A PHYLOGENETIC PERSPECTIVE OF EVAPORATIVE WATER LOSS IN BIRDS

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ABSTRACT.—Allometry, the study of the consequences of body size on form and function, has been a powerful investigative tool in avian biology. Comparison of phenotypic data with allometric reference equations permits the identification of possible adaptations and the formulation of hypotheses for testing. The standard allometric equation that relates total evaporative water loss (TEWL) to body mass in birds, published more than two decades ago, was based on a relatively small sample size, and was constructed using procedures which may have biased parameter estimation. In this report, I have analyzed data for TEWL for 102 species of birds ranging in size from hummingbirds to Ostriches (*Struthio camelus*) using both least-squares regression and phylogenetically independent contrasts. Both approaches suggest that: (1) the slope of the relationship between TEWL and body mass is higher than the value originally proposed; (2) birds from arid environments have a statistically lower TEWL than do birds from more mesic environments; and (3) small birds have similar ratios of TEWL to oxygen consumed compared to larger species. The latter finding negates the idea that small desert birds replenish proportionately less of their TEWL with metabolic water than do larger species. *Received 19 June 1995, accepted 22 September 1995.*

BECAUSE the chemical reactions that are sine qua non for life require an aqueous environment, maintenance of water balance has been a fundamental problem in the evolutionary development of land animals. By virtue of their diurnal, nonfossorial, behavior, high mass-specific metabolic rates (Aschoff and Pohl 1970), and attendant high body temperatures (Calder and King 1974), birds are particularly prone to high rates of water efflux. Total evaporative water loss (TEWL), the sum of evaporative water losses through skin and from respiratory passages, is the major avenue of water loss in birds, especially small species where TEWL is five times greater than urinary-fecal water loss (Lee and Schmidt-Nielsen 1971, Bartholomew 1972, Dawson 1982). High water loss necessitates regular water ingestion through the avenues of drinking, water in food, and metabolic water production. Considerations of water balance restrict some species to areas with free-standing water, whereas others that rely on succulent foods seem to be independent of the requirement of drinking water. Given the central importance of water balance to patterns of distribution and survival, one would expect to find physiological adaptations that would minimize TEWL, especially for species that occupy hot, dry environments (Bartholomew 1972, Dawson 1982).

The study of the consequences of body size on form and function in living organisms, termed allometry, has been an important investigative tool in many ecological, physiological, and evolutionary research programs (Calder 1984, Schmidt-Nielsen 1984). In most studies, variables of interest are measured along with body mass, both of these transformed to logarithms, and a linear equation fit to the data. Sometimes the biological implications of the observed slope are of primary interest, but more often the equation is used as a standard for comparison. Species that deviate widely from predictions are considered candidates for further study into the possible adaptive significance of this variation.

A commonly cited allometric analysis of TEWL at thermally neutral temperatures is that of Crawford and Lasiewski (1968), who tabulated data for 42 species ranging in size from a 3-g hummingbird to a 100 kg Ostrich (*Struthio camelus*). These authors regressed TEWL (ml H_2O/day) against body mass to produce the equation:

$$\log \text{TEWL} = -0.365 + 0.585 \log M, \quad (1)$$

where here and throughout the text M is body mass in grams. Comparative physiologists have used this equation to ascertain the relative magnitude of TEWL in additional species with the underlying purpose of documenting adaptive

traits which might be involved in minimizing this phenotypic trait (Taylor et al. 1971, Dawson and Bennett 1973, Calder and King 1974, Weathers 1977, Dawson 1982, Schleucher et al. 1991).

Several limitations inherent to analysis of Crawford and Lasiewski (1968), as well as the advent of other comparative approaches, suggest that the relationship between TEWL and body size might usefully be reevaluted. As Crawford and Lasiewski pointed out, the data they used for the three largest birds—the Ostrich, Emu (*Dromaius novaehollandiae*, and Greater Rhea (*Rhea americana*)—were collected using a flow-through mask, a procedure that yields estimates of respiratory water loss only, not TEWL. If cutaneous water loss is a significant component of TEWL in these three species, as it is for other smaller birds (Bernstein 1971, Lasiewski et al. 1971, Withers and Williams 1990), then Crawford and Lasiewski may have underestimated the slope of the relationship between TEWL and body mass in birds. For the Ostrich, more recent reports document that cutaneous water loss in the thermal-neutral zone equals about 40% of TEWL (Withers 1983). In addition, Crawford and Lasiewski included in their data set six measurements of TEWL for the chicken (*Gallus gallus*), three for the Rock Pigeon (*Columba livia*), and duplicate measurements for several other nondomestic species. Multiple data for the same species not only inflates the degrees of freedom for statistical tests, but also adds bias in the estimation of the slope and intercept in regression analysis. The problem is exacerbated by the fact that it is unknown whether artificial selection has influenced TEWL in domestic birds.

Despite the above limitations, reliance on the Crawford and Lasiewski equation has influenced the development of several concepts about the water economy of birds. Noting that the slope of the Crawford and Lasiewski equation (0.59) was less than the slope of the line for avian standard metabolic rate and body mass (0.72; Lasiewski and Dawson 1967), Bartholomew (1972) proposed that, in the absence of thermal stress, the quantity of water evaporated per unit oxygen consumed was greater in small birds compared to larger species. Consequently, the former replenish proportionately less of their evaporative water losses by metabolic-water production, a source of water thought to be an important determinant of survival of desert species (Dawson 1982, MacMillen 1990). A high ratio of TEWL to metabolic-water production mandates that small birds are more dependent on preformed water for their survival than are larger birds. In conflict with this reasoning, Bartholomew (1972) pointed out the paradox that some species of xerophilous birds, all less than 50 g, could survive in captivity on a diet of dry seeds in the absence of drinking water (see also Lindgren 1973).

Even though some arid-adapted species can live on a diet of air-dried seeds without any drinking water, at least in the laboratory, unique adaptations that reduce TEWL remain undocumented (Bartholomew and Dawson 1953, Dawson 1982). In an early study, Bartholomew and Dawson (1953) examined the TEWL of 13 species—some inhabitants of arid regions—and concluded that TEWL did not differ between mesic and arid-adapted forms.

Investigators often seek to identify adaptive traits of individual species and the possible mechanisms responsible for the evolutionary development of those traits by examining interspecific phenotypic variation over a range of body sizes. Some practitioners have proffered the idea that multispecies allometric analyses contain an inherent statistical flaw because species-specific phenotypic values are assumed to represent statistically independent values (Pagel and Harvey 1988, Harvey and Pagel 1991). In fact, it is argued, each species cannot be considered statistically independent of all others because manifestations of phenotypic traits in extant species may reflect phyletic heritage rather than adaptation to recent selective pressures (Burt 1990, Miles and Dunham 1993). In effect, this phylogenetic nonindependence reduces the degrees of freedom available for hypothesis testing and affects parameter estimation in statistical analyses (Grafen 1989, Harvey and Pagel 1991, Martins and Garland 1991; but see Pagel 1992). Techniques, such as nested analysis of variance, phylogenetic autocorrelation, and phylogenetically independent contrasts, have been developed that attempt to control for the influence of phylogeny when analyzing quantitative traits across a range of species (Cheverud et al. 1985, Felsenstein 1985, Felsenstein 1988, Gittlemand and Kot 1990, Edwards and Naeem 1993). Felsenstein's (1985) method of phylogenetically independent contrasts fulfills assumptions of parametric statistics and has received wide acceptance (Grafen 1989, Martins and Garland 1991).

At present, there is disagreement concerning

the use of these techniques that purportedly eliminate historical bias (Grafen 1992, Pagel and Harvey 1992, Miles and Dunham 1993, Purvis et al. 1994). There is no consensus as to which procedure should be implemented to control for phylogeny in a given study. In some cases, when results from alternate methods that control for phylogeny have been compared, authors have arrived at conflicting conclusions (Oaks 1992, Miles and Dunham 1992). Some argue that, in many comparative studies, abandonment of traditional methods for alternative procedures of phylogenetic analyses is unwarranted (Weathers and Siegel 1995), while others go so far as to say that all comparative methods, no matter which analytical techniques are used, will fail to elucidate adaptations (Leroi et al. 1994). During this time when investigators disagree about which comparative method is appropriate, the best approach may be to employ several methods in attempting to make meaningful interpretations about adaptation.

In this paper, I use two comparative approaches to examine the relationship between TEWL and body mass in birds. First, I use least-squares regression to regress TEWL on body mass, a tactic that assumes a model where all species have radiated from a single common ancestor, a star phylogeny (Purvis and Garland 1993). Second, I assume that species are part of a branching hierarchial phylogeny, and use Felsenstein's (1985) method of phylogenetically independent contrasts to evaluate TEWL, controlling for genealogical influences (also using least-squares regression). Specifically, I address the following questions: (1) What is the relationship between TEWL and body mass in birds? (2) Do birds from arid regions have a lower TEWL than birds from more mesic areas? (3) Do small birds have a higher rate of TEWL relative to their oxygen consumption than do larger birds?

MATERIALS AND METHODS

Numerous studies have reported laboratory measurements of TEWL of birds; most have used open-circuit respirometry to make determinations. The different experimental conditions under which measurements were made along with the diverse techniques used to quantify water loss add considerable variation to the data. I included data from studies without regard to: levels of illumination in the chamber; the nutritional plane of birds (postabsorptive vs. nonpostabsorptive); the time of measurement (diurnal or nocturnal activity phase); or the time of year

that subjects were captured (summer or winter). However, I eliminated studies where subjects were water-stressed prior to measurement of TEWL.

Evaporative water loss in birds is relatively independent of temperatures below the lower critical point, but dramatically escalates at temperatures above the upper critical temperature (Dawson and Bennett 1973, Withers and Williams 1990). My reasons for selecting data taken at 25°C were that this temperature is: (1) at or near the lower critical temperature for many birds; (2) thermally unstressful for most birds; and (3) consistent with that chosen by Crawford and Lasiewski (1968) for their analysis. Because in three cases data were not available for a temperature of 25°C— the Humboldt Penguin (*Spheniscus humboldti*; 10°C), Brown-necked Raven (*Corvus ruficollis*; 30°C), and Bedouin Fowl (*Gallus gallus*; 30°C)—I included data taken at different temperatures, but still in the thermal-neutral zone.

I eliminated some early studies where reduced air flow likely influenced measurement of TEWL because variation in ambient water-vapor pressure within metabolism chambers can significantly alter values of TEWL, thereby hindering interspecific comparisons (Lasiewski et al. 1966). By adjusting flow rates of ambient air and, thus, maintaining low water-vapor pressures within metabolism chambers, Bernstein et al. (1977) found that TEWL in pigeons at 20°C was independent of absolute humidity.

Classification of a species' environment as either arid or mesic presents a problem because environmental aridity is a continuum based on a combination of factors including solar insolation, rainfall, air temperature, relative humidity, and prevailing wind conditions. My intent in classifying the environment of a species as arid was guided by the idea that species experiencing hot, dry, and desiccating conditions face unusual problems in maintaining water balance. Assignment of a species to an environmental category typically was based on the location identified in each study and distribution maps of arid regions of the world (McGinnies et al. 1968). In many cases, the judgement of the original author or authors regarding the environment of the species was followed.

Phylogenetic comparative methods that attempt to remove the confounding effects of correlated traits due to common genealogical history assume that the cladistic relationships between species are known. To construct a phylogenetic diagram of the 102 species for which I assembled data on TEWL (Figs. 1 and 2), I used the topology for birds generated by Sibley and Ahlquist (1990) using DNA-DNA hybridization techniques. Branch lengths were based on $\Delta T_{50}H$ values. For taxonomic names and common names of species, I relied on Sibley and Monroe (1990). In some cases, the tapestry of Sibley and Ahlquist (1990) did not contain species for which I had data. I placed these species in the topology as closely as possible to sister species, often with the aid of advice from specialists (see Acknowledgments). I connected each species to
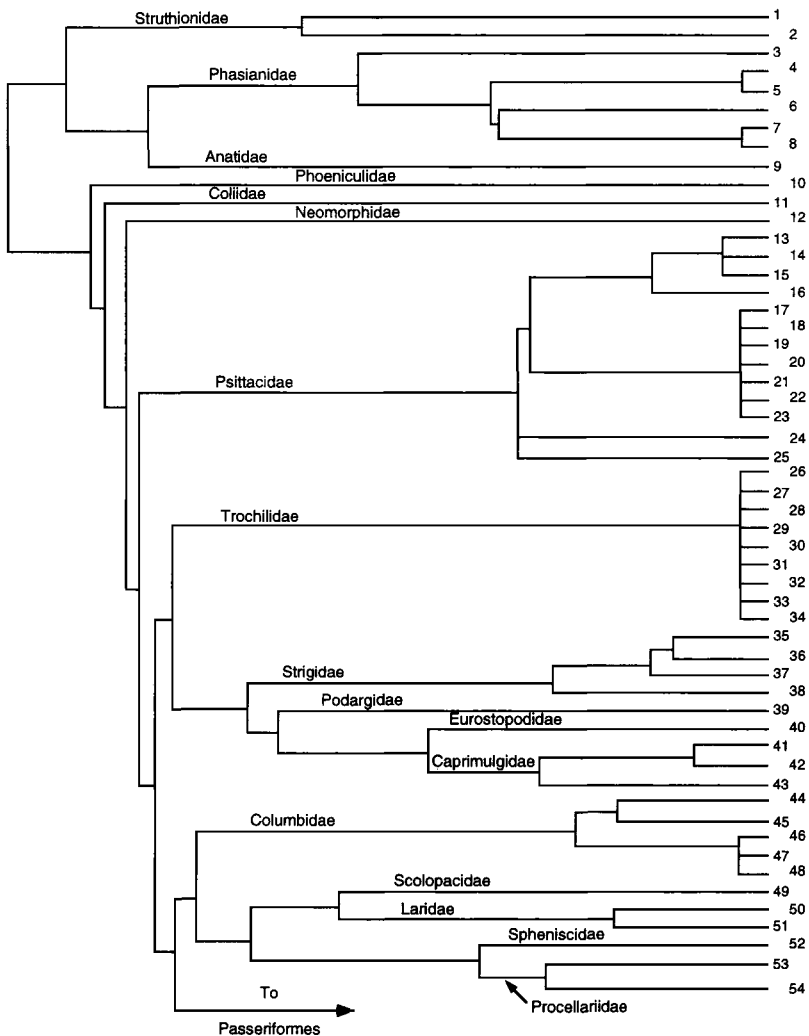
Nonpasserines

Fig. 1. Hypothesized phylogenetic relationships of nonpasserine species. Branch lengths are $\Delta T_{50}H$ values based on DNA-DNA hybridization (Sibley and Ahlquist 1990). All polytomy branch lengths arbitrarily set to 1. Total $\Delta T_{50}H$ units = 28.0.

its presumed most recent ancestor and assigned an arbitrary branch length of one (T. Garland pers. comm.).

I used the PDTREE module of the Phylogenetic Diversity Analysis Program (version 2.0; Garland et al. 1993) to calculate Felsenstein's (1985) standardized independent contrasts for log-transformed values of TEWL (ml H_2O/day) and body mass (g; Garland pers. comm.). A plot of the absolute values of standardized contrasts versus standard deviations showed no linear trends for either variable suggesting that contrasts were adequately standardized (Garland et al. 1992, Garland 1992).

I regressed the standardized independent contrasts

for log TEWL against those for log body mass with the regression line forced through the origin (Garland et al. 1992, Garland and Janis 1993). This procedure yields an estimate of the slope and its 95% confidence interval of the relationship between log TEWL and log body mass with the effects of phylogenetic history removed. For degrees of freedom, I have followed the maximally conservative recommendation of Purvis and Garland (1993) by taking the degrees of freedom as equal $(N - P_u)$, where N is the number of independent contrasts and P_u is the number of unresolved polytomies. To define an allometric relation between log TEWL and log body mass, I solved the equation $Y = a + bX$ for the inter-
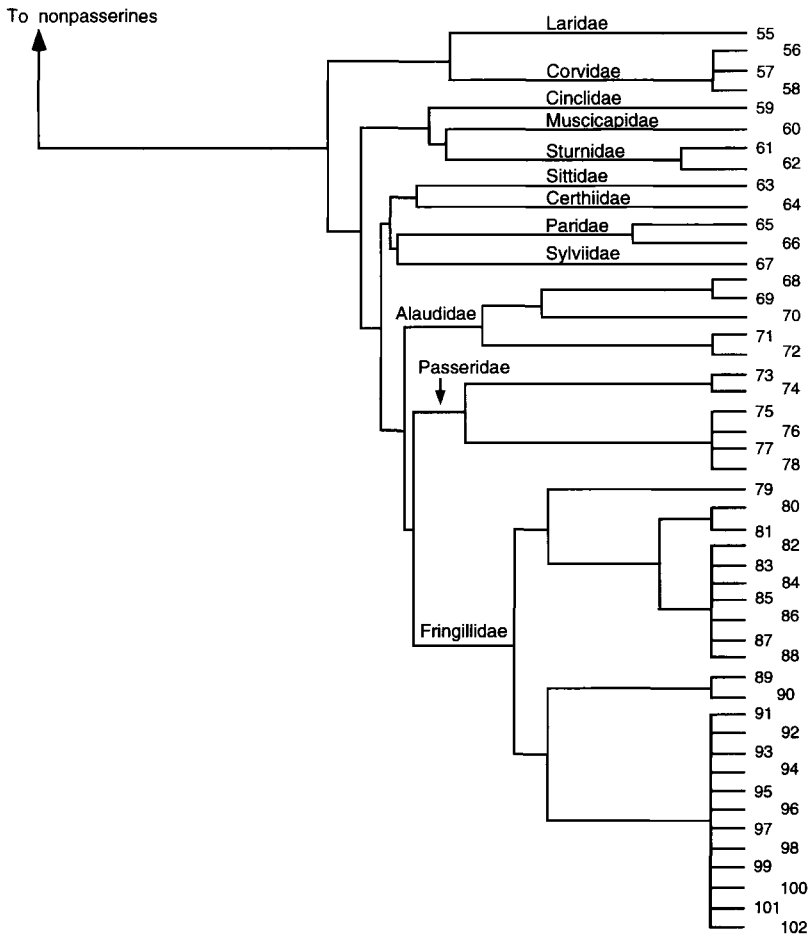
Passeriformes

Fig. 2.   Hypothesized phylogenetic relationships of species of passerines. Branch lengths are $\Delta T_{50}H$ values bases on DNA-DNA hybridization (Sibley and Ahlquist 1990). Polytomy branch lengths arbitrarily set to 1. Total $\Delta T_{50}H$ units = 21.6.

cept. Here b equals the previously determined slope, and Y and X are the root-node contrast values for log TEWL and log body mass, respectively. When computing independent contrasts, the estimated value at the root node represents an estimate of the overall mean for all species in the phylogeny, weighted by topology and branch lengths (Garland et al. 1993). To date, no one has proposed a method to estimate a confidence interval for the intercept in such an equation, so elevations of different equations can not be compared, although jackknifing or bootstrapping might be used in a heuristic fashion (Garland pers. comm.).

To determine whether TEWL of birds from arid environments differed from birds from mesic envi-

ronments, I computed independent constrasts for environment scored as 1 for arid and 0 for mesic. A plot of standardized independent contrasts and their standard deviations disclosed a significant negative trend. Hence, I square-root-transformed branch lengths to correct this problem (Garland et al. 1992). I then used multiple regression through the origin to test for the influence of environment on TEWL in birds with the standardized contrasts of log TEWL as the dependent variable and the standardized contrasts of log body mass and environment as the independent variables. The entry criteria for selection of variables in the equation was a P of 0.05. The significance of partial correlation coefficients was determined using a t-test (Zar 1984).
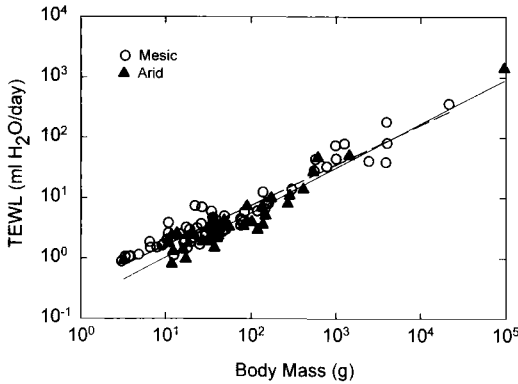
Fig. 3. Logarithmic plot of total evaporative water loss in birds versus body mass.

The assumptions underlying Felsenstein's phylogenetically independent contrasts method are: First, it is assumed that an accurate phylogeny is known (Felsenstein 1985), a supposition that constitutes a limitation to the procedure because, undoubtedly, the true phylogeny is not known. I have used the topology of Sibley and Ahlquist (1990) because it is the only complete estimate of the phyletic relationships of birds. Recent data based on more advanced molecular techniques lend support to the overall topology of Sibley and Alhquist (Bleiweiss et al. 1994, Mooers and Cotgreave 1994). However, Feduccia (1995) has recently challenged whether DNA-DNA hybridization provides an accurate view of the genealogical history of birds because of apparent conflict with the fossil record. Of the few studies that have attempted to compare results using alternative phylogenies, some have reported consistent results in subsequent statistical tests (Gittleman and Kot 1990, Miles and Dunham 1992), while others have arrived at conflicting conclusions (Garland et al. 1991). Second, it is assumed that the evolution of continuous traits is modeled appropriately as Brownian motion (Felsenstein 1985, 1988, Martins and Garland 1991). If the Brownian-motion model is incorrect, then contrasts are no longer independent of phylogeny (Miles and Dunham 1993).

RESULTS

ALLOMETRIC ANALYSIS

Evaporative water loss-considering all birds.—I addressed my first question concerning the relationship between TEWL and body mass by collating data on TEWL at thermally neutral temperatures (mostly 25°C) for 102 species of birds (Table 1). The equation that describes TEWL (ml H_2O/day) in birds is:

$$\log \text{TEWL} = -0.523 + 0.678 \log M, \quad (2)$$

where M is body mass (g) as before ($r^2 = 0.90$, $F_{slope} = 865.5$, $P < 0.001$). Here I incorporated only one value for each species. For the chicken and House Finch numbers 4 and 80 of Table 1), I have excluded the arid forms.

Arid vs. mesic comparisons.—I separated the data on TEWL based on the environment of respective species and determined whether statistical differences exist between species from arid and mesic regions (Fig. 3). The equation that describes the association between TEWL and body mass in birds from mesic areas is:

$$\log \text{TEWL} = -0.438 + 0.661 \log M \quad (3)$$

($n = 64$, $r^2 = 0.92$, $F_{slope} = 671.8$, $P < 0.001$). For birds from arid regions, the equation is:

$$\log \text{TEWL} = -0.754 + 0.750 \log M \quad (4)$$

($n = 38$, $r^2 = 0.93$, $F_{slope} = 441.5$, $P < 0.001$). By analysis of covariance (ANCOVA), the slopes of these two equations are significantly different ($F_{slope} = 4.0$, $P < 0.05$). Birds from arid regions have a statistically lower TEWL at thermally neutral temperatures than birds from more mesic areas.

Comparisons among passerines.—Does this finding that arid-zone birds have a reduced TEWL apply when only passerines are examined? The equation that describes TEWL among passerines from arid regions is:

$$\log \text{TEWL} = -0.860 + 0.868 \log M \quad (5)$$

($n = 15$, $r^2 = 0.85$, $F_{slope} = 72.4$, $P < 0.001$). The equation for passerines from mesic areas is:

$$\log \text{TEWL} = -0.174 + 0.443 \log M \quad (6)$$

($n = 33$, $r^2 = 0.41$, $F_{slope} = 21.1$, $P < 0.001$). By ANCOVA, these equations are statistically distinct ($F_{slope} = 9.1$, $P < 0.001$). The steeper slope and lower elevation of arid-zone passerines conforms to the general conclusion that arid-zone birds have reduced TEWL.

Passerines vs. other birds.—Because the basal metabolic rate of passerines exceeds that of nonpasserines (Aschoff and Pohl 1970), one might expect that TEWL of the former also would be demonstrably higher. I tested this idea by comparing the TEWL for passerines and nonpasserines by ANCOVA, and found no significant differences ($F_{slope} = 0.7$, $P > 0.2$; $F_{intercept} = 0.52$, $P > 0.5$).

TABLE 1. Body mass and total evaporative water loss of birds from mesic and arid environments (taken at 25°C).

Species	Environment	Body mass (g)	Total evaporative water loss (ml H_2O/day)	Source
STRUTHIONIFORMES				
Struthionidae				
1. Ostrich (*Struthio camelus*)	Arid	95,400.0	1,420.0	Withers 1983
Rheidae				
2. Greater Rhea (*Rhea americana*)	Mesic	21,500.0	364.7	Taylor et al. 1971
GALLIFORMES, Phasianidae				
3. California Quail (*Callipepla californica*)	Arid	147.1	5.14	Bartholomew and Dawson 1953
4. Chicken (*Gallus gallus*)	Arid	1,427.0	49.7	Marder 1973a
5. Chicken	Mesic	2,430.0	40.8	Barott and Pringle 1946
6. Blue-breasted Quail (*Coturnix chinensis*)	Mesic	42.7	3.08	Crawford and Lasiewski 1968
7. Chukar (*Alectoris chukar*)	Arid	412.0	13.8	Frumkin et al. 1986
8. Sand Partridge (*Ammoperdix heyi*)	Arid	172.0	9.92	Frumkin et al. 1986
ANSERIFORMES, Anatidae				
9. Domestic goose (*Anser anser*)	Mesic	4,000.0	81.0	Romijn and Lokhorst 1961
UPUPIFORMES, Phoeniculidae				
10. Green Woodhoopoe (*Phoeniculus purpureus*)	Mesic	75.9	4.21	Williams et al. 1991
COLIIFORMES, Coliidae				
11. Speckled Mousebird (*Colius striatus*)	Mesic	46.1	2.75	Brown and Foster 1992
CUCULIFORMES, Neomorphidae				
12. Greater Roadrunner (*Geococcyx californianus*)	Arid	284.7	10.9	Calder and Schmidt-Nielsen 1967
PSITTACIFORMES, Psittacidae				
13. Galah (*Eolophus roseicapillus*)	Arid	268.7	8.0	Williams et al. 1991
14. Sulphur-crested Cockatoo (*Cacatua galerita*)	Mesic	776.1	32.7	Williams et al. 1991
15. Long-billed Corella (*C. tenuirostris*)	Mesic	549.9	28.0	Williams et al. 1991
16. Cockatiel (*Nymphicus hollandicus*)	Arid	80.7	3.4	Dawson 1965
17. Red-rumped Parrot (*Psephotus haematonotus*)	Arid	55.0	3.3	MacMillen and Baudinette 1993
18. Budgerigar (*Melopsittacus undulatus*)	Arid	33.7	1.9	Weathers and Schoenbaechler 1976
19. Bourke's Parrot (*Neopsephotus bourkii*)	Arid	35.3	2.7	Dawson 1965
20. Port Lincoln Parrot (*Barnardius zonarius*)	Arid	137.0	3.6	Dawson 1965
21. Red-tailed Black Cockatoo (*Calyptorhynchus banksii*)	Arid	535.3	26.4	Williams et al. 1991
22. Rock Parrot (*Neophema petrophila*)	Mesic	48.4	5.0	Williams et al. 1991

TABLE 1. Continued.

Species	Environment	Body mass (g)	Total evaporative water loss (ml H$_2$O/day)	Source
TROCHILIFORMES, Trochilidae				
23. Rainbow Lorikeet (Trichoglossus haematodus)	Mesic	137.1	12.5	Williams et al. 1991
24. Monk Parakeet (Myiopsitta monachus)	Mesic	83.1	5.8	Weathers and Coccarnise 1978
25. Rosy-faced Lovebird (Agapornis roseicollis)	Arid	48.1	4.2	Kendeigh et al. 1977
26. Costa's Hummingbird (Calypte costae)	Arid	3.2	0.93	Crawford and Lasiewski 1968
27. Anna's Hummingbird (C. anna)	Mesic	4.8	1.15	Lasiewski 1964
28. Black-chinned Hummingbird (Archilochus alexandri)	Mesic	3.3	1.07	Lasiewski 1964
29. Rufous Hummingbird (Selasphorus rufus)	Mesic	3.8	1.09	Lasiewski 1964
30. Allen's Hummingbird (S. sasin)	Mesic	3.7	1.07	Lasiewski 1964
31. Calliope Hummingbird (Stellula calliope)	Mesic	3.0	0.89	Lasiewski 1964
32. Magnificent Hummingbird (Eugenes fulgens)	Mesic	6.6	1.51	Lasiewski and Lasiewski 1967
33. Blue-throated Hummingbird (Lampornis clemenciae)	Mesic	7.9	1.52	Lasiewski and Lasiewski 1967
34. Giant Hummingbird (Patagona gigas)	Mesic	19.1	2.98	Lasiewski et al. 1967
STRIGIFORMES				
Strigidae				
35. Spotted Owl (Strix occidentalis)	Mesic	571.0	43.3	Ganey et al. 1993
36. Great Horned Owl (Bubo virginianus)	Mesic	1,000.0	43.9	Ganey et al. 1993
37. Screech Owl (Otus asio)	Arid	101.3	4.0	Bartholomew and Dawson 1953
38. Burrowing Owl (Speotyto cunicularia)	Arid	132.4	6.9	Coulombe 1970
Podargidae				
39. Marbled Frogmouth (Podargus ocellatus)	Mesic	145.0	6.61	Lasiewski et al. 1970
Eurostopodidae				
40. Spotted Eared-Nightjar (Eurostopodus argus)	Arid	88.0	4.01	Dawson and Fisher 1969
Caprimulgidae				
41. Common Nighthawk (Chordeiles minor)	Mesic	75.0	4.5	Lasiewski and Dawson 1964
42. Lesser Nighthawk (C. acutipennis)	Mesic	40.2	3.0	Bartholomew and Dawson 1953
43. Common Poorwill (Phalaenoptilus nuttallii)	Arid	40.0	2.45	Lasiewski and Bartholomew 1966
COLUMBIFORMES, Columbidae				
44. Mourning Dove (Zenaida macroura)	Arid	118.7	2.96	Bartholomew and Dawson 1953
45. Rock Pigeon (Columba livia)	Mesic	300.0	13.9	Kayser 1939
46. Diamond Dove (Geopelia cuneata)	Arid	34.0	2.47	Schleucher pers. comm.
47. Spinifex Pigeon (Geophaps plumifera)	Arid	89.0	7.3	Withers and Williams 1990

TABLE 1. Continued.

Species	Environment	Body mass (g)	Total evaporative water loss (ml H₂O/day)	Source
48. Namaqua Dove (*Oena capensis*)	Arid	37.0	1.49	Schleucher pers. comm.
CICONIIFORMES				
Scolopacidae				
49. Red Knot (*Calidris canutus*)	Mesic	118.0	6.1	Verboven and Piersma 1994
Laridae				
50. South Polar Skua (*Catharacta maccormicki*)	Mesic	1,249.5	78.7	Morgan et al. 1992
51. Kelp Gull (*Larus dominicanus*)	Mesic	980.3	73.2	Morgan et al. 1992
Spheniscidae				
52. Humboldt Penguin (*Spheniscus humboldti*)	Mesic	3,870.0	39.0	Drent and Stonehouse 1971
Procellariidae				
53. Wilson's Storm-Petrel (*Oceanites oceanicus*)	Mesic	34.1	6.0	Morgan et al. 1992
54. Antarctic Giant Petrel (*Macronectes giganteus*)	Mesic	3,928.8	181.4	Morgan et al. 1992
PASSERIFORMES				
Laniidae				
55. Loggerhead Shrike (*Lanius ludovicianus*)	Arid	40.8	2.37	Bartholomew and Dawson 1953
Corvidae				
56. Brown-necked Raven (*Corvus ruficollis*)	Arid	610.0	46.1	Marder 1973b
57. Black-billed Magpie (*Pica pica*)	Mesic	158.9	8.14	Hayworth and Weathers 1983
58. Yellow-billed Magpie (*P. nuttalli*)	Mesic	151.9	8.33	Hayworth and Weathers 1983
Cinclidae				
59. American Dipper (*Cinclus mexicanus*)	Mesic	50.2	3.01	Murrish 1970
Muscicapidae				
60. European Robin (*Erithacus rubecula*)	Mesic	16.7	1.85	Shilov 1968
Sturnidae				
61. Northern Mockingbird (*Mimus polyglottos*)	Arid	39.6	2.14	Bartholomew and Dawson 1953
62. California Thrasher (*Toxostoma redivivum*)	Mesic	74.7	3.51	Bartholomew and Dawson 1953
Sittidae				
63. Wood Nuthatch (*Sitta europaea*)	Mesic	21.0	2.18	Shilov 1968

TABLE 1. Continued.

