ALTITUDINAL VARIATIONS IN NESTS OF THE HAWAIIAN HONEYCREEPER *HEMIGNATHUS VIRENS VIRENS*

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ABSTRACT.—We examined more than 90 nests of the Common Amakihi (*Hemignathus virens virens*) from the Island of Hawaii to determine if their placement, composition, or insulation varied with meteorological conditions at the time of nesting. Common Amakihi nest chiefly during the wet season. The nests were always within the canopy of the nest trees and consequently were probably shielded from rain. The nests from a warm rain forest on Kohala Mountain were significantly higher in the canopy and nearer each tree's center than the nests from Mauna Kea, a cold upland savannah. On Mauna Kea, nests were nearer the edge of the canopy at higher elevations, i.e., in a location where they would benefit from radiant solar energy.

Nests from Kohala Mountain lacked liners and were more porous than those from Mauna Kea. These features permitted the nests to dry rapidly. Nests from Mauna Kea, in contrast, were always lined, which retarded drying and increased their insulating capacity—features appropriate for the drier, colder conditions in areas where they were built. All of the nests were excellent windscreens.

The thermal conductance of nests from Mauna Kea diminished with altitude, i.e., nests at higher elevations had more insulation than those at lower elevations. This trend was associated with differences in the nests' walls, which were denser (but not thicker) at higher elevations.

The nest's thermal conductance can be used to estimate the energetic expense of incubation. For Common Amakihi, the energy required to keep a clutch at incubation temperature may be as much as 0.115 W or 47% of the birds' metabolic rate at rest.

The Common Amakihi (*Hemignathus virens*, family Drepanididae) is an abundant and widespread forest bird of the Hawaiian islands. The subspecies from the Island of Hawaii (*H. v. virens*) occurs at elevations between 650 and 3,000 m. Some populations nest in areas that are extremely wet and warm (rain forests), whereas others nest in relatively dry cold areas (upland savannahs); all commonly do so during the rainy season (Berger 1969, Eddinger 1970, van Riper 1978). On the Island of Hawaii, their breeding season extends from late October through August.

We speculated that the small size of the amakihi (13–14 g), coupled with the extreme variations in moisture and temperature to which populations are exposed while nesting, might have led to altitudinal differences in nest structure. For example, breeding success in rain forests might require a nest that will drain readily and dry quickly, but one that need not be highly insulated because of the mild and fairly constant temperatures in such habitats. In fact, amakihi on the Island of Kauai sometimes brace their nests against tree trunks where they are soaked by water running down the bark during heavy rains. In contrast, amakihi nesting at high elevations on the Island of Hawaii, where it is decidedly drier and colder, may require a more highly insulated nest, but one that is still capable of drying efficiently. Here, a nest with a liner might be more adaptive. In order to address these possibilities, we conducted qualitative and quantitative studies of more than 90 amakihi nests collected at many different elevations on the Island of Hawaii.

MATERIALS AND METHODS

STUDY SITES

Most of our nests came from elevations between 1,600 and 2,600 m above sea level, around Puu Laau on the Island of Hawaii (20°N, 155.5°W). Puu Laau is on the southwestern or leeward slope of a dormant volcano, Mauna Kea, which rises 4,205 m above sea level. Since the mountain effectively blocks out the tradewinds, our study sites were in its rain shadow. The area is relatively dry and cold: rainfall is about 51 cm annually and temperatures frequently fall below 0°C in most months of the year; they rarely exceed 30°C (van Riper 1980). Puu Laau is one of the few remaining native dry forest ecosystems in Ha-

waii. The dominant trees are mamane (*Sophora chrysophylla*) and naio (*Myoporum sandwicense*).

For comparative purposes, we also examined nests collected at much lower elevations (650–1,000 m) in the rain forest on Kohala Mountain near the northern tip of the island. Here, precipitation is much higher (about 229 cm annually) and ambient temperatures more moderate (9–25°C) than at Mauna Kea (van Riper 1976, unpubl. data). Dominant plants are the giant tree fern (*Cibotium glaucum*), and the trees ohia (*Metrosideros collina polymorpha*) and olapa (*Cheirodendron trigynum*). Introduced species, particularly the Norfolk Island pine (*Araucaria excelsa*), ironwood (*Casuarina equisetifolia*), and *Eucalyptus* spp. occur along the forest edges (van Riper 1976).

MEASUREMENTS ON SITE AT PUU LAAU

At monthly intervals between 1973 and 1975, van Riper measured the density of the canopy in mamane trees at Puu Laau by standing under them and recording the percentage of open sky visible. He also determined the composition of the forest at 1,980, 2,130, and 2,290 m above sea level, using five contiguous 30- × 30-m plots arranged in the shape of a *T* at each elevation. He identified and numbered all the mamane and naio trees that were more than 2 m high in these plots and measured their heights with a clinometer. Additional details of his methods are in van Riper (1980).

Van Riper also periodically measured air temperatures and precipitation both at Puu Laau and on Kohala Mountain using maximum-minimum thermometers and a National Weather Service rainfall gauge.

NEST COLLECTION

Van Riper collected the Common Amakihi nests on which this report is based and recorded (1) the species of tree in which they were located, (2) nest height, (3) distance of the nest from the tree's central axis, and (4) the height of the nest tree. Where possible, he also noted the stage of the birds' breeding cycle when he collected their nests, and measured the dimensions and mass of the nests. Most of them were collected in 1971–1975 and 1980–1981.

MEASUREMENTS IN THE LABORATORY

Nest dimensions and area of the nest cup. Kern made detailed studies of these nests in the laboratory. He reweighed them and made the following measurements: (1) nest height: with the top of the nest in a horizontal position, (2) **average** thickness of the nest wall: based on measurements from eight locations spaced equally around the nest's circumference, (3) width of the **thinnest** region of the nest's wall, (4) thickness of the nest's floor: a fine wire was passed through the floor and the length enclosed by the nest was measured with a ruler, (5) major and minor diameters of the nest and nest cavity, and (6) depth of the nest cavity.

Kern also determined the surface area of the nest cavity by cutting a piece of thin rubber sheeting to fit it, making a copy of this on paper of known, uniform composition, weighing the copy to the nearest 0.1 mg, and using a predetermined mathematical relationship between paper weight and surface area.

Thermal conductance and thermal conductivity of the nests. Kern measured the thermal conductance (h) of the nest's floor (h_f) and thinnest wall (h_w) and used this information to estimate the overall h of the nest (h_{wf}), which is the average of the values for floor and wall. Using h_{wf} and the nest's dimensions, he then calculated the thermal conductivity (k) of the nest. Details of his methods are in Skowron and Kern (1980). In brief, he assumed that the nest was hemispheric. Heat was pumped through its floor and walls under steady state ambient conditions by means of a balloon of hot water, the temperature of which was held constant, placed in the nest cavity. (The balloon contained 60–85 ml of water, but did not visibly compress the nest.) Under such conditions, the nest's h_w or h_f can be determined using the equation $h = Q_n/(A)(T_i - T_o)$ in which Q_n is heat flow across the nest's wall or floor, A is the area of the nest cavity across which this heat flows, and $(T_i - T_o)$ is the difference between the temperature of the nest cavity (T_i) and the temperature at the surface of the nest (T_o) directly opposite. The nest's k was obtained by rearranging the equation for conductive heat transfer across a sphere (Birkebak 1966): $Q_n = (4\pi)(r_i r_o)(T_i - T_o)(\delta)(k)/(r_o - r_i)$ in which r_i is the radius of the sphere of which the nest cavity is part; r_o is the radius of the nest itself; and δ is a constant whose size is related to the part of the sphere across which heat flow occurs, i.e., the surface area of the nest cup (A) divided by the total surface area of a sphere of which the nest cup is part ($=4\pi r_i^2$). To use this equation, Kern assumed that the nest was part of a hollow sphere with walls and floor of uniform thickness.

Q_n was measured directly using heat flux transducers (Thermonetics Corp.) placed on the floor and the thinnest wall of the nest cavity, and connected to a sensitive voltmeter. Nest temperatures were measured with thermistors (models 402 and 427, Yellow Springs Instrument Co.) placed under each heat flux

transducer and on the external surface of the nest directly opposite. They were connected through a 12-channel switch box to a YSI tele-thermometer (model 43 TD). Kern also measured the h_f of 13 nests in the presence and absence of their nest liners.

Nest density. Kern estimated the weave or porosity of the nests in three different ways. (1) He directed a laminar airstream at the sides and bottom of the nest. The velocity of the air at its point of impact with the nest (v_o) was held constant at 3.7 m/s; the velocity of air was then determined inside the nest (v_i) directly opposite the point where v_o was measured. A hair dryer connected to a variac provided the airstream. Airspeed was measured with a hotwire anemometer (model HWA-103, Thermonetics Corp.). The top of the nest was covered to prevent air from flowing over the nest's walls and into the nest cavity while v_i was being determined. By this method, porosity is a function of the ease with which air penetrates the nest's wall or floor (P_{air}), penetrability being the ratio of airspeed on the two sides of the structure expressed as a percent, i.e., % $P_{air} = (v_i/v_o) \times 100$. The porosity of the walls was the average of measurements made on the four sides of the nest. (2) Kern also inverted the nest over a small 10-W lightbulb and measured the amount of light that passed through the structure using a sensitive light meter equipped wth an adapter for the tube of a microscope. Light was measured with the tube of the photometer adjacent to the outside surface (wall or floor) of the nest; the nest was then removed and the light again measured at the same distance from the bulb. In this case, porosity is a function of the ease with which light penetrated the nest (P_{light}), penetrability being the ratio of light in the nest's presence (lux_{np}) and absence (lux_{na}) expressed as a percent, i.e., % $P_{light} = (lux_{np}/lux_{na}) \times 100$. Values for the wall were averages of measurements made on the four sides of the nest. Because the materials that made up the amakihi nests were opaque, we assumed that this method accurately measured porosity in terms of the ease with which light passed **between** the materials of which the nest was made. (3) Finally, Kern lined the nest cavity with photographic printing paper and then exposed the outside of the nest to a 1-s pulse of light. Any light that passed through the nest exposed the paper on contact. Unlike methods (1) and (2), which measure the nest's weave at a few discrete points, method (3) measures the porosity of the entire nest in terms of light penetration. To measure the density of the nest's floor, the nest was placed upside down on a piece of photographic printing paper under an enlarger, which was turned

on for one second. When the paper was developed, it exhibited a pattern of light and dark spots within the outline of the nest. Dark spots were points where light had penetrated the matrix. To measure the density of the nest's walls, strips of photographic paper were placed along the inside of the nest cavity, emulsion-side facing out. Each strip of paper had a black backing to prevent exposing the emulsion from the back. The opening of the nest cavity was also covered with black paper. A circular fluorescent light was then set up around the nest at wall level and turned on for one second. The strips were removed from the nest cup and developed. Kern made three separate sets of these strips for each nest. After development, all of them exhibited a pattern of light and dark spots similar to those described above for the floor. To quantify the amount of light and dark on each strip of paper, the strip was overlaid with a grid consisting of 5-mm squares. The number of intersections in the grid that fell on light (n_l) and dark (n_d) areas of the paper were counted. In this case, nest porosity is a function of the area of photographic paper that was exposed to light ($A_{exposed}$) expressed as a percent, i.e., % $A_{exposed} = (n_d/[n_l + n_d]) \times 100$.

We are aware that methods involving light penetration are not altogether precise in measuring the nest's weave. For example, light is scattered by fibers and in some cases transmitted by them. Nonetheless, other methods that do not destroy or mutilate a nest are not currently available for assessing weave. We adopted these methods because they do not alter the nest's morphology, an important consideration when using nests from museums or private collections. Furthermore, Skowron and Kern (1980) showed that the amount of light that penetrated a nest was highly correlated with Q_n and h. Similar correlations existed between % P_{light} or % $A_{exposed}$ and h for the amakihi nests in our study (wall: $r = 0.50$ and 0.35, respectively, 40 df, $P < 0.001$ and 0.05; floor: $r = 0.40$, but 0.09, 39 and 40 df, $P < 0.01$ and NS).

Nest's rate of drying. Because Common Amakihi breed in the rainy season and at least on Kohala Mountain commonly experience heavy downpours, we speculated that the nest is probably built to both drain readily and dry quickly. To test that hypothesis, Kern submerged each nest under water for 2 min and then suspended it on large-mesh netting in an environmental chamber (Percival) at a temperature (31.4 ± 0.25°C) approximating the daily high at Puu Laau and Kohala Mountain during the peak of the breeding season. He weighed the nest before immersing it, and reweighed it at periodic intervals while it dried

(at 15-min intervals for the first 2 h and at 30-min intervals for the next 2 h after immersion) and again 24 h later (at which time the nest was dry).

