RESPIRATORY AND CUTANEOUS EVAPORATIVE WATER LOSS AT HIGH ENVIRONMENTAL TEMPERATURES IN A SMALL BIRD

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Summary

We measured rates of respiratory and cutaneous evaporative water loss as a function of air temperature in a small desert bird, the verdin *Auriparus flaviceps*. Birds were placed in a two-compartment metabolic chamber that separately collected water evaporated from the bird's head and body. Cutaneous and respiratory evaporative water loss, as well as CO_2 production, were measured in resting birds at 2 °C intervals between 30 and 50 °C. Metabolic rate was lowest at 38 °C ($19\,\mathrm{mW\,g^{-1}}$) and increased to $28\,\mathrm{mW\,g^{-1}}$ at 50 °C. At the lowest air temperature, 30 °C, resting metabolic rate was $34\,\mathrm{mW\,g^{-1}}$. As air temperature increased from 30 to 50 °C, cutaneous water loss increased from 3.3 to $10.3\,\mathrm{mg\,g^{-1}\,h^{-1}}$ and respiratory water loss increased from 2.1–$64.1\,\mathrm{mg\,g^{-1}\,h^{-1}}$. At moderate air temperatures (30–36 °C), water loss was divided almost evenly between respiratory and cutaneous components. As air temperature increased, however, verdins became heavily dependent on respiratory evaporation for heat dissipation. Evaporative water loss data for other species at high air temperatures suggest that partitioning of water loss may follow two different patterns. Evaporative heat dissipation may depend primarily on either cutaneous or respiratory modes of evaporative heat transfer. The physiological mechanisms and functional significance of these contrasting patterns of evaporative heat loss remain unknown.

Key words: water loss, heat dissipation, evaporation, respiration, verdin, *Auriparus flaviceps*, cutaneous evaporation, thermoregulation, metabolic heat production.

Introduction

Evaporative water loss is an essential means of heat transfer for birds when ambient temperatures exceed body temperature, and birds dwelling in subtropical deserts during the summer are routinely exposed to these conditions. For example, air temperature (T_{air}), which is best regarded as a *minimum* index of environmental temperature because it does not include radiative effects, often exceeds 50 °C in subtropical deserts and is commonly above 40 °C for 5–6 h each day. Initial observations of panting and gular flutter in birds during heat stress, and their lack of sweat glands, led researchers to consider respiratory evaporative water loss (REWL) as the only significant avenue of evaporation (Bartholomew and Cade, 1963; Dawson and Bartholomew, 1968). Smith (1969) and Bernstein (1969) later demonstrated that, at low to moderate air temperatures (0–40 °C), rates of cutaneous water loss (CEWL) were equal to or exceeded evaporation from the respiratory system. Further investigations showed that cutaneous evaporation accounts for 40–75 % of total evaporative water loss (TEWL) in those species tested (Dawson, 1982; Webster, 1991; Webster and King, 1987). However, the majority of these studies quantified water loss in the absence of severe heat stress (e.g. T_{air}=20–40 °C) (Bernstein, 1971*a,b*; Bouverot *et al.* 1974; Lasiewski *et al.*

1971; Lee and Schmidt-Nielsen, 1971; Richards, 1976; van Kampen, 1971; Webster and Bernstein, 1987; Webster and King, 1987; Withers and Williams, 1990). Few studies have measured or estimated CEWL during extreme heat stress (e.g. T_{air}>40 °C) and these studies have been restricted to a few species of medium to large (i.e. body mass exceeding 100 g) columbiform and galliform birds (Marder and Arieli, 1988; Marder and Ben-Asher, 1983; Marder and Gavrieli-Levin, 1986).