Species	Environment	Body mass (g)	Total evaporative water loss (ml H_2O/day)	Source
Certhiidae				
64. House Wren (Troglodytes aedon)	Mesic	10.8	3.89	Kendeigh 1939
Paridae				
65. Black-capped Chickadee (Parus atricapillus)	Mesic	10.8	2.63	Shilov 1968
66. Great Tit (P. major)	Mesic	16.7	2.01	Shilov 1968
Sylviidae				
67. Blackcap (Sylvia atricapilla)	Mesic	16.7	1.85	Shilov 1968
Alaudidae				
68. Stark's Lark (Eremalauda starki)	Arid	16.0	1.38	Willoughby 1968
69. Crested Lark (Galerida cristada)	Arid	35.8	4.36	Adams pers. comm.
70. Dune Lark (Certhilauda erythrochlamys)	Arid	27.3	1.90	Williams unpubl.
71. Desert Lark (Ammomanes deserti)	Arid	19.8	2.43	Adams pers. comm.
72. Grey-backed Sparrow-lark (Eremopterix verticalis)	Arid	16.0	1.38	Willoughby 1968
Passeridae				
73. House Sparrow (Passer domesticus)	Mesic	26.0	3.74	Kendeigh 1944
74. Eurasian Tree Sparrow (P. montanus)	Mesic	21.3	2.21	Shilov 1968
75. Dusky Munia (Lonchura fuscans)	Mesic	9.5	1.75	Weathers 1977
76. White-throated Silverbill (Lonchura malabarica)	Arid	10.9	1.78	Willoughby 1969
77. Zebra Finch (Taeniopygia guttata)	Arid	11.7	1.89	Lee and Schmidt-Nielsen 1971
78. Black-rumped Waxbill (Estrilda troglodytes)	Mesic	6.5	1.87	Cade et al. 1965
Fringillidae				
79. Chaffinch (Fringilla coelebs)	Mesic	19.7	1.88	Shilov 1968
80. House Finch (Carpodacus mexicanus), desert population	Arid	17.2	0.97	MacMillen and Hinds pers. comm.
81. House Finch, coastal population	Mesic	17.9	1.50	MacMillen and Hinds pers. comm.
82. European Greenfinch (Carduelis chloris)	Mesic	24.9	1.70	Shilov 1968
83. European Goldfinch (C. carduelis)	Mesic	16.4	1.81	Shilov 1968
84. Eurasian Siskin (C. spinus)	Mesic	12.4	1.12	Shilov 1968
85. Eurasian Bullfinch (Pyrrhula pyrrhula)	Mesic	29.2	2.40	Shilov 1968
86. Laysan Finch (Telespiza cantans)	Mesic	32.8	3.01	Weathers and Van Riper 1982
87. Palila (Loxioides bailleui)	Mesic	36.0	3.39	Weathers and Van Riper 1982
88. Apapane (Himatione sanguinea)	Mesic	14.5	2.52	Weathers et al. 1983
89. Northern Cardinal (Cardinalis cardinalis)	Mesic	41.3	3.60	Hinds and Calder 1973

TABLE 1. Continued.

Species	Environment	Body mass (g)	Total evaporative water loss (ml H$_2$O/day)	Source
90. Pyrrhuloxia (C. sinuatus)	Arid	32.0	3.20	Hinds and Calder 1973
91. Brewer's Sparrow (Spizella breweri)	Arid	12.2	1.30	Dawson et al. 1979
92. Yellowhammer (Emberiza citrinella)	Mesic	26.4	7.04	Wallgren 1954
93. Ortolan Bunting (E. hortulana)	Mesic	22.0	7.38	Wallgren 1954
94. Chipping Sparrow (S. passerina)	Arid	11.8	0.80	Dawson et al. 1979
95. Blue-black Grassquit (Volatinia jacarina)	Mesic	9.1	1.63	Weathers pers. comm.
96. Variable Seedeater (Sporophila americana)	Mesic	10.4	2.04	Weathers pers. comm.
97. White-crowned Sparrow (Zonotrichia leucophrys)	Mesic	23.2	3.16	Bartholomew and Dawson 1953
98. Savannah Sparrow (Passerculus sandwichensis)	Mesic	17.4	3.26	Williams and Hansell 1981
99. Canyon Towhee (Pipilo fuscus)	Mesic	39.3	2.35	Bartholomew and Dawson 1953
100. Abert's Towhee (P. aberti)	Arid	38.2	2.94	Bartholomew and Dawson 1953
101. Rufous-sided Towhee (P. erythrophthalmus)	Mesic	35.4	4.71	Bartholomew and Dawson 1953
102. Black-throated Sparrow (Amphispiza bilineata)	Arid	13.5	2.59	Bartholomew 1972

* Value taken at 30°C.

PHYLOGENETIC ANALYSIS

Evaporative water loss considering all birds.—the estimated phylogenetic relationships of species in Table 1 are presented in Figures 1 and 2. Note that numbers in these figures correspond to those assigned to species in Table 1.

A regression of the standardized independent contrasts of log body mass and log TEWL through the origin (Garland et al. 1992, Garland and Janis 1993) yielded a slope of 0.789 with a 95% confidence interval of ±0.11 (Fig. 4). I then solved the linear equation $Y = a + bX$ for the intercept, where X and Y are contrast values for the root node. The allometric equation given by this procedure is:

$$\log \text{TEWL} = -0.833 + 0.789 \log M. \quad (7)$$

Judging by the confidence interval, the slope of this line does not differ significantly from the slope of the line generated by the previous allometric method. Even so, predictions made by each equation markedly differ for larger species (see Discussion).

Arid vs. mesic comparisons.—A stepwise multiple regression through the origin of standardized contrasts for log TEWL as the dependent variable and standardized contrasts of log body mass and environment as the independent variables revealed that environment had a significant affect in the equation ($t = -2.82, P < 0.006$). The negative value of the partial correlation coefficient indicated that birds from arid regions had a reduced TEWL.

Comparisons among passerines.—I tested for the effect of environment on TEWL among passerines, while controlling for phylogeny using Felsenstein's (1985) method of independent contrasts. Regression through the origin for standard contrasts of log TEWL and log body mass yielded a slope of 0.819 with a 95% confidence interval of ±0.24 ($n = 48$). The allometric equation for passerines is:

$$\log \text{TEWL} = -0.752 + 0.819 \log M. \quad (8)$$

A multiple-regression procedure with standard contrasts for log TEWL as the dependent variable and standard contrasts for log body mass and environment as independent variables revealed that the partial correlation coefficient for environment was significant ($t = 2.24, P < 0.04$). Again the general conclusion is confirmed: arid-zone birds have a significantly lower TEWL.

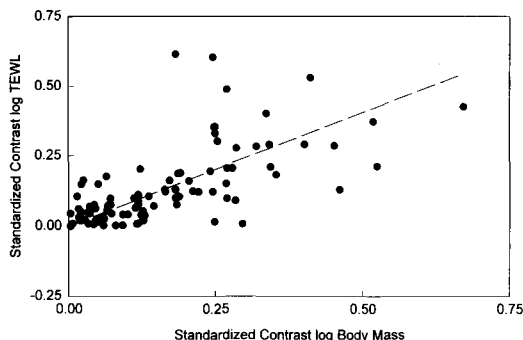　　　　　　　　　JOSEPH B. WILLIAMS　　　　　　　　

Fig. 4. Standardized independent contrasts for log total evaporative water loss and log body mass. Body-mass values positivized according to Garland et al. (1992).