Since five types of amakihi nests (described further on) exist, Kern dried five or six nests in the environmental chamber simultaneously, each type being represented in the group. This caused the chamber's humidity (which initially averaged 25.3%, but ranged from 20 to 32% on different days) to increase by between 15.1 and 20.0% (or an average of 17.6%). Such increases in humidity undoubtedly retarded the rate of drying, but we reasoned that all types of nests would be affected similarly and that this source of error would be minimized by having representatives of each type drying simultaneously.

The temperature of the chamber was measured (by means of a mercury thermometer suspended at nest level within it) each time the nests were removed for weighing. Chamber humidity was also periodically measured, by means of a sling psychrometer, while the nests were in the chamber. No attempt was made to reduce air flow around the nests while they were drying in the chamber.

Composition of the nests. After all physiological measurements had been made, van Riper dismantled 15 lichen type nests to determine the materials of which they were made. Nest liners and outer frames were analyzed separately. All materials except grasses were sorted by species and were weighed. Nests of other types were not dismantled because of their scarcity. For example, sheep were removed recently from Mauna Kea (van Riper and van Riper 1982) and it is unlikely that nests of the wool type will be built in the near future, if ever again.

Statistical analyses. The data were analyzed with one-way analysis of variance followed by Student-Newman-Keuls (multiple range) tests to separate means, Student's t-tests, or least squares analyses, depending on the data set (Zar 1974). Percentages were converted to their arcsin equivalents before analysis. The values that appear in the text and tables of this paper are means ±95% confidence limits ($\bar{x} \pm CI_{95}$). Only nests of average or better-than-average quality were used in this study.

RESULTS

NEST SITE

Mauna Kea. Most Common Amakihi (86.3%) at Mauna Kea built their nests in mamane trees as Berger (1969) found in 1966. Almost all of the other nests (12.1%) were in naio trees, again consistent with Berger's findings.

Amakihi selected trees that were predominantly 4.5–9.0 m high, the mean height being about 6 m (Table 1). Nest trees were significantly taller than would be expected if these birds used trees of various heights solely on the basis of their availability (height of 174 nest trees *vs.* height of a random sample of 265 mamane and 352 naio trees in the same area: $\chi^2 = 28.19$, $P < 0.01$, 1 df; Fig. 1). The nests were usually 4–5 m above the ground and consequently well below the surface of the canopy (Table 1). Their internal location may explain why peak nesting activity was not correlated with the density of the canopy as illustrated at our 2,290-m study site during 1974 and 1975 (Fig. 2). Neither the height of the nest tree nor the nest height varied significantly with elevation, regardless of whether the nests were in mamane ($r = 0.09$ and 0.11, $P > 0.50$, 70–71 df) or naio trees ($r = 0.59$ and 0.52, $P > 0.10$, 5–6 df). However, the distance of the nest from the tree's center (Table 1) was related to elevation in the case of mamane trees ($r = 0.29$, $P < 0.001$, 71 df); no such relationship existed for naio trees ($r = 0.16$, $P > 0.50$, 6 df). In other words, nests were closer to the edge of the canopy in mamane trees at higher elevations.

The birds apparently selected specific sites in these trees in which to place the nest since significant correlations existed between (1) the height of the nest and nest tree: for mamane trees, $r = 0.69$ ($P < 0.001$, 88 df) and for naio trees, $r = 0.77$ ($P < 0.01$, 8 df), and (2) the height of the nest tree and the horizontal distance of the nest from the tree's center, at least for nests in mamane trees ($r = 0.35$, $P < 0.001$, 88 df; but for naio trees, $r = 0.42$, $P > 0.20$, 8 df).

Kohala Mountain. Nests on Kohala Mountain were built almost exclusively in ohia trees, as they are in other mesic areas of the Hawaiian Islands (Berger 1981; e.g., on the Island of Kauai [Eddinger 1970]). The nest trees were nearly twice as high as those on Mauna Kea, as was nest height, but the nests were much closer to the trees' center (Table 1).

NEST TYPES

Amakihi on the Island of Hawaii build at least five types of nests that differ in external appearance (Fig. 3). All are cup-shaped, open bowls saddled in upright forks in the nest tree. Four types were found in the Puu Laau area and the fifth on Kohala Mountain.

Those from Puu Laau had similar outer frames (consisting of mamane parts, woody twigs, grass stems, and occasionally tufts of sheep's wool), but different linings. Nests of the **lichen** type were lined with *Usnea*; the **root-**

TABLE 1. Characteristics of the amakihi's nest site. Values in the table are $\bar{x} \pm CI_{95}(n)$.

Breeding area[a]	Nest site	Height (m) of		Distance of nest from tree's center (cm)	Source
		Nest tree	Nest		
Puu Laau, Island of Hawaii	Mamane trees	6.08 ± 0.40 (79)	4.32 ± 0.27 (82)	63.63 ± 9.74 (79)	This study
	Naio trees	6.43 ± 0.91 (11)	4.84 ± 0.84 (12)	45.98 ± 19.69 (10)	
	Mamane and naio trees	. . .	4.15 (60)	. . .	Berger (1981)
Kohala Mountain, Island of Hawaii	Ohia trees	11.22 ± 1.61 (5)	8.35 ± 3.78 (5)	24.13 ± 6.86 (5)	This study
Kokee State Park, Island of Kauai	Ohia trees	. . .	5.64 (23)	. . .	Eddinger (1970)

[a] Amakihi on the Island of Hawaii belong to the subspecies *H. v. virens*; those on the Island of Kauai to the subspecies *H. v. stejnegeri*.

let type with tiny rootlets, bits of fine plant material, and pig's hair; the **lichen-rootlet** type with roughly equal amounts of *Usnea* and fine rootlets; and the **wool** type with fine rootlets and considerable sheep's wool.

The **Kohala** nest had an outer frame of woody twigs, fern leaves, and many and large rootlets from ohia trees and tree ferns. It was lined with bits of fine plant material, small rootlets, animal hair, and occasionally with some *Usnea*.

Fifteen nests of the lichen type, when dismantled, had outer frames consisting of *Lythrum maritimum*, a prostrate shrub with thin branches that break easily, but still add rigidity to the nest; small branches and leaf petioles of mamane; *Gnaphalium japonicum*, a small composite; and coarse grasses (e.g., *Dactylis glomerata* and *Holcus lanatus*) which were used to bind the other materials together (Table 2). The nest linings contained fine rootlets and delicate grasses (e.g., *Lolium perenne* and *Poa annua*), which were woven into the underlying frame, and large amounts of *Usnea*. This li-

chen was not woven into the nest, but simply piled into the nest bowl and then compressed by the bird into a lining. Feathers, pig's hair, and sheep's wool were also present in a few liners.

The distributions of the nest types at Mauna Kea overlapped considerably (Fig. 4). Wool nests were confined to elevations above 2,164 m.

QUANTITATIVE MEASUREMENTS ON AMAKIHI NESTS

Although the above five types of nests differed perceptibly in external appearance, they did *not* differ significantly in mass, dimensions, surface area of the nest cavity, or thermal conductance (Tables 3 and 4; Fig. 4). Furthermore, we found no evidence that the nest tree or the position of the nest within it differed at Puu Laau according to nest type (Table 4).

The average h_{wf} of amakihi nests was 5.78 ± 0.26 W m^{-2} °C^{-1}, a value that is somewhat higher than the 4.14 W m^{-2} °C^{-1} published
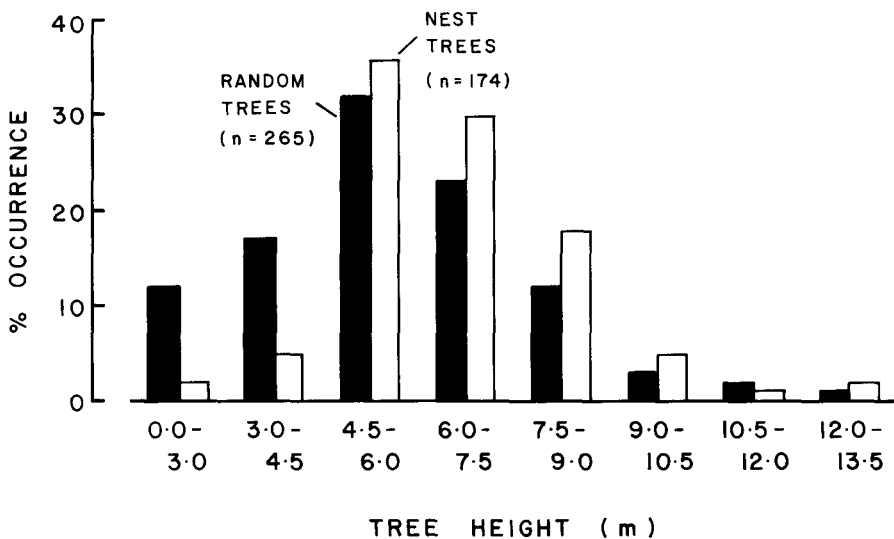

FIGURE 1. Distribution of mamane trees by size at Puu Laau, Island of Hawaii. The closed columns represent a random sample of trees in the study area; the open columns a sample of trees that contained nests of Common Amakihi. Nest trees were significantly taller than would be expected on the basis of the availability of trees of various heights.

PERCENT CANOPY COVER
IN EACH MAMANE TREE

FIGURE 2. Monthly changes in the canopy cover of mamane trees at Puu Laau, an area where Common Amakihi nest. The density of the canopy cover in these trees did not apparently determine when the peak of the nesting season (black parts of the horizontal bars) occurred in the study area. In 1974, nesting peaked when the canopy was closed, but in 1975 when the canopy was still relatively open.

earlier for the floor of four amakihi nests, one of which was from Kauai (Whittow and Berger 1977; our h_f averaged 5.37 W m^{-2} °C^{-1}). The walls leaked heat only slightly more readily (by a factor of 1.14) than the floor of the nest, which is not surprising since the two had about the same thickness (Table 3).

The average h_f of 13 nests with and without their liners was 4.77 and 7.53 W m^{-2} °C^{-1}, respectively. Hence, the liner (averaging 3.76 g or 35.6% of the nest's mass) reduced the rate of heat loss from the nest by 36.6%. This saving was not a simple function of the liner's size since there was no significant correlation between the percent reduction of heat loss when the liner was present and the percent of the nest's mass constituted by the liner.

Thirty-nine nests from Mauna Kea had a thermal conductivity that averaged 0.069 ± 0.003 W m^{-1} °C^{-1}. In other words, the nest's thermal properties are intermediate to those of wood ($k = 0.048$–0.159 W m^{-1} °C^{-1}) and animal fur ($k = 0.037$ W m^{-1} °C^{-1}; Weast 1975).

NEST INSULATION AS A FUNCTION
OF ELEVATION

We were able to examine altitudinal differences in nests collected on Mauna Kea during 1973 because we had a large sample (23) from 11 different elevations between 1,615 and 2,377

m above sea level. Our samples for other years were too limited for such analyses. Moreover, we did not think it justifiable to combine years for analysis because marked annual variations in rainfall could have affected this honeycreeper's building behavior and the resulting thermal quality of its nests. For example, 1973 was an unusually dry year and almost no rain fell at Puu Laau during the peak of the breeding season (van Riper 1980).

We found no significant changes in the mass or morphology of the 1973 nests in relation to elevation. However, h_{wf} diminished significantly with increasing altitude ($r = -0.43, P < 0.05$, 21 df); i.e., nests from higher elevations had more insulation than those from lower elevations. Although much anecdotal evidence suggests that such gradients exist in birds' nests (reviewed by Collias 1964, Drent 1975), to our knowledge this is the first time that such a gradient has been described in quantitative physical terms.

The coefficient for determination (r^2) for the 1973 data indicated that differences in elevation accounted for about 18% of the variation in the thermal properties of the nests. The elevational gradient was apparently due to differences in the wall of these nests, rather than their floors, since (1) h_w was more strongly correlated with elevation ($r = -0.49, P < 0.02$, 21 df) than h_{wf}, and (2) h_w was not significantly
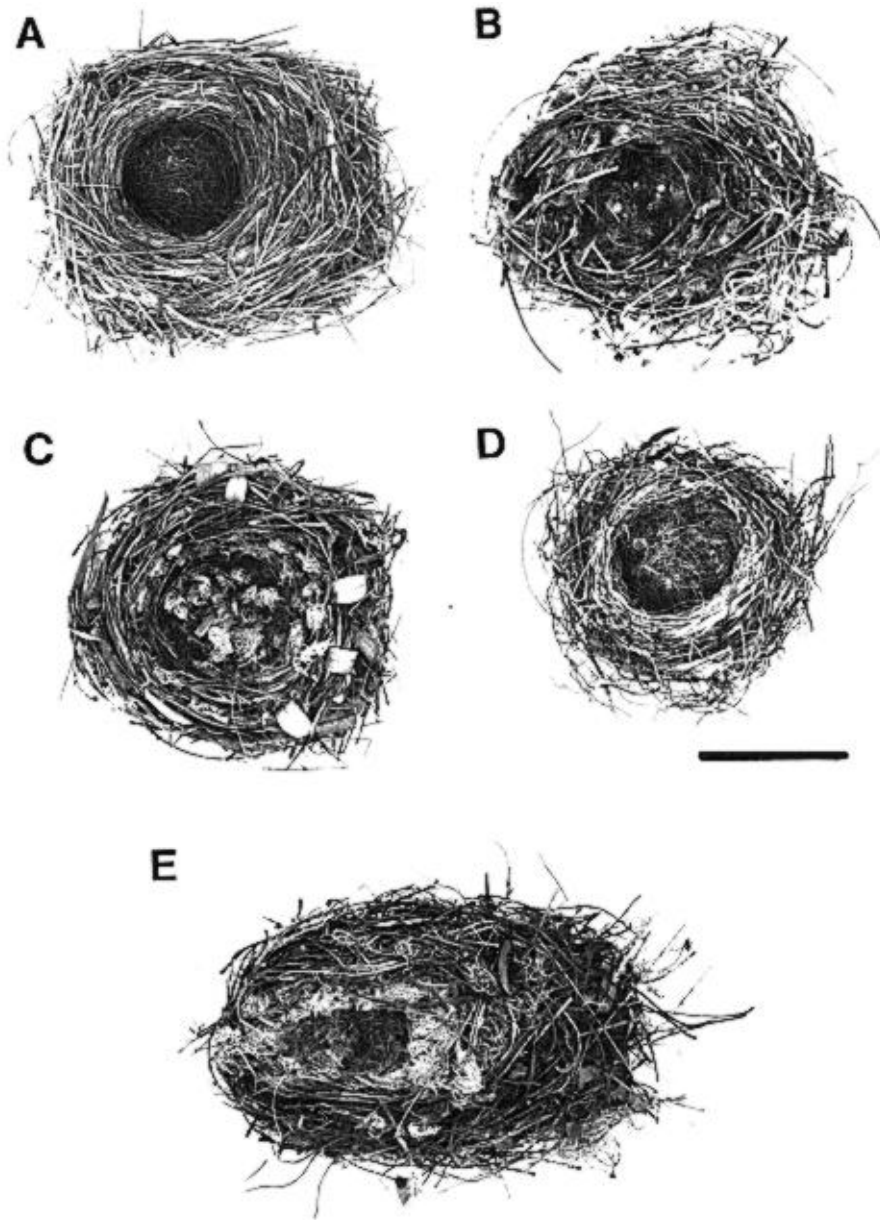
FIGURE 3. Nests of the Common Amakihi: A, rootlet type; B, wool type; C, lichen-rootlet type; D, Kohala type; E, lichen type. The scale line represents 6 cm.

correlated with elevation ($r = 0.04$, $P > 0.50$, 21 df). However, the gradient was not a simple function of the wall's thickness ($r = 0.12$) or height ($r = -0.06$). Rather, it appeared to be related to the porosity or size of the air spaces in the walls since significantly less light penetrated the wall (but not the floor) of the nest at higher elevations (% P_{light} vs. elevation: $r = -0.66$, $P < 0.005$, 15 df). Our data suggest, therefore, that the walls of the nest were more tightly woven at higher elevations and that this, rather than changes in nest size, accounted for the nest's greater insulation there.

NEST DENSITY

The amount of light that penetrated the walls and floor of the amakihi's nest (% P_{light}) averaged 0.33% (range: 0.00–4.84%) and 0.03% (range: 0.00–0.14%; $n = 46$ nests), respectively, and did not differ significantly among nest types. The area of photographic paper exposed by light passing through the nests' walls and floor (% $A_{exposed}$) averaged 29.64% (range: 0.00–85.14%) and 5.65% (range: 1.20–13.53%, $n = 42$ nests), respectively. The walls of all five types of nest admitted similar amounts of light

TABLE 2. Materials used by amakihi in 15 lichen-type nests from Mauna Kea, Hawaii. Values of mass in the table are $\bar{x} \pm CI_{95}$. T = trace.

	Total mass (g)		Nest material							
		Lythrum maritimum	Grasses	Sophora chrysophylla	Rootlets	Lichens (Usnea sp.)	Gnaphalium japonicum	Sheep's wool	Pig's hair	Feathers
Outer frame[a]										
Mass (g)	6.50 ± 0.72	0.79 ± 0.60	3.32 ± 0.46	0.75 ± 0.42	0.38 ± 0.33	0.61 ± 0.30	0.13 ± 0.17	0.17 ± 0.25	T	T
Range of mass (g)	4.96–8.79	0.00–4.31	1.26–4.82	0.05–2.42	T–2.36	T–2.03	0.00–1.04	0.00–1.56	...	...
% of frame's mass	...	12.0	52.1	12.2	5.2	9.4	1.9	2.5	...	...
Lining of nest cup[a]										
Mass (g)	3.56 ± 0.88	T	0.81 ± 0.27	0.08 ± 0.12	0.43 ± 0.32	2.06 ± 0.66	0.02 ± 0.03	0.02 ± 0.03	...	...
Range of mass (g)	1.04–6.66	...	0.08–1.83	0.00–0.86	T–2.14	0.06–4.38	0.00–0.22	0.00–0.20	...	...
% of lining's mass	...	...	53.9	2.0	12.8	54.8	0.02	1.1	...	...
Whole nest										
Mass (g)	10.06 ± 1.14	0.79 ± 0.60	4.13 ± 0.60	0.77 ± 0.36	0.81 ± 0.55	2.67 ± 0.84	0.15 ± 0.17	0.20 ± 0.27	T	T
Range of mass (g)	6.90–14.24	0.00–4.31	1.61–5.56	0.05–2.44	T–2.97	0.06–5.65	0.00–1.04	0.00–1.76	...	...
% of nest's mass	...	8.1	41.4	9.4	7.3	26.0	1.4	2.1	...	...
Nests containing item		12	15	15	15	15	5	4	5	2
Frames containing item		12	15	15	15	15	4	4	3	0
Linings containing item		1	15	9	15	15	2	4	4	2

[a] In terms of mass, the outer frame was on average 65.5% of the entire nest; the lining 34.5% of it.

into the nest cup, but the floor of the Kohala type allowed in significantly ($P < 0.001$) more (10.4%) than did the floor of the other nests, which did not differ significantly among themselves (means ranging from 4.0 to 5.8%).