Current data suggest that birds use two contrasting patterns of evaporative water loss as air temperature increases and approaches body temperature: (1) an increasing dependence on CEWL as the primary mode of heat loss (Marder and Arieli, 1988; Marder and Ben-Asher, 1983; Webster and King, 1987; Withers and Williams, 1990), or (2) an increasing dependence on REWL as the primary mode of heat loss (Bouverot *et al.* 1974; Marder and Ben-Asher, 1983; Richards, 1976; van Kampen, 1971). Unfortunately, these observations are based on measurements from only three orders of birds (pattern 1, Columbiformes; pattern 2, Anseriformes and Galliformes) that represent less than 10 % of bird species.

Although the pre-eminence of REWL in passerines during heat stress has been assumed, there are no data that quantify

how such species partition evaporative water loss at high temperatures. Indeed, our understanding of respiratory and cutaneous water loss, how it is partitioned and the physiological implications of this for birds remain largely unexplored. Here, we report data on metabolic rate and respiratory and cutaneous evaporative water loss of a very small passerine, the verdin (*Auriparus flaviceps*), over a range of moderate to very high air temperatures.

Materials and methods

Experimental animals

Verdins *Auriparus flaviceps* are small (about 7.0 g) insectivorous passerines that reside all year in the deserts of the southwestern United States and northern Mexico. They were captured from their roost nests in the Superstition Mountains of central Arizona in May and June 1994. Birds were transported to Tempe, Arizona, where they were housed individually in BioQuip $0.2 m \times 0.2 m \times 0.2 m$ folding insect cages in a walk-in environmental room. The room temperature and photoperiod were reprogrammed weekly to simulate the current environment of the nearby desert. We maintained the birds on a diet of mealworms and seedless grapes, supplemented once weekly with vitamins (Webster and Weathers, 1988). All birds maintained body mass while in captivity. Measurements were made on eight adult birds during August and September 1994.

Metabolic chamber

A two-compartment metabolic chamber was used which was 16.0 cm long, 14.0 cm high and 9.0 cm wide (Fig. 1). It was constructed from 7.0 mm aluminum plate, except for the front and top of the chamber, which were Plexiglas and which represented about 20 % of chamber interior surface area. The lower half of the chamber (body chamber) had a volume of 660 ml and contained a perch of 1.0 cm square stainless-steel mesh placed above a 2.0 cm deep layer of paraffin oil for collection of feces. The wire mesh was adjusted to a height that allowed the bird to perch. The bird's head protruded through
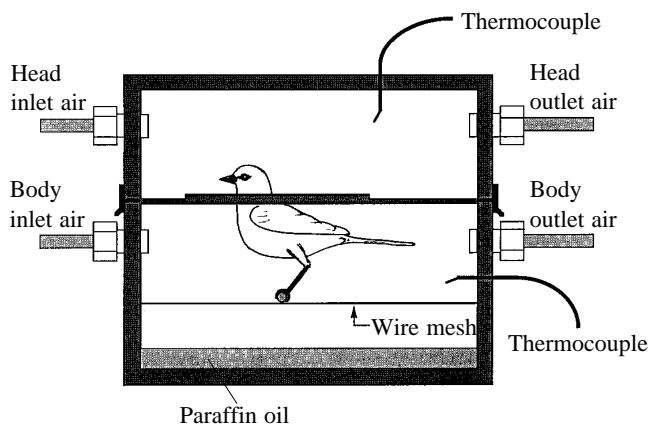

Fig. 1. Two-compartment metabolic chamber used for partitioning respiratory and cutaneous evaporative water loss.

a 0.25 mm thick latex membrane that was stretched over its head and fitted snugly around its neck before placing the bird in the chamber. The membrane was mounted on a thin aluminum frame bolted to a partition separating the respiratory and cutaneous compartments (Fig. 1). The upper half of the chamber (head chamber) had a volume of 560 ml and was sealed to the lower chamber using a rubber gasket to provide an air-tight seal. Chamber temperature was adjusted by placing the metabolic chamber in an environmental room that controlled temperature and lighting.

Carbon dioxide measurement system

A Puregas model CDA1112 air dryer/CO_2 scrubber system provided dry, CO_2-free air that ventilated the upper and lower halves of the metabolic chamber at a rate of 300–1240 ml min^{-1} to maintain chamber vapor densities below a dew point of 5 °C. Incurrent flow for head and body chambers was measured using two Omega FL 3402C-HRV rotameters, calibrated to ± 1 % of full scale with a 1 l soap-bubble flowmeter. These flow rates allowed the metabolic chamber to reach 99 % equilibrium in 2–10 min, calculated using the equation of Lasiewski *et al.* (1966). A sample of upper or lower chamber effluent air passed through a column of Drierite at 50 ml min^{-1} and into a LiCor 4 model 6252 CO_2 analyzer that determined CO_2 concentration to ± 1 p.p.m. The CO_2 analyzer was calibrated daily using CO_2-free air and calibration gas known to contain 0.2840 p.p.m. CO_2.

A second sample of upper or lower chamber effluent air passed through a Thunder Scientific Corp. model PC-2101 humidity evaluation module at 50 ml min^{-1}. A calibration curve for the humidity probe was developed using saturated solutions of calcium chloride and solid CO_2 to form slurries with different freezing points. Humidified air at room temperature (24 °C) was passed through a series of copper coils resting in the slurry at approximately 50 ml min^{-1} and then through the humidity probe. The vapor density of the effluent air leaving the coils varied with the slurry temperature. A nine-point calibration curve was generated between −35 °C (vapor density 0.1 g m^{-3}) and 11 °C (vapor density 10.0 g m^{-3}). Instrument signals were recorded on a Campbell model CR21x datalogger, which collected 40 data points per minute and averaged values for each minute.

Experimental protocol

Eight birds were used for measurements of carbon dioxide production and respiratory and cutaneous evaporative water loss at each of the following temperatures: 30, 34, 36, 38, 40, 42, 44, 46, 48 and 50±0.5 °C. The experimental period started 0.5 h after the lights had been turned off in the evening and continued for 6 or 7 h. Birds were used only once during a 24 h period and at a single temperature on any given day. The bird was weighed to ± 0.01 g and placed inside the chamber in the dark. After at least 20 min and two chamber equilibrium periods, measurements were started. The bird's activity was continuously monitored under infrared light with a Magnavox CCD camera surveillance system. If a bird

struggled continuously for more than 30–40 s, it was removed from the chamber and the run was terminated. Each experiment typically lasted 0.5–1.0 h, and the order in which the birds were used and the temperatures selected were varied nightly. Cutaneous and respiratory water loss were measured sequentially. Consequently, because of the lag time in the sample sytem, 3 min separate these measurements. We believe that this lag produced no appreciable differences when compared with simultaneous measurements because (1) cutaneous water loss was stable after the chamber had reached equilibrium and only varied if the bird struggled violently for an extended period, and (2) except at the highest temperatures measured, the equilibrium time for the system was equal to or greater than the time lag between measurements. Carbon dioxide production and evaporative water loss were calculated from 1 min averages obtained from the sequential measurements from the cutaneous and respiratory chambers using the last 1 min cutaneous average and the first 1 min respiratory average after the 3 min sample system transient.

Analyses

Carbon dioxide production was calculated using equation 3 of Walsberg and Wolf (1995) and corrected to standard conditions (0 °C, 101 kPa) using equation 6.5 of Mclean and Tobin (1987) for flow measurements using rotameters. Respiratory quotient (RQ) and total evaporative water loss were measured at 10 °C in a separate series of experiments because the high flow rates precluded accurate measurements of oxygen consumption (Walsberg and Wolf, 1995). Mean RQ was 0.76 (N=7) measured from 0.5 h to 12 h after removal from food (Walsberg and Wolf, 1995). On the basis of this value, the thermal equivalent of carbon dioxide produced is estimated as 26.2 J ml^{-1} (Gessaman and Nagy, 1988; Kleiber, 1961). All values presented represent means ±95 % confidence intervals.

