO₂.

RESULTS AND DISCUSSION

NUMBERS OF OCCUPANTS

The nest was observed for five calm, clear nights in December. On three of these nights, the roost was occupied by 15 birds (two nights) or 16 birds (one night). The birds entered the roost asynchronously over approximately 15- to 25-min periods between sunset and the end of dusk. Most birds emerged from the roost nearly simultaneously within a 1- to 3-min period at dawn prior to sunrise, although a few individuals strag-

gled out up to 20 min after sunrise. The roost was unoccupied on two of the five nights. These two nights did not differ noticeably from periods in which the roost was occupied, suggesting that the gnatcatchers may have been occupying an alternative roost. At the beginning of a fourth night of data collection on the occupied roost, the nest was accidentally disturbed. The gnatcatchers left immediately and did not return on subsequent evenings.

OXYGEN AND CARBON DIOXIDE CONCENTRATIONS

Maximum differences between the gas concentration of the roost and that of the general atmosphere should occur near dawn, when low temperatures elevate metabolic rates and typically windless conditions minimize nest ventilation. It is remarkable, therefore, that oxygen concentration within the roost was reduced an average of only 0.32% (range = 0.28%–0.38%) to 20.61% of dry, CO₂-free air volume. Assuming that the animals are catabolizing fat with a resultant respiratory quotient of 0.71 moles of CO₂ produced per mole of O₂ consumed and that gas exchange is dominated by convection predicts that CO₂ should be elevated an average of only 0.23% (= 0.71 × 0.32%) to 0.27% of air volume. Such changes in O₂ and CO₂ concentrations are moderate compared to those observed in a variety of other bird species occupying cavities and are unlikely to elicit changes in respiratory parameters (e.g., Withers 1977, Wickler and Marsh 1981, Birchard et al. 1984, Howe et al. 1987).

In contrast to the modest changes in gas concentrations, roost temperature was elevated 8.6°C–30.2°C (average = 21.0°C) above that of the surrounding air during the period in which the nest was occupied (18:00–07:00 MST; Fig. 1). Such high temperatures should produce major energetic savings to roosting gnatcatchers. The relation of metabolism to environmental temperature (T_A) has not been measured in this species, but can be estimated assuming a typical body mass of 5 g (Weathers 1983) and using the allometric equations of Aschoff and Pohl (1970) and Calder and King (1974). Equation 13 of Calder and King predicts a whole-body thermal conductance (h) of 0.011 W °C⁻¹. Assuming that body temperature (T_B) equals 40°C, standard metabolic rate below thermal neutrality may be predicted as

$$M = h(T_B - T_A). \quad (1)$$

The expected lower critical temperature equals the point (29°C) at which the line predicted by equation 1 intercepts the basal metabolic rate of 0.12 W predicted by the equation of Aschoff and Pohl (1970). Assuming 20.1 kJ is produced per liter of oxygen consumed, these predicted values for basal metabolism and thermal conductance in gnatcatchers are 5% and 12%, respectively, above those measured for the similarly sized (5.5 g) Common Bushtit, *Psaltriparus minimus* (Chaplin 1982).

Predicted metabolic parameters and equation 1 were used to estimate the power consumption required at prevailing roost temperatures separately for each of the 14 hr the roost was occupied (18:00–07:00 MST) for each of 3 days. Averaging these 42 separate estimates

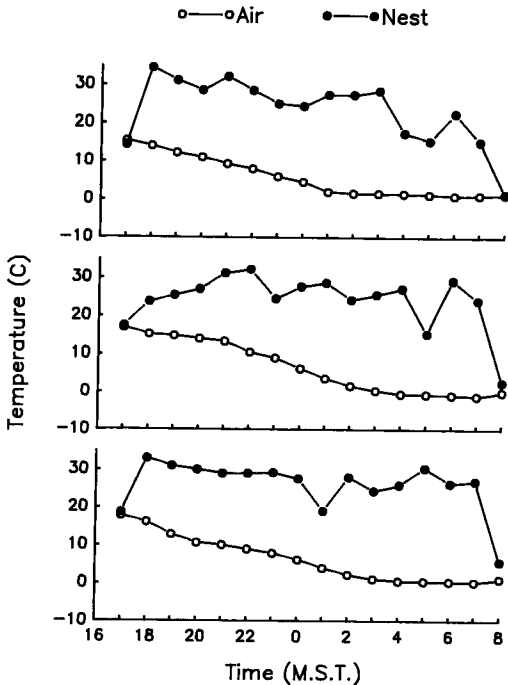


FIGURE 1. Temperatures inside and outside of a communal roost of Black-tailed Gnatcatchers on three different days. Roost was occupied from approximately 18:00 MST to 07:00 MST. Values for 17:00 MST and 07:00 MST are for the unoccupied roost.

predicts mean metabolic rates of 0.38 W bird^{-1} at prevailing air temperatures outside the nest (range = $0.27\text{--}0.46 \text{ W}$) and 0.15 W bird^{-1} at roost temperatures (range = $0.12\text{--}0.28 \text{ W}$). This 61% reduction in power consumption associated with roost use is substantially greater than that previously reported for other species, which generally range from 4–43% (Walsberg 1985). Although large, a 61% reduction in power consumption probably is a substantial underestimate of the savings accrued in gnatcatchers. In addition to the benefits of elevated air temperature, birds within the enclosed nest experience reduced convective and radiative heat loss and may additionally benefit by direct contact with other individuals. These effects should amplify the thermal benefits of roost occupation.

These large energetic savings are associated with substantial numbers of birds occupying a single, enclosed roost. One week after data were collected, the Verdun nest was dissected and the inner chamber found to measure 8.3 cm long and 7.4 cm wide. Modeling the nest chamber as a prolate spheroid (Hodgman 1960) yields a chamber volume of 238 cm^3 . The body volume of a Black-tailed Gnatcatcher can also be modeled as a prolate spheroid, with length (excluding the beak and tail) of 4.5 cm and maximum width (midtorso) of 2.2 cm. This predicts a body volume of 11 cm^3 , suggesting that 15 gnatcatchers occupy roughly 72% of chamber volume. Clearly, this is only a crude estimate and ignores feather erection and compression, postural

changes, and the awkward geometry of limbs. It does suggest, however, that roosting birds must be rather tightly packed into the nest chamber.

If communal roosting presents such a major energetic advantage, why has it not been previously observed in this species? One possibility, of course, is that it occurs only rarely because of countervailing disadvantages, perhaps including increased danger of detection by predators. However, it also is notable that Black-tailed Gnatcatchers do not form flocks and population densities normally are low, averaging only $0.27 \text{ bird ha}^{-1}$ in similar wash habitats studied by Weathers (1983). This low density suggests that the 15–16 birds occupying this roost inhabit about 56–59 ha of suitable habitat distributed linearly along the wash. It is therefore possible that communal roosting in this species is not uncommon but has previously been undetected simply because of the very low density of occupied roosts.

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CAROTENOIDS PRODUCE FLUSH IN THE ELEGANT TERN PLUMAGE¹

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Key words: Feather flush; carotenoids; astaxanthin; *Elegant Tern*.

Adult Elegant Terns (*Sterna elegans*), Roseate Terns (*S. dougallii*), many gulls (Laridae), several pelicans (*Pelecanus* spp.), the Common Merganser (*Mergus merganser*), and ptarmigans (*Lagopus* spp.) display a pink flush on their white body feathers (Stegmann 1927-1934; see also Völker 1964, Höhn and Singer 1980, Harrison 1983). Called variously "flush," "blush," "bloom," "tint," "wash," or "cast," the color is generally confined to the ventral surface. Characteristically, the color is ephemeral, and fades rapidly (within a few weeks to several years) after the death of the bird (Völker 1964). Neither the origin of the coloration nor its chemical nature have been conclusively elucidated (Höhn and Singer 1980). The ephemeral nature of the coloration is particularly challenging.

Stegmann (1956) suggested that the color might originate from a substance produced by the uropygial gland and deposited on the bird's plumage by preening. He proposed that oxidation and breakdown of the substance could account for the rapid color loss (Stegmann 1956). The secretion of the gland in some gulls and the White Pelican (*Pelecanus onocrotalus*) is bright red (Stegmann 1956). However, not all flushed species produce colored uropygial gland secretions (Höhn and Singer 1980), and other causes of the flush are possible. Colored substances are not mentioned in recent reviews of uropygial gland secretions (Jacob 1978, Jacob and Ziswiler 1982). To our knowledge, no feather pigments or environmentally derived substances have been identified as responsible for the pink flush. Also, struc-

tural modifications of the flushed feathers have not been demonstrated (Höhn and Singer 1980). Adventitious, yellow colors found in a variety of birds are produced by environmental ferrous oxide adsorbed to the feathers (Berthold 1967).

The availability of colored feathers from an Elegant Tern gave us the opportunity to investigate the factors responsible for the feather flush. We were interested especially in the possibility that it might be a carotenoid that was applied to the feather surface. Carotenoid pigments are widely distributed in birds and are responsible for many of their brightest colors (reviewed in Brush 1981). Adventitious carotenoids would be particularly sensitive to oxidation. However, carotenoid pigments are commonly deposited inside feathers, not on the surface (Lucas and Stettenheim 1972). We found that carotenoids were indeed implicated in the flush, and were deposited inside the feathers.

MATERIAL AND METHODS

An adult Elegant Tern in full molt with a distinct salmon pink flush was collected at the Bolsa Chica Ecological Reserve (Orange County, California) on 15 September 1988. Flushed contour feathers which originated from unspecified areas on the body were plucked and sent to us for analysis. The feathers were tinted uniformly over both vanes and the rachis. Some of the flushed feathers were kept intact for comparison with washed and decolorized feathers.

We first washed the flushed feathers (ca. 1 g) with a soapy solution (ca. 0.1% v/v, Sweet Life lotion detergent) for 24 hr. About 50 ml of this and subsequent solvents were used for the washes. After the soap treatment the feathers were washed repeatedly with distilled water, and once with acetone for several minutes to remove the water (first acetone wash), and air-dried. We also washed the feathers once with petroleum ether for 24 hr. Subsequently, the feathers were soaked in methanol for an additional 24 hr. We again rinsed the feathers once in acetone (second wash) and redried them. The methanol and second acetone washes were combined for analysis. The remaining pigment was

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