The walls and floor of the nest blocked out 97.40% (range: 86.67–99.67%) and 98.71% (range: 84.03–99.87%, $n = 42$ nests), respectively, of the airstreams to which they were exposed. All five nest types were equally effective in this regard.

In summary, our measurements revealed that the walls and floor of the nests were dense enough to act as effective windscreens, but still had spaces large enough to allow light to penetrate. The floor and wall differed by ratios of 1:11, 1:5.35, and 1:1.01 for % P_{light}, % $A_{exposed}$, and % P_{air}, respectively.

RATE OF DRYING OF NESTS

Amakihi nests dried at an exponential rate (i.e., in log-linear fashion; the distribution of points around the decay curve was very tight, r values ranging between -0.92 and -0.99 [13–14 df] depending on the nest). The actual rate of drying, $(\log M_2 - \log M_1)/(t_2 - t_1)$, in which M_1 and M_2 are the nest's masses at times t_1 and t_2, respectively, averaged -0.001222 g min^{-1}. Nests were 80% dry after 5.4–18.6 h. Those of the lichen type dried significantly ($P < 0.025$) more slowly than the others: they required 11.9 ± 3.0 h ($n = 7$) to dry by 80%, whereas other types required only 8.0 ± 0.4 h ($n = 23$).

DISCUSSION

NEST COMPOSITION

The five types of nests that Common Amakihi fabricate may be phenotypic expressions of genetic differences in the behavior of individual birds or populations that are broadly sympatric on Mauna Kea (Fig. 3). More likely, however, the birds simply use materials that are pliable and readily available. Van Riper (1978), for example, found that most items in amakihi nests were collected within a pair's territory. The latter explanation for differences among the nests is also consistent with differences between the Kohala type and the others. Kohala type nests do not contain mamane parts, although the latter are common in other types of nests (Table 2). Mamane trees do not occur in the mesic forest on Kohala Mountain, but they and naio are the dominant tree species around Puu Laau (van Riper 1980). The wool type of nest was restricted to high elevations on Mauna Kea, which is not surprising since sheep populated the uplands of this volcano until recently (van Riper and van Riper 1982). However, amakihi decidedly prefer wool and
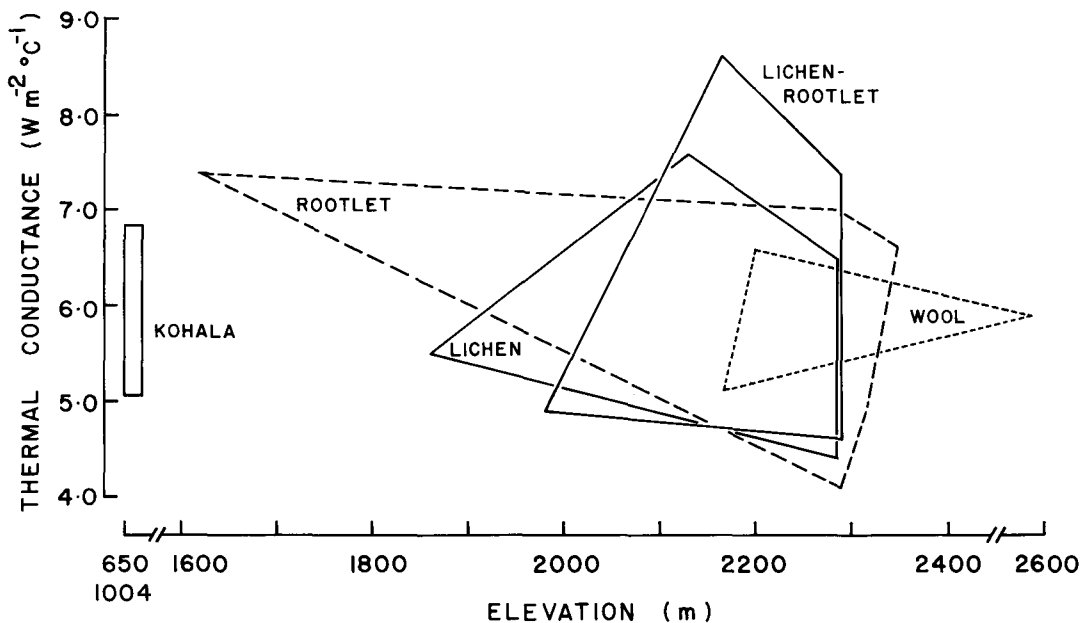
FIGURE 4. Distribution and thermal conductance of five types of nests built by Common Amakihi on the Island of Hawaii.

will travel beyond their territorial limits to get it (van Riper 1977).

Judging from the similarities in thermal conductance among the five nest types (Table 3), van Riper (1977) was probably correct in suggesting that amakihi seek out sheep's wool for its lightness and binding qualities, rather than its insulation value. However, given the ability of these nests to stop airstreams and block the passage of light, we were surprised at how rapidly they dried after being saturated with water. They would probably not dry quite as rapidly in the field because ambient humidity there (at least on Kohala Mountain) is considerably higher than the 20–52% that we used in our experiment. Nonetheless, the nests do dry rapidly, a property with probable selection value even on Mauna Kea—since amakihi commonly nest there during the wet season—and certainly on Kohala Mountain, where heavy downpours drench the forest during the peak of breeding. The particularly porous floor of the Kohala type nest and the near absence of *Usnea* in its cup must collectively permit nests of this type to dry very rapidly under such moist conditions.

It is also probably no accident that lichen type nests were found only on Mauna Kea, since they dried slowly and had small values of *h*. Moreover, the nests were nearer the edge of the canopy at high elevations there, although still well protected by the canopy (Table 1). The relatively light rainfall at Puu Laau, coupled with the placement of the nest where it might benefit from the radiant energy of the

sun and yet be protected from rain, may permit amakihi to use lichen in the nest cup for insulation without exposing their eggs to potentially lethal amounts of moisture.

One reason for the Common Amakihi's success in such a diverse spectrum of habitats in Hawaii may therefore be its ability to alter the insulative quality of its nest to fit the environmental situation in which it breeds. The bird selects readily available nesting materials, but the pieces are pliable so that in colder areas the nest's walls can be more tightly woven, thus increasing the structure's insulative quality. This presumably enables the female to transfer more metabolic heat to the eggs than would otherwise be possible.

USING NESTS TO PREDICT THE ENERGY REQUIRED TO INCUBATE A CLUTCH OF EGGS

The overall thermal conductance (h_{wf}) of a nest can be used to estimate the energy required to keep a clutch of eggs at incubation temperature, just as eggs have been used in the past (Kendeigh 1973). In so doing, we make the assumption that to keep the temperature of a clutch of eggs constant, the incubating bird must produce heat (via metabolism) and add it to the eggs at a rate ($\dot{H}_p$, in W) that equals the rate of heat loss from the clutch ($\dot{H}_L$, in W; Fig. 5). Consequently, by determining the rate of heat loss from a nest, we simultaneously measure the energetic cost of keeping the eggs warm.

Heat is lost from the clutch through an area

TABLE 3. Characteristics of amakihi nests and nest sites. Values in the table are $\bar{x} \pm CI_{95}$. Numbers in parentheses are sample sizes that differ from those listed in the column designated "n."

Island and nest type	n	Characteristics of nest site			Thermal conductance of nest (W m⁻² °C⁻¹)		
		Height of nest tree (m)	Height of nest (m)	Distance of nest from tree's center (cm)	Wall	Floor	Overall[a]
Hawaii							
Lichen	16	6.95 ± 0.73 (15)	4.36 ± 0.45 (15)	66.50 ± 20.05 (11)	5.75 ± 0.81	5.29 ± 0.73	5.53 ± 0.50
Rootlet	15	6.49 ± 0.84 (10)	4.78 ± 0.51 (11)	97.03 ± 32.60 (10)	6.33 ± 0.85	5.48 ± 0.66	5.91 ± 0.48
Lichen-rootlet	11	6.77 ± 1.20 (10)	5.41 ± 1.47 (10)	90.80 ± 35.10 (8)	6.50 ± 1.47	5.31 ± 0.49	5.93 ± 0.81
Wool	5	5.18 (1)	5.18 (1)	17.78 (1)	6.01 ± 2.08	5.39 ± 1.52	5.70 ± 0.74
Kohala	5	11.22 ± 1.61	8.35 ± 3.78	24.13 ± 6.86	6.48 ± 1.72	5.36 ± 0.90	5.92 ± 0.99
Combined	52	6.88 ± 0.55 (41)	4.98 ± 0.57 (42)	79.72 ± 15.36 (35)	6.17 ± 0.46	5.37 ± 0.30	5.78 ± 0.26
Kauai[b]	5	...	5.64 (23)	...	...	...	...
Hawaii and Kauai[c]	4	...	4.15[d] (60)[d]	...	...	4.14	...

[a] Overall thermal conductance (h_{wf}) = average for values of thermal conductance of wall and floor.
[b] Data for the subspecies H. v. stejnegeri (Eddinger 1970).
[c] Data for the subspecies H. v. virens and H. v. stejnegeri (Whittow and Berger 1977).
[d] Data for the subspecies H. v. virens (Berger 1981).

TABLE 4. Mass, dimensions, and area of various types of amakihi nests. Values in the tables are $\bar{x} \pm CI_{95}$. Numbers in brackets were derived from other dimensions of the nest.

Island and nest type	n	Mass of nest (g)	Dimensions of the nest (cm)						Surface area of nest cavity (cm²)
			Inner diameter	Outer diameter	Height	Depth	Thickness of floor	Thickness of walls	
Hawaii									
Lichen	16	20.5 ± 3.5	5.06 ± 0.23	11.37 ± 0.68	5.84 ± 0.45	2.54 ± 0.26	3.16 ± 0.38	2.94 ± 0.34	39.5 ± 3.2
Rootlet	15	13.8 ± 3.2	5.10 ± 0.26	11.03 ± 0.79	5.46 ± 0.62	2.55 ± 0.28	2.65 ± 0.43	2.64 ± 0.21	40.2 ± 2.8
Lichen-rootlet	11	16.4 ± 4.0	5.37 ± 0.36	11.42 ± 0.71	5.42 ± 0.78	2.47 ± 0.51	2.70 ± 0.60	2.92 ± 0.38	42.0 ± 3.7
Wool	5	15.8 ± 3.0	5.00 ± 0.36	10.90 ± 1.03	6.66 ± 4.47	2.76 ± 1.22	4.48 ± 6.08	2.80 ± 0.33	41.3 ± 15.5
Kohala	5	15.4 ± 3.3	4.66 ± 0.67	11.27 ± 1.64	5.62 ± 0.64	2.72 ± 0.58	2.64 ± 0.58	2.72 ± 0.64	44.9 ± 18.5
Combined	52	16.9 ± 1.7	5.09 ± 0.14	11.23 ± 0.34	5.70 ± 0.40	2.57 ± 0.16	2.99 ± 0.46	2.82 ± 0.14	40.9 ± 2.1
Kauai[b]	5	...	6.35	11.43	6.35	3.81	[2.54]	2.54[a]	...
Hawaii and Kauai[c]	4	...	5.32	[7.45]	[6.98]	3.50	3.48	2.12[a]	...

[a] Thickness of the wall at the rim of the nest.
[b] Data for the subspecies H. v. stejnegeri (Eddinger 1970).
[c] Data for the subspecies H. v. virens and H. v. stejnegeri (Whittow and Berger 1977).

of the nest cup that equals the area of it occupied by the eggs. We make a second assumption here that this area is roughly the same as the area of the bird's brood patch (A_{bp}, in cm^2). If we then know the temperature of the nest cup under the eggs (T_n, in °C) and the temperature on the outside of the nest directly opposite (roughly equal to ambient temperature, T_a, in °C), h_{wf} of the nest (in W m^{-2} °C^{-1}) specifies $\dot{H}_L$ for the amount of time the bird is on the nest daily (t_n, expressed as a percent of 24 h).

Since the female is occasionally absent from the nest during the day, we need to include whatever heat she produces to rewarm the clutch daily, which is the heat added to rewarm eggs after each absence ($\dot{H}_R$, in W) × the number of absences per day (t_r).