TABLE 2. Comparison of predicted rates of evaporative water loss from allometric equations.

| Body mass (g) | Total evaporative water loss (ml H_2O/ day) | | |
	Crawford and Lasiewski	Allometric	Phylogenetic
10	1.7	1.4	0.9
100	6.4	6.8	5.6
1,000	24.6	32.4	34.2
10,000	94.4	154.2	210.4
100,000	363.1	732.8	1,294.2

DISCUSSION

My analysis suggests that the slope of the Crawford and Lasiewski (1968) equation, 0.58, should be steeper for the relationship between TEWL and body mass for birds. I found a slope of either 0.678 or 0.789, depending on the method used. For the three equations (i.e. the Crawford and Lasiewski equation, the equation based on allometric analysis, and the equation generated from phylogenetically independent contrasts), the Crawford and Lasiewski equation yields the lowest predictions of TEWL at larger body sizes (Table 2). Though the slopes of the two equations constructed in this study for TEWL and body mass did not statistically differ, the one given by phylogenetically independent contrasts yielded much higher predictions at larger body masses. At this point, it is not possible to distinguish between the intercepts of the two equations.

Evidence from both of the comparative methods that I used in this paper lends credence to the hypothesis that arid-zone birds generally have a reduced TEWL. For both the allometric approach and the method of phylogenetically independent contrasts, comparisons between arid and mesic species were highly significant. When the analysis was restricted to passerines only, the same trends were evident.

Suprisingly few intraspecific comparisons have been made for TEWL for species that live in both mesic and arid regions. Hinds and MacMillen (pers. comm.) have studied the TEWL of populations of House Finches from the coast of southern California and from the much drier Mojave Desert. The desert population had a mean TEWL of 0.97 ml H_2O/day, whereas the coastal population had a significantly higher TEWL, 1.50 ml H_2O/day (Table 1). The advantage of the Hinds and MacMillen study was that measurements were made by the same investigators using the same equipment. Although pairwise comparisons make less convincing evolutionary arguments (Garland and Adolph 1994), the findings of the study by Hinds and MacMillen are consistent with the hypothesis of reduced TEWL in arid-zone birds.

What are the physiological mechanisms acted upon by natural selection to bring about an adaptive reduction in evaporative water loss. Although a definitive answer to this question is not possible, it could be that selection has reduced cutaneous water loss in arid forms by increasing the lipid layer in the skin, which would increase the resistance to water-vapor diffusion (Webster and Bernstein 1987). Another possibility is that desert forms have increased their ability to minimize water lost during expiration. Cactus Wrens recover 74% of the water lost from nasal passages on inspiration before air is exhaled (Schmidt-Nielsen et al. 1970). It seems possible that desert forms might have an increased number of convolutions of nasal chonchae and, thus, increased surface area; in this way they could recover more water from expired air than mesic forms. Another possibility is that some desert birds could have an unknown physiological trait that would allow them to exhale unsaturated air. One case of an arid-adapted bird, the Ostrich, exhaling unsaturated air has been reported, although the mechanism was not resolved (Withers et al. 1981).

In a seminal essay, Bartholomew (1972) concluded that small birds have greater preformed

TABLE 3. Comparison of oxygen consumption and total evaporative water loss of birds.

Body mass (g)	Oxygen consumption[a] (liters O_2/day)	TEWL[b] (ml H_2O/day)	TEWL/ O_2	MWP[c]/ TEWL
Passerines				
10	0.85	0.9	0.94	0.54
100	4.50	5.6	1.24	0.46
1,000	23.90	34.2	1.43	0.40
Nonpasserines				
10	0.5	0.9	1.73	0.33
100	2.8	5.6	2.00	0.29
1,000	15.3	34.2	2.23	0.26
10,000	83.0	210.4	2.53	0.23
100,000	449.8	1,294.2	2.88	0.20

[a] Metabolic rate calculated from Aschoff and Pohl (1970) for nocturnal phase. Metabolic rate converted to oxygen consumption using 1 Kcal = 4.8 liter O_2 (Schmidt-Nielsen 1983).

[b] Total evaporative water loss calculated as log TEWL (ml H_2O/day) = $-0.833 + 0.789 \log M$.

[c] Metabolic water production calculated using the relationship 0.576 ml H_2O/liter O_2 (Schmidt-Nielsen 1983).

water requirements than do larger birds, an idea based on the fact that the slope of the Crawford and Lasiewski equation was significantly lower than the slope for standard oxygen consumption (Lasiewski and Dawson 1967, Aschoff and Pohl 1970). Ratios of TEWL to oxygen consumption were thought to be higher in smaller birds and, as a result, smaller species replace less of their evaporative water with metabolic water production. The results from my analysis indicate that small birds do not have greater TEWL relative to their oxygen consumption than do larger species. To illustrate this concept, I have computed oxygen consumption for various sizes of birds and calculated ratios of both TEWL and metabolic water production to oxygen consumption using the equation for all birds from my phylogenetically-independent-contrasts analysis to predict TEWL (Table 3). I find no evidence that small birds replenish proportionately less of their TEWL with metabolic water than do larger birds.

In summary, I have found that the slope of the relationship between TEWL and body mass in birds is higher than originally reported by Crawford and Lasiewski (1968), and nearly approximates or exceeds the slope for basal or standard metabolic rate in birds. Even at thermally unstressful temperatures, arid-adapted species have a reduced TEWL, a diminution amounting to as much as a third less than more

mesic counterparts. This indicates selection has operated to reduce water loss in these species even when they are experiencing moderate temperatures. Small birds are not disadvantaged when it comes to the amount of water lost per unit oxygen consumed. This finding is consistent with the fact that many species inhabiting deserts have a mass of less than 50 g.

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