TEMPERATURE REGULATION IN TWO ENDANGERED HAWAIIAN HONEYCREEPERS: THE PALILA (*PSITTIROSTRA BAILLEUI*) AND THE LAYSAN FINCH (*PSITTIROSTRA CANTANS*)

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ABSTRACT.—The closely related, morphologically similar Palila (*Psittirostra baileui*) and Laysan Finch (*P. cantans*) are natives of thermally dissimilar habitats. The 34.8-g Palila is confined to the cool, montane forests of Hawaii Island, whereas the 31-g Laysan Finch is restricted to a low, treeless atoll. To study their climatic adaptation, we measured their body temperature, oxygen consumption, and evaporative water loss at stable air temperatures between 3 and 40°C. Bioenergetically, these species are most distinct in their response to heat. The Palila's upper critical temperature (31°C) is 7°C lower than the Laysan Finch's, and its heat-strain coefficient is 31% higher (1.76 versus 1.34 mW·g^{-1}·°C^{-1}). The Palila is much less heat tolerant than the Laysan Finch (which, in its heat tolerance, resembles other passerines). Consequently, the Palila probably is restricted physiologically to cool, mountain forests and is not a suitable candidate for lowland introductions. The Palila's lower critical temperature (17.5°C), thermal conductance (0.612 mW·g^{-1}·°C^{-1}), and nighttime basal metabolic rate (BMRρ) (12.87 mW/g) were all within 8% of levels predicted from mass, indicating that its cold tolerance is not unusual for a passerine of its size. The Laysan Finch's BMRα averaged 15.2 mW/g H$_2$O/day, 80% of the value predicted from mass. Its evaporative water loss ($\dot{m}_{we}$) also was lower than expected, 2.22 versus 3.31 g H$_2$O/day. Reductions in BMR and $\dot{m}_{we}$ have adaptive value for small birds living in waterless environments. *Received 4 January 1982, accepted 12 March 1982.*

CLIMATE can affect birds directly (i.e. physiologically), through its impact on energy and water balance, and/or indirectly (i.e. ecologically), through its influence on vegetation and food availability. Birds exhibit a remarkable degree of physiological adjustment to differing climates, and, except for truly extreme environments such as hot, waterless deserts or the frigid Arctic, they are thought to be limited most often by the effect of climate on vegetation structure and food availability (Dawson and Bartholomew 1968). Nevertheless, significant thermoregulatory differences do exist in similar species from dissimilar climates (Dawson 1954, Wallgren 1954, Hudson and Kimzey 1966, Rising 1969, Blem 1974, Hinds and Calder 1973, Hayworth 1980). These findings, together with the fact that avian basal metabolic rate (BMR) is climatically adaptive (Weathers 1979), suggest that physiological capacity may play a greater role in determining bird distribution than is generally believed. Further thermoregulatory studies of closely related species from differing climates are needed to resolve this issue.

The Laysan Finch (*Psittirostra cantans*) and Palila (*P. baileui*) are finch-billed members of the endemic Hawaiian honeycreeper family Drepanididae. Closely related, they share many physical, myological, and osteological traits (Raikow 1977, Pratt 1979), but occupy quite different habitats. The Laysan Finch is restricted to Laysan Island (25°N), a treeless atoll whose highest point is 5 m above sea level. Laysan Island contains a hypersaline lake but no standing fresh water. Its landscape is dominated by clumps of bunch grass, in which Laysan Finches nest, and intervening patches of bare sand. The Laysan Finch's diet—insects, seeds, flower buds, and birds' eggs (Berger

1972)—and the open terrain that it inhabits suggest that it is often subjected to direct solar radiation while foraging.

The Palila is restricted to Hawaii Island (20°N), where it occupies fairly dry mamane (*Sophora chrysophylla*) and mamane-naio (*Myoporum sandwicense*) forests on Mauna Kea volcano (see van Riper 1980a for a description of the habitat). Its range has contracted greatly since 1900 (van Riper et al. 1978), and it is currently restricted to Mauna Kea's higher forests, from treeline (2,900 m elevation) down-mountain to about 2,000 m. Historically, the Palila occurred at somewhat lower elevations (down to 1,220 m, Perkins 1903), but it is essentially a montane bird. It feeds extensively on mamane seed pods, using its powerful bill to tear open the pods and extract the seeds (van Riper 1980b). While feeding, the Palila is often shaded from the sun by the mamane tree canopy.

Weathers (1977, 1979) pointed out that BMR often is reduced in tropical birds that forage in the sun but is normal in shade-foraging species. Because little of the heat gained by sun-foraging, lowland, tropical birds can be dissipated by evaporation (owing to high ambient humidity), possessing a reduced BMR increases the time available for foraging. Hence, thermal influences—high heat load coupled with reduced evaporative capacity—act as selective forces favoring a reduced BMR in these birds. Shade-foraging tropical birds do not confront exogenous thermal loads and thus do not require reduced BMRs. Nevertheless, BMR is reduced in some shade-foraging species. For example, MacMillen (1981) found that the BMR of four Hawaiian honeycreeper species departs from the usual mass dependency (i.e. BMR was not proportional to mass$^{3/4}$), with shade-foraging species having lower than expected BMRs. The selective forces operating in this case were the species' social position in an interspecific dominance hierarchy and their relative success at nectar exploitation.

Unlike the honeycreepers that MacMillen studied, the Palila and Laysan Finch do not compete for food and are not members of a dominance hierarchy. Because they inhabit quite different thermal environments and experience different solar heat loads while foraging, they provide an opportunity to test further the hypothesis that, in the absence of competitive interactions, thermal influences will constrain avian BMR. Furthermore, both species are currently listed as endangered by the U.S. Fish and Wildlife Service (1976), and it is imperative that resource managers have an adequate data base upon which to base their preservation strategies.

METHODS

We studied four male Palilas and 12 Laysan Finches (mixed sexes) during November and December 1980 at the Hawaii Field Research Center (elev. 1,220 m), Hawaii Volcanoes National Park. The birds had been held in flight cages at the park for approximately 1 yr. The roofed cages provided protection from the frequent rains but exposed the birds to prevailing temperatures and photoperiods. In body mass, Palilas ranged from 33.5 to 40.0 g (mean = 36.0 ± 1.6 SD), Laysan Finches from 24.4 to 37.9 g (mean = 32.8 ± 3.6 SD).

Rates of oxygen consumption ($\dot{V}O_2$) and evaporative water loss ($\dot{m}_{we}$) were determined on postabsorptive birds that had been in darkened 4-l metabolism chambers for at least 1 h. Each chamber was equipped with a thermistor probe, perch, hardware cloth floor, and mineral oil trap for urine and feces. Temperature control was attained by submerging the chamber in a water bath. Rates of $\dot{V}O_2$ were calculated by equation 2 of Hill (1972) from the fractional O_2 concentration change in dry, CO_2-free inlet and outlet airstreams, as measured (to the nearest 0.005%) with an Applied Electrochemistry S-3A O_2 analyzer (N-22M sensor). Oxygen concentration was monitored with a Heath/Schlumberger recorder. Chamber air flow rate was kept constant at between 470 and 600 cm^3/min (STPD), when air temperature (T_a) was less than 35°C, and at 950 cm^3/min (STPD), when T_a was greater than 35°C. Chamber air-flow rate was measured with upstream Matheson rotameters (603 tube). Rotameters were calibrated against Brooks Mass Flow Meters (NBS traceable). Because the "perfect" gas laws alone do not correct rotameter flows measured at reduced pressures, we corrected indicated air flow rates to standard conditions (STPD) using viscosity factor data provided by Matheson. Body temperature (intestinal) was determined immediately after the metabolic run with a YSI telethermometer (Series 511 probe), which was calibrated against a NBS thermometer. Rates of $\dot{m}_{we}$ were determined by collecting water vapor from the downstream airline with a series of three drierite-filled U-tubes.

Our initial metabolism measurements were made during the rest phase (ρ) of the circadian cycle. Comparing the two species' results was confounded, however, by their differing response to the measurement apparatus. Palilas readily accepted confinement in the metabolism chamber and typically slept during the metabolic determinations. Most
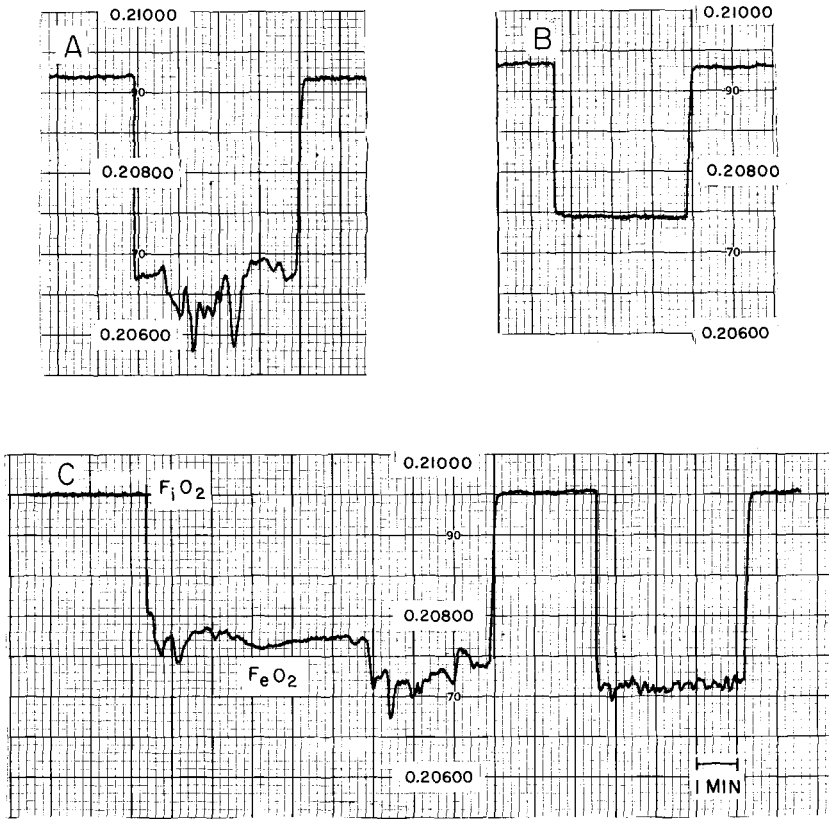
Fig. 1. Representative fractional O_2 concentration records obtained during metabolism measurements. Contrast the records for an active (A) and sleeping (B) Palila with comparable Laysan Finch records (C). F_iO_2 = O_2 concentration in air upstream from the metabolism chamber; F_eO_2 = O_2 concentration in downstream air.

Laysan Finches, in contrast, tended to remain awake and active, even after 9 h in the chambers. This made it difficult to obtain truly basal metabolic rates for the Laysan Finches. Figure 1 illustrates the two species' differing responses to rest-phase determinations. The O_2 trace of an active Palila (Fig. 1A), recorded less than 1 h after the bird was placed in the metabolism chamber, exhibits the widely fluctuating O_2 concentration typical of an active animal. In contrast, a flat O_2 record was typical of sleeping Palilas (Fig. 1B). Figure 1C presents strip-chart records for two Laysan Finches. The left trace represents an obviously active animal, the right-hand trace a seemingly quiescent bird. Note, however, that the quiescent Laysan Finch record exhibits considerable "noise," unlike the flat trace of the sleeping Palila (Fig. 1B). This "noise" indicates minor postural adjustments typical of awake birds. Obviously, Laysan Finches were remaining active during the "rest" phase of the circadian cycle. To avoid this confounding variable, we altered our protocol and measured Laysan Finches during the active phase (α) of the circadian cycle, when birds are normally awake and/or active.

An unanticipated problem arose during this study. The U.S. Fish and Wildlife Service abruptly transferred the Palilas to the Honolulu Zoo before we completed our studies. This accounts for the paucity of low-temperature Palila data.

RESULTS

Figure 2 presents values for the Laysan Finch's metabolic heat production ($\dot{H}_m$) and body temperature (T_b) measured at different temperatures. The Laysan Finch's thermoneutral zone extended from 23.5 to approximately 36.5°C. Within this zone, T_b increased an average of 0.75°C. The least squares regression equation for $\dot{H}_m$ as a function of T_a below 25°C is $\dot{H}_m$ (mW/g) = 28.46 − 0.54T_a (r^2 = 0.777,
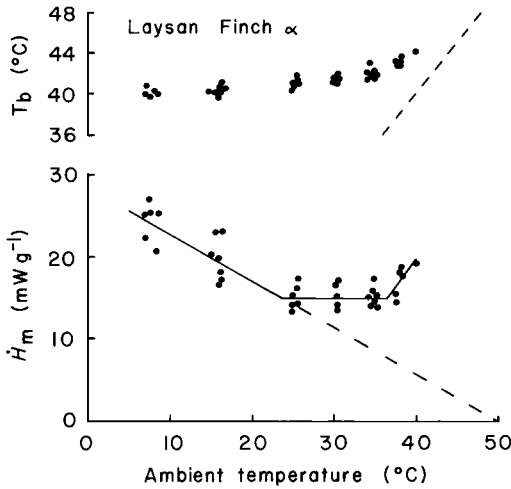
Fig. 2.　Relation of body temperature (T_b) (above) and metabolic heat production ($\dot{H}_m$) (below) of post-absorptive Laysan Finches to ambient temperature. Measurements made during the active phase of the circadian cycle. Dashed line represents $T_b = T_a$. Solid lines were fitted to $\dot{H}_m$ data by the method of least squares.
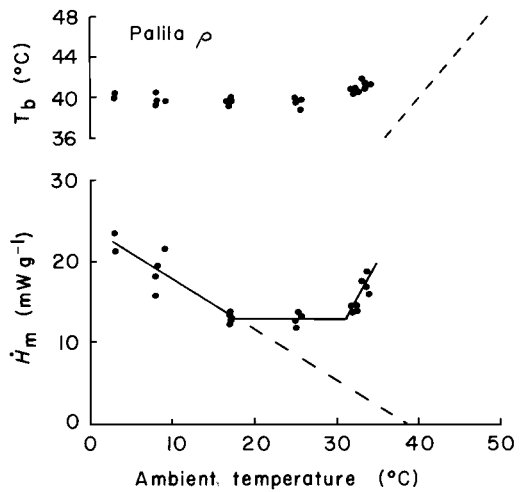

Fig. 3.　Relation of body temperature (T_b) (above) and metabolic heat production ($\dot{H}_m$) (below) of post-absorptive Palilas to ambient temperature. Measurements made during the rest phase of the circadian cycle. Dashed line represents $T_b = T_a$. Solid lines were fitted to $\dot{H}_m$ data by the method of least squares.

$S_{y \cdot x} = 2.121$, $S_b = 0.070$, $n = 19$). Note that this line, fitted to the low temperature $\dot{H}_m$ data in Fig. 2, does not extrapolate to $\dot{H}_m = 0$ at $T_a = T_b$. By statistically forcing the line through $\dot{H}_m = 0$ at 41°C, the equation becomes $\dot{H}_m = 30.90 - 0.75T_a$. The least squares regression equation for $\dot{H}_m$ above 36°C is $\dot{H}_m = 1.34T_a - 34.07$ ($r^2 = 0.390$, $n = 6$). The correlation coefficient (r) for this relation is not statistically significant ($P > 0.05$), however. Consequently, the apparent upper critical temperature ($T_{uc} = 36.5°C$) is unreliable. Values of $\dot{H}_m$ determined at 38°C are not significantly higher than those determined at 35°C ($P < 0.10$, Mann-Whitney U-test), indicating that the Laysan Finch's T_{uc} probably exceeds 38°C. Because of the Laysan Finch's activity during metabolic determinations, $\dot{H}_m$ measurements at high T_a's involved a large risk. We chose not to risk killing any Laysan Finches rather than to try and refine the T_{uc} estimate.

Figure 3 presents $\dot{H}_m$ and T_b values for Palilas measured at various temperatures. The Palila's thermoneutral zone extends from 17.5 to 31.0°C. Within this zone, T_b remained constant and averaged 39.4°C. The least squares regression equation for $\dot{H}_m$ as a function of T_a below 18°C is $\dot{H}_m$ (mW/g) $= 23.92 - 0.61T_a$ ($r^2 = 0.38$, $n = 6$). The correlation coefficient for this relation

is not statistically significant. (We described above the unfortunate circumstances surrounding our limited low temperature Palila data.) Note, however, that this line does extrapolate to $\dot{H}_m = 0$ at $T_a = T_b$ and that the lack of a significant correlation between $\dot{H}_m$ and T_a results mainly from the scattered data at 8°C. Consequently, we believe this relation reasonably approximates the Palila's true metabolic response. The least squares regression equation for $\dot{H}_m$ above 31°C is $\dot{H}_m = 1.76T_a - 42.12$ ($r^2 = 0.52$, $n = 8$). The correlation coefficient (r) for this relation is statistically significant ($P < 0.05$).

Figure 4 presents the relation of evaporative heat loss ($\dot{H}_e$)—calculated from steady-state measurements of evaporative water loss—to T_a. The lines shown in Fig. 4 are the theoretical relations calculated from body mass by Calder and King's (1974) equation 56. At 25°C, Palila evaporative water loss average 3.92 mg·g^{-1}·h^{-1} versus 2.92 mg·g^{-1}·h^{-1} for the Laysan Finch. Evaporative water loss of Laysan Finches measured during the day (α) at 25°C averaged 3.83 mg·g^{-1}·h^{-1}.

Measuring $\dot{H}_m$, $\dot{H}_e$, and T_b simultaneously enables one to calculate the rate of dry heat transfer (h') between the animal and environment (see King and Farner 1961, Calder and
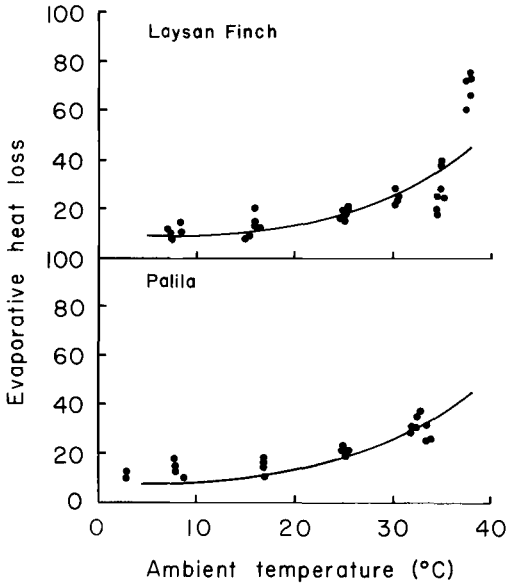
Fig. 4. Relation of evaporative heat loss (calculated from steady state water loss measurements) to ambient temperature. Curves represent relations predicted by Calder and King's (1974) equation 56.
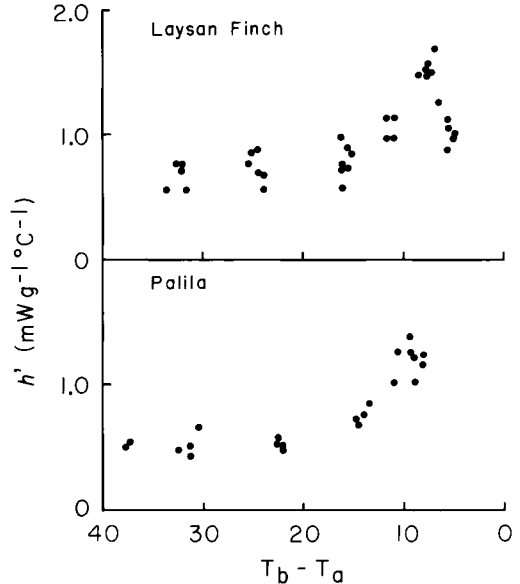

Fig. 5. Relation of the dry heat transfer coefficient, h' (dry conductance), to the difference between body and ambient temperature.

Schmidt-Nielsen 1967). Values of h' for the Palila and the Laysan Finch are presented in Fig. 5. At low air temperatures (i.e. $T_b - T_a > 20°C$), the Laysan Finch lost 35% more heat through nonevaporative pathways than the Palila (0.51 ± 0.05 versus 0.69 ± 0.10 mW·g^{-1}·$°C^{-1}$). This reflects the Laysan Finch's reduced rate of evaporative water loss. In both species, h' increased as T_a approached T_b (i.e. as $T_b - T_a$ approached zero). In the Laysan Finch, h' appeared to decrease when the $T_b - T_a$ gradient reached 5°C, indicating a decrease in the rate of heat lost by radiation, conduction, and convection.

Discussion

Quantitatively comparing the Palila and the Laysan Finch's native climates is difficult because data for Laysan Island are unavailable— the nearest weather station is on Midway Island, 265 km north and 600 km west of Laysan. Climatic data are available for the Palila's habitat (Puu Laau), however, and these are compared with data for Midway Island in Table 1. Assuming the climates of Midway and Laysan Island are similar (a reasonable assumption for these mid-oceanic islands), the Palila experiences cooler and drier conditions than those encountered by the Laysan Finch (Table 1). In terms of continental climates, the mean annual air temperature of Laysan Island equals that of Tampa, Florida, whereas that of Puu Laau is equivalent to that of Columbus, Ohio (Ruffner and Bair 1977). But unlike their continental counterparts, these oceanic islands exhibit little seasonal variation in air temperature. Nighttime air temperature at Puu Laau, for example, approaches freezing throughout the year, but maximum daytime temperatures rarely exceed 22°C (van Riper 1980a). Thus, the Palila experiences cool temperatures year round, unlike the birds of Columbus, Ohio.

Based on the climates to which they are exposed, we expected the Laysan Finch's BMR to be about 25% lower than predicted from its mass and the Palila's BMR to be normal or slightly elevated. The Laysan Finch's daytime BMR was indeed 20% lower than would be predicted for a 31-g passerine (Table 2). A reduction in metabolism of this magnitude would be expected in a sun-foraging, lowland, tropical bird (Weathers 1979) and confirms our hypothesis. Unlike daytime BMR, the Laysan

TABLE 1. Weather data for Midway Island and Puu Laau, Hawaii Island.

	Elevation (m)	Annual temperature (°C) mean (range)	Annual precipitation (mm)
Midway[a]	3	22.2 (9.5–31.5)[b]	1,080
Puu Laau[c]	2,290	11.2 (−5–29)[d]	603[e]

[a] Twenty-eight years of record (NOAA 1980).
[b] Range for 1980.
[c] Data from van Riper (1978, unpubl. obs.).
[d] Records for 1973–1975.
[e] Records for 1965–1974.

Finch's nighttime BMR is nearly normal (94% of predicted), reflecting the bird's activity during nighttime metabolic determinations. The Palila's BMR was 8% less than predicted. Apparently the Palila's cool habitat does not require an increase in BMR, such as that seen in many high-latitude birds (Weathers 1979).

Endotherm thermal adaptation manifests itself not only through variations in BMR, but through other thermoregulatory parameters as well, especially thermal conductance (h) and lower critical temperature (T_{lc}), both of which tend to be low in cold-climate species (Calder and King 1974). Table 3 presents these values, along with other observed thermoregulatory parameters, for the two honeycreeper species.

Thermal conductance.—The slope of the metabolism curve on air temperature equals conductance only when the curve extrapolates to body temperature (McNab 1980). Although the Laysan Finch's thermal conductance seems much lower than expected (Table 3), its curve does not extrapolate to T_b. Forcing the metabolism curve through T_b increases the Laysan Finch's thermal conductance but still leaves conductance 22% lower than predicted (Table 3). Low conductance, indicating high insulation, is considered adaptive in cold-climate birds. Lower than expected thermal conductance, however, is not restricted to cold climate birds: tropical birds with reduced BMRs also have low thermal conductances (Weathers 1977). As is obvious from equation 1 (below), when BMR is reduced there must be a corresponding reduction in thermal conductance if T_b is to remain normal. Because the Laysan Finch's T_b is normal, it would require a 20% reduction in conductance to compensate for its 20% lower BMR. The force-fit metabolism curve closely matches the expected reduction in conductance.

The Palila's thermal conductance does not deviate from the level predicted from body mass (Table 3). The predictive conductance equation is based largely on data for temperate species. As was the case for BMR, the Palila's thermal niche is not sufficiently cool to require an increase in insulation.

Lower critical temperature.—The Palila's T_{lc} is 6°C lower than the Laysan Finch's, a finding seemingly consistent with the difference in these species' native climates. But because T_{lc} is lower in larger birds, or when metabolism is measured during the rest phase of the circadian cycle (Calder and King 1974), we need to account for size and circadian-cycle effects before we can conclude that the difference in these species' T_{lc} reflects climatic adaptation.

TABLE 2. Observed and predicted basal metabolic rates of Hawaiian honeycreepers.[a]

	Mass (g)	NA	N	Basal metabolism (mW/g)		
				Observed	Predicted[b]	Percentage predicted
Laysan Finch						
Daytime	31.0 ± 3.08	8	18	15.20 ± 1.40	19.09	80
Nighttime	31.6 ± 3.05	5	9	13.46 ± 1.09	14.34	94
Palila						
Nighttime	34.8 ± 1.41	4	8	12.87 ± 0.65	13.97	92

[a] Values are means ± standard deviations. NA = number of animals; N = number of observations.
[b] Predicted by appropriate equation of Aschoff and Pohl (1970).

TABLE 3. Observed and expected (for passerine birds) physiological parameters for *Psittirostra baileui* and *P. cantans*.

	P. baileui		P. cantans	
	Observed	Expected	Observed	Expected
Thermal conductance [mW(g°C)$^{-1}$]^a	0.612	0.618	0.638 (0.751)^e	0.957
Heat strain coefficient [mW(g°C)$^{-1}$]^b	1.76	1.24	1.34	1.33
Evaporative water loss (g H$_2$O/day)^c	3.27	3.38	2.22	3.31
Lower critical temperature (°C)^d	17.5	17.4	23.5	23.5

^{a} Calculated from the relation mW(g°C)$^{-1}$ = 4.784 g$^{-0.463}$ for α measurements and mW(g°C)$^{-1}$ = 3.215 g$^{-0.461}$ for ρ measurements after Aschoff (1981).
^{b} Calculated from the relation mW(g°C)$^{-1}$ = 12.5 g$^{-0.65}$ from Weathers (1981).
^{c} Calculated from the relation g H$_2$O/day = 1.56 g$^{0.217}$ from Crawford and Lasiewski (1968); expected value at T_a = 25°C.
^{d} See text for derivation of expected values.
^{e} Regression line forced through $\dot{H}_m$ = 0 at 41°C.

An endotherm's T_{lc} can be related to its metabolism ($\dot{H}_m$) and thermal conductance (h) through the Scholander model (see Calder and King 1974: 278) as follows:

$$\dot{H}_m = h(T_b - T_{lc}). \quad (1)$$

By substituting predictive equations for $\dot{H}_m$ and h into the above relation, the expected T_{lc} can be calculated. For night-resting passerines, Aschoff and Pohl's (1970) equation for metabolic rate may be converted to units of mW/g and combined with Aschoff's (1981) equation for thermal conductance (converted to units of mW/g°C) to yield

$$36.9 \, g^{-0.274} = 3.21 \, g^{-0.461}(T_b - T_{lc}), \quad (2)$$

which can be rearranged as

$$T_{lc} = T_b - 11.50 \, g^{0.187}. \quad (3)$$

Similarly, for day-resting passerines,

$$45.2 \, g^{-0.296} = 4.78 \, g^{-0.463}(T_b - T_{lc}). \quad (4)$$

Rearranging gives

$$T_{lc} = T_b - 9.46 \, g^{0.167}. \quad (5)$$

Given a passerine bird's T_b and body mass (g), its expected T_{lc} can be predicted from equation 3 or 5.

At T_a's below the T_{lc}, the Palila's T_b averaged 39.7°C, the Laysan Finch's 40.3°C. Using these values together with the body masses given in Table 2 and solving equations 3 and 5 for the expected T_{lc} reveal that the difference in the Palila's and Laysan Finch's T_{lc} can be completely accounted for by size and circadian effects (Table 3).

Responses to heat.—Palilas are remarkably heat intolerant. Their upper critical temperature, 31°C, is one of the lowest among birds (see Weathers 1981). Consequently, Palilas are heat stressed at ambient temperatures that correspond to thermoneutral levels in most species. Additionally, the Palila's heat-strain coefficient (the metabolism-temperature slope above T_{uc}) is 42% higher than predicted from mass (Table 3). Thus, not only are Palilas heat stressed at moderate T_a's, but they expend proportionately more energy on thermoregulation in the heat than other birds of similar size. Lack of heat tolerance correlates with the Palila's cool habitat. Palila's seldom experience T_a's above 30°C (Table 1), and they evidently have lost the usual avian tolerance to high temperatures. Accordingly, heat intolerance may restrict this species to Hawaii's cool, montane forests.

Another Hawaiian honeycreeper, the Amakihi (*Loxops virens*), is similarly heat intolerant (MacMillen 1974). Like the Palila, it is a high forest bird and seldom encounters T_a's above 27°C. Lacking the appropriate selective pressure, the Amakihi has either lost or never evolved the usual avian tolerance of high temperature. Indeed, four of six Amakihis died following exposure to 38.9–40.4°C for 1.5 h (MacMillen 1974), a degree of heat stress easily endured by most passerines.

In contrast with its montane relatives, the Laysan Finch possesses a more typical level of heat tolerance. Its T_{uc} (38°C) is about 7°C higher than the Palila's, and its heat-strain coefficient is 24% lower (Table 3). Clearly, the Palila and Amakihi's heat intolerance reflects their thermally cool habitats rather than a taxonomic trait of the family Drepanididae.

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