Cutaneous and respiratory evaporative water loss rates were corrected for water loss from the skin of the head and neck in the upper chamber. The contribution of the head to cutaneous evaporation and the effects of cutaneous evaporation from the head on respiratory water loss estimates have been considered to be small and have been ignored by previous workers using two-compartment metabolic chambers (Bernstein, 1971*b*; Webster and King, 1987; Smith, 1969). The skin surface area represented by the head and neck was estimated by measuring neck diameter, neck length and head diameter and calculating the area. The surface area of the head was assumed to be equal to that of a sphere of the same diameter and the surface area of the neck was equated to a cylinder of the same dimensions. This value, which averaged about 16 % of total skin surface area, was subtracted from the total skin surface area estimated using the equation of Walsberg and King (1978). The head and neck area was multiplied by the surface-area-specific water loss rate for the body, and this value was subtracted from the EWL value from the head chamber and added to the EWL value from the body chamber to calculate the corrected REWL and CEWL, respectively.

Although the latex membrane fitted snuggly around the bird's neck, small quantities of carbon dioxide were detected in the body chamber in most experiments. We assume that this represented leakage between the head and body chambers, although it could have been partially due to fecal or cutaneous losses of CO_2. Corrections were made to REWL and CEWL values in experiments where CO_2 was detected in the body chamber. We assumed that water vapor was introduced into the body chamber at the same fractional rate as CO_2. The percentage total CO_2 in the lower chamber was used to calculate the evaporative water loss adjustment. This value was added to respiratory evaporation in the head chamber and subtracted from the values for cutaneous evaporation in the body chamber. The average percentage of total CO_2 produced found in the lower chamber was 7.5 %. If it exceeded 12 % of the total CO_2 produced, data from the experiment were discarded.

Results

Metabolic heat production was lowest at 19 mW g^{-1} at 38 °C and increased to 28 mW g^{-1} at 50 °C. At the lowest experimental temperature, 30 °C, resting metabolic rate was 34 mW g^{-1} (Fig. 2).

Respiratory evaporative water loss increased with increasing air temperature from 2.1 mg g^{-1} h^{-1} at 30 °C to 64.1 mg g^{-1} h^{-1} at 50 °C (Fig. 3). The water vapor density within the head chamber varied from a minimum of 0.9 g m^{-3} at 30 °C to 6.1 g m^{-3} at 50 °C. From 30 to 36 °C, the rate of REWL is described by equation 1 (r^2=0.902), as fitted using a least-squares algorithm:

$$REWL = 0.282 T_{air} - 6.471. \qquad (1)$$

Between 38 and 50 °C respiratory evaporation rate is described by (r^2=0.995):

$$REWL = 4.791 T_{air} - 176.93. \qquad (2)$$

At 30 °C, CEWL was minimal at 3.3 mg g^{-1} h^{-1} and increased to 10.3 mg g^{-1} h^{-1} at 50 °C (Fig. 3). The water vapor density of the body chamber ranged from 0.9 to 1.5 g m^{-3} between 30 and 50 °C. Cutaneous evaporative water loss increased exponentially (r^2=0.959) with increasing chamber air temperature as fitted using a least-squares algorithm:

$$CEWL = 0.547 \log^{-1}(0.025 T_{air}). \qquad (3)$$

Discussion

Variation in metabolic heat production and respiratory evaporation

We provide the first data quantifying the relative contributions of respiratory and cutaneous evaporative water loss in a small passerine at moderate and high air temperatures. Respiratory evaporation becomes increasingly important with increasing heat stress and is the primary mode of heat dissipation at high ambient temperatures. Cutaneous evaporation increases more
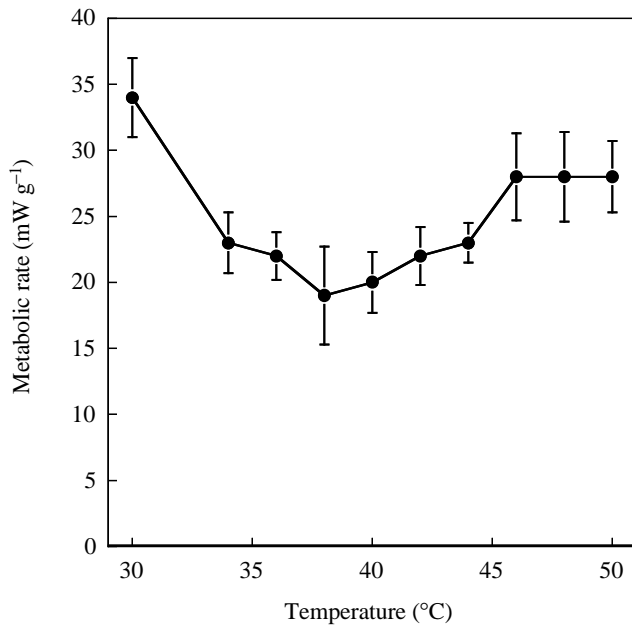
Fig. 2. Metabolic rate of verdins (mW g^{-1}, mean body mass 6.74 g) as a function of air temperature. Data are presented as means ±95 % confidence limits for eight animals at each temperature.

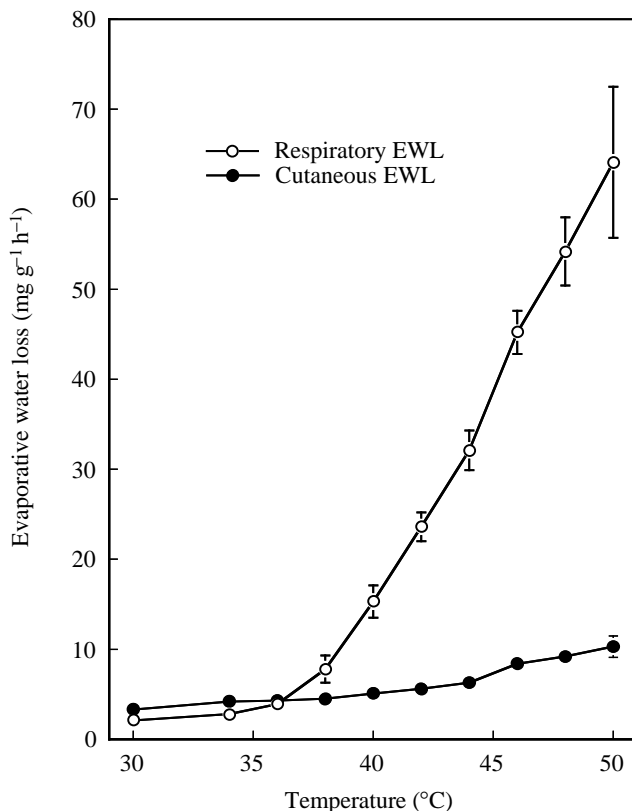Fig. 3. Respiratory and cutaneous evaporative water loss (EWL) in the verdin as a function of air temperature. Data are presented as means ±95 % confidence limits for eight animals (mean body mass 6.74 g) at each temperature.

modestly, but does not appear simply to increase passively with increasing skin temperatures. Rather, tissue resistances to water vapor diffusion are apparently reduced with increasing heat stress. Metabolic rates measured during these experiments are similar to values for previous measurements of resting metabolic rate in verdins (Buttemer *et al.* 1987; Wolf and Walsberg, 1996), particularly considering differences in birds used, their acclimation history, the time of year and experimental conditions. For example, RMR at 36 °C for the present investigation was 22 mW g^{-1} compared with an RMR of 25.9 mW g^{-1} for our earlier study (Wolf and Walsberg, 1996). These values are close to the basal metabolic rates for verdins of 22.2 mW g^{-1} at 36 °C (Wolf and Walsberg, 1996) and 24.2 mW g^{-1} at 35 °C (Buttemer *et al.* 1987). These similarities indicate that the restraint imposed on the verdins by the latex membrane in the metabolic chamber in the present study did not produce measurable additional stress and probably did not result in elevated rates of evaporative water loss.

Changes in respiratory evaporation were qualitatively similar to those observed for birds in other studies (Dawson, 1982; Webster and King, 1987; Withers and Williams, 1990). Rates of respiratory evaporation increased modestly between 30 and 36 °C (Fig. 3) and then sharply between 36 and 50 °C. Panting and gular flutter are important mechanisms for enhancing respiratory evaporation in heat-stressed birds (Calder and King, 1974; Dawson, 1982). Although ventilatory parameters were not measured, visual observations indicated that birds panted intermittently at air temperatures between 40 and 44 °C. Continuous or near-continuous panting was observed at chamber temperatures above 44 °C. Between 30 and 50 °C, there was a more than 30-fold increase in respiratory evaporation. Respiratory evaporative heat dissipation varied from approximately 3 W m^{-2} at 30 °C to 100 W m^{-2} at 50 °C, assuming a latent heat of vaporization of 2.45 J mg^{-1} water. From 46 to 50 °C, there was no change in metabolic rate (Fig. 2), although respiratory evaporative water loss continued to rise steeply (Fig. 3). This suggests some increase in the efficiency of the evaporation of water or a rise in body temperature at the higher ambient temperatures. If Q$_{10}$ effects on metabolism were not overwhelming, an increase in body temperature in a bird already panting at a resonant frequency might elicit this response.

Cutaneous evaporation and variation in resistance to water vapor diffusion

Rates of cutaneous water loss, although modest when compared with respiratory evaporation, do increase almost threefold between 30 and 50 °C (Fig. 3). Cutaneous evaporative heat loss was 5.6 W m^{-2} at 30 °C and 17 W m^{-2} at 50 °C, giving surface-area-specific evaporative water losses comparable to values for other species (Fig. 4). Webster and King (1987) observed a threefold increase in cutaneous evaporation between 20 and 40 °C in rock doves and Bernstein (1982) estimated that cutaneous evaporation increased 3.5-fold between 25 and 42 °C in painted quail. These workers measured cutaneous evaporation in pigeons and doves

(Webster and King, 1987; Webster and Bernstein, 1987) and the Pekin duck (Bouverot *et al.* 1974) at about 2–4 times higher than in verdins at any given temperature. In contrast, pigeons, doves and sand grouse have CEWL rates 10 or more times greater than those of verdins (Marder and Ben-Asher, 1983; Marder *et al.* 1986). The data of Marder *et al.* (1986) are not direct measurements of evaporative water loss and we have chosen not to use them for comparative purposes in Fig. 4 because their measurements of skin resistance were for a few discrete body areas (e.g. pectoral area, torso under wing, and back). Furthermore, plumage and boundary layer resistances were not measured directly, and plumage surface areas (as opposed to skin surface area) were used to generate values for whole-body cutaneous evaporation. Nonetheless, pigeons and doves may be exceptional in their ability to evaporate water from the skin. Marder and Arieli (1988) have demonstrated that pigeons can dissipate essentially all of their internal and external heat loads through CEWL at ambient temperatures of 60 °C. Using their TEWL data to estimate cutaneous evaporation, based on the assumption that 80–100 % of TEWL is cutaneous, suggests that heat-acclimated pigeons may evaporate 4–5 times as much water across the skin as that measured for verdins.
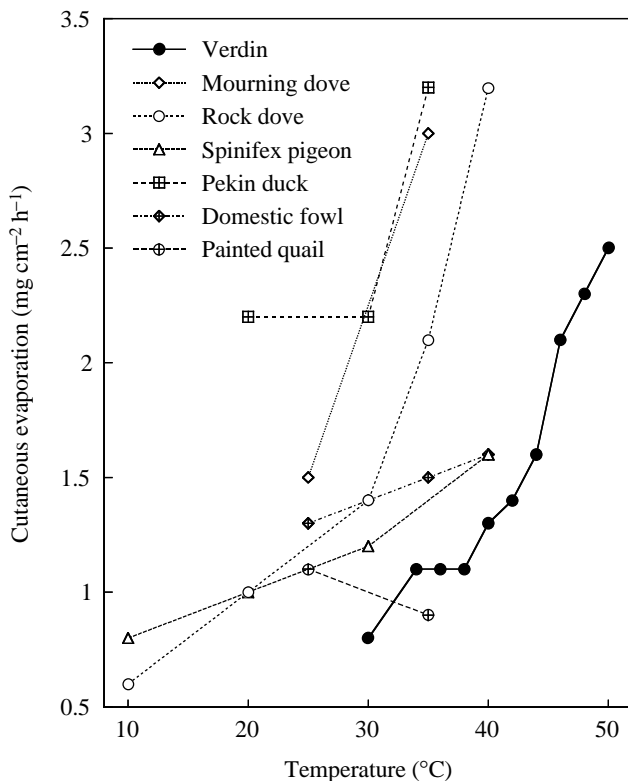

Fig. 4. Surface-area-specific cutaneous evaporative water loss as a function air temperature. Skin surface areas were estimated from equation 1 of Walsberg and King (1978). Data are from the following sources: verdins, this study; mourning dove, Webster and Bernstein (1987); rock dove, Webster and King (1987); spinifex pigeon, Withers and Williams (1990); Pekin duck, Bouverot *et al.* (1974); domestic fowl, Richards (1976); painted quail, Bernstein (1971*a*).

Changes in cutaneous water loss can result either from changes in the skin's resistance to water movement or from changes in the skin-to-environment water vapor pressure gradient. Changes in the skin-to-air water vapor gradient as a result of changes in skin temperature probably cannot explain all of the substantial elevation of CEWL with increasing environmental temperatures in verdins. Using equation 1 of Webster *et al.* (1985), we examined the effects of skin temperature on cutaneous evaporation if skin resistance to water vapor diffusion were held constant. Taking CEWL values for 30 °C and assuming a skin temperature of 34 °C, we calculated a whole-body water vapor diffusion resistance of 197 s cm^{-1}. Using this value and an estimated skin temperature of 44 °C (Webster *et al.* 1985) to predict CEWL at an environmental temperature of 50 °C, we conclude that such increases in skin temperature would account for only 53 % of the observed increase in cutaneous evaporation (1.1 mg cm^{-2} h^{-1} predicted *versus* 2.1 mg cm^{-2} h^{-1} observed). These calculations strongly suggest that water vapor diffusion resistance in the skin–plumage boundary layer complex decreases with increasing heat stress.

In birds, the skin is apparently the primary barrier to water vapor diffusion, comprising approximately 75–94 % of the total vapor resistance over the range of temperatures studied by Webster *et al.* (1985). The remaining resistance is divided between the plumage and boundary layer, but the total of these components is not likely to exceed 10–15 s cm^{-1} in a small bird (Webster *et al.* 1985). Although plumage and boundary layer resistances are of minor importance at low to moderate air temperatures when tissue resistances are high, they become increasingly important as environmental temperatures increase above body temperature. To lower plumage resistance, birds may sleek their feathers (McFarland and Baher, 1968). In addition, they may also employ several mechanisms to lower tissue resistances by altering either the path length for diffusion (Webster *et al.* 1985) or the barrier properties (Appleyard, 1979). Epidermal lipids are widely regarded to have a primary barrier function in a variety of terrestrial organisms, including birds (Hadley, 1989), and conformational changes in the structure of lipids in the stratum corneum may serve to reduce tissue resistance. Increased hydration of the thin epidermis through increases in dermal blood flow (Edwards and Haines, 1978) or increased capillary permeability (Smith, 1969) have also been suggested as a means of reducing tissue resistance. Increased epidermal hydration may result in increased rates of CEWL through hydration and swelling of the dry and keratinized stratum corneum, as occurs in some mammals (Scheuplein and Blank, 1971). The physiological mechanisms and control of cutaneous diffusion resistance in birds, however, remain essentially unknown.

The relative importance of the respiratory and cutaneous components of total evaporative water loss varies with environmental temperature. From 30 to 36 °C, verdins partition respiratory and cutaneous EWL in a similar way to other species (Fig. 5). Evaporative water loss is of little
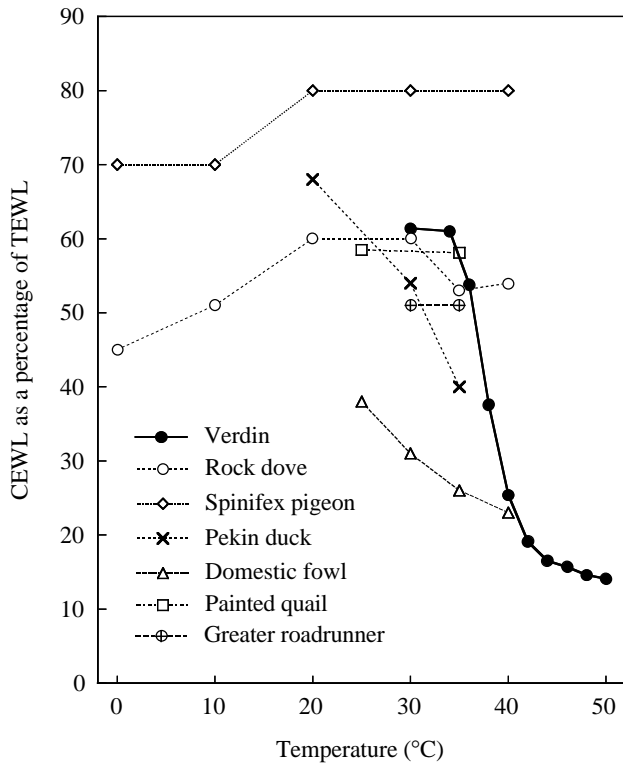
Fig. 5. The percentage of total evaporative water loss (TEWL) attributable to cutaneous evaporation (CEWL) as a function of air temperature. Data are from the following sources: verdins, this study; rock dove, Webster and King (1987); spinifex pigeon, Withers and Williams (1990); Pekin duck, Bouverot *et al.* (1974); domestic fowl, Richards (1976); painted quail, Bernstein (1971*a*); greater roadrunner, Lasiewski *et al.* (1971).

thermoregulatory importance at these lower temperatures and is presumably at a minimum level enforced by respiration and the presence of a thin epidermis. However, evaporation of water becomes an essential means of heat loss when air temperatures exceed body temperature. In verdins, the respiratory system is increasingly responsible for heat dissipation with increasing heat stress. At 36 °C, only 40 % of TEWL is respiratory. As air temperature rises, respiratory evaporation quickly assumes the major role in heat defense and at 50 °C is responsible for 86 % of TEWL. At least some Anseriformes and Galliformes also depend primarily on respiratory evaporation for heat dissipation at high temperatures (Fig. 5). Pigeons and doves appear to utilize a contrasting pattern in which the skin is the primary organ of heat loss at high air temperatures when environmental humidites are low. The verdin's pattern of respiratory pre-eminence in heat dissipation contrasts with that of columbids, which can apparently dissipate almost their entire heat load through cutaneous evaporation. The physiological mechanisms and functional significance of these contrasting patterns of evaporative heat loss remain unknown.

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