Accordingly, in mathematical terms (also see Fig. 5), the *total* daily cost in incubation is

$$\dot{H}_P = \dot{H}_L = (h_{wf})(A_{bp})(T_n - T_a)(t_n) + (\dot{H}_R)(t_r) \quad (1).$$

If amakihi are like other songbirds, the brood patch occupies about 10% of their skin surface (Walsberg and King 1978, Kern and Coruzzi 1979). We can calculate an amakihi's surface area (A_{skin}) using Meeh's equation that relates it to mass (M): $A_{skin} = 10M^{0.667}$ (Drent and Stonehouse 1971). The average mass of a female amakihi is 13.4 g (van Riper 1978). Hence, $A_{skin} = 56.5$ cm^2 and $A_{bp} = 5.65$ cm^2. Whittow and Berger (1977) indicated that 12.5 cm^2 is roughly the area of the nest cup in contact with the eggs and incubating amakihi. We use the smaller value because this is the area through which heat enters the clutch.

Nest temperature has not been measured for the amakihi, and depends on the insulation of the nest and T_a (Kendeigh 1963). However, the average T_n for 11 small passerines is 33.6°C (Drent 1975) and we have used this value in estimating this honeycreeper's incubation costs.

The average minimal and maximal T_as that an incubating female experiences at Puu Laau at 2,290 m elevation during peak breeding months (March–May) are 0.4 and 21.3°C, respectively (based on data for 1973–1975 in van Riper [1980]). Our model estimates only the *minimal* and *maximal* energy expended for incubation daily since we use values of T_a representing the lowest and highest likely experienced by an incubating amakihi. Her actual energetic costs should lie between these extremes.

Nest attentiveness varies during the incubation period (van Riper 1978), the female sitting on the eggs 55–88% of the day (except on day 0 of incubation when her attendance is only 15%). We averaged her attendance for
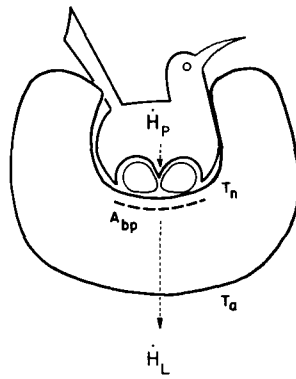
$$\dot{H}_P = \dot{H}_L = (h_{wf})(A_{bp})(T_n - T_a)(t_n) + (\dot{H}_R)(t_r)$$

FIGURE 5. Information about the thermal properties of a bird's nest permits one to estimate the energetic cost of incubating a clutch of eggs. In order for a female amakihi to keep her eggs at a temperature appropriate for embryonic development, she must add heat to them at a rate ($\dot{H}_P$) equal to the rate at which they lose heat ($\dot{H}_L$). The latter depends on the thermal conductance of the nest (h_{wf}), the area of the nest cup occupied by the eggs (A_{bp}), the difference between nest temperature (T_n) and ambient temperature (T_a), and the amount of time the female is on the nest daily (t_n). Her energetic expense also includes the heat required to rewarm the eggs ($\dot{H}_R$) following her absences from the nest (t_r is the number of times she leaves the nest each day).

days 1–14 of incubation to obtain the value 73.4% for use with equation (1).

Eddinger (1970) found that incubating female amakihi on the Island of Kauai left their nests for periods of 3–4 min and were away from them 24 min of each 3–4 h period of daylight. At most then, they were absent eight times in a 3-h period. Van Riper's unpublished observations of incubating amakihi on the Island of Hawaii indicate that they leave the nest an average of 1.88 times per hour during the day (females incubate continuously at night). Since daylength on the Island of Hawaii during March–May is about 12 h (Ruffner 1978), the female is away from her nest 23 (according to van Riper) to 32 (according to Eddinger) times daily, and must rewarm her clutch on each return.

The rate at which eggs cool when amakihi leave the nest is also unknown, but those of seven passerines cool 4–8°C when unattended (unpubl. obs. of C. Vleck, see Walsberg and King 1978). We assume a decrease of 6°C. Ricklefs (1974) estimated that 3.3 J g^{-1} °C^{-1} are required to reheat an egg. Clutches of two or three eggs are the most common for *H. virens* (Eddinger 1970, van Riper 1978, Berger 1981). The fresh mass of an amakihi's egg is 1.60 g (range: 1.25–1.90 g; $n = 21$ eggs; van Riper, unpubl. data). Hence, 63 and 95 J are

required to reheat 2- or 3-egg clutches, respectively, to incubation temperature each time the female returns to the nest. (Our model neglects the metabolic heat produced by embryonic chicks late in the incubation period.)

Substituting the above values into equation (1), we calculate that a female Common Amakihi spends energy at the rate of 0.046–0.096 W to keep a 2-egg clutch at incubation temperature if she is absent 23 times daily; 0.053–0.103 W if absent 32 times daily. If she leaves 23 times, her caloric expense is 19–40% of her metabolic rate during the rest phase of the day (MR_r) which we obtained from her mass (M) using the equation $(MR_r) = 114.8M^{0.726}$ (Aschoff and Pohl 1970), MR_r being in kcal day^{-1} and M in kg (this transforms to 0.243 W for a 13.4-g female amakihi). On the other hand, if she is gone 32 times a day, her incubation cost is 22–42% MR_r.

For 3-egg clutches, amakihi expend somewhat more energy: 0.055–0.105 W or 23–43% MR_r if the number of absences is 23 per day; 0.065–0.115 W or 27–47% MR_r if the number is 32 per day.

These estimates may be too low since Macmillen (1981) showed that the amakihi's MR during the time of day when it is active is only 74.1% of the value predicted by the equation of Aschoff and Pohl (1970). If the MR_r of Common Amakihi is also 74.1% of the predicted 0.243 W, then keeping a 2-egg clutch warm requires energy equivalent to 26–53 or 29–57% MR_r, depending on whether the female leaves the nest 23 or 32 times daily. For 3-egg clutches, energetic costs increase to 31–58 and 36–64% MR_r under the same conditions.

Our estimates, based on the thermal properties of the nest, are equivalent to or somewhat higher than those reported for other small songbirds and based on properties of eggs or direct measurements of oxygen consumption during incubation: 10–22% MR_r for House Wrens (*Troglodytes aedon*; Kendeigh 1963), 21–37% for Zebra Finches (*Poephila guttata*; Vleck 1981), and 62–68% for Great Tits (*Parus major*; Mertens 1977).

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