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# The Adjustment of Avian Metabolic Rates and Water Fluxes to Desert Environments

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## ABSTRACT

We tested the hypothesis that birds in arid environments, where primary productivity is low and surface water is scarce, have reduced energy expenditure and water loss compared with their mesic counterparts. Using both conventional least squares regression and regression based on phylogenetically independent contrasts, we showed that birds from desert habitats have reduced basal and field metabolic rates compared with species from mesic areas. Previous work showed that desert birds have reduced rates of total evaporative water loss when exposed to moderate environmental temperatures in the laboratory. We tested whether reduced rates of total evaporative water loss translate into low field water fluxes. Conventional ANCOVA indicated that desert birds have reduced water fluxes, but an analysis based on phylogenetically independent contrasts did not support this finding, despite the wide array of taxonomic affiliations of species in the data set. We conclude that the high ambient temperatures, the low primary productivity, and the water scarcity in desert environments have selected for or resulted in reduced rates of energy expenditure and evaporative water loss in birds that live in these climes.

## Introduction

High ambient air temperatures ( $T_a$ ), low primary productivity, and lack of surface water place deserts among the most extreme terrestrial environments on earth. One might expect that birds living in desert conditions require specific physiological and behavioral adaptations. Low primary productivity could con-

strain energy intake and potentially favors individuals with low rates of energy expenditure (Louw and Seely 1982; Williams and Tieleman 2000b). Likewise, lack of surface water ostensibly limits water intake and could select for low evaporative and excretory water losses. Despite these predictions, early work on metabolism and water flux of birds did not show any general physiological differences between desert and nondesert species (Bartholomew and Cade 1963; Bartholomew 1964; Dawson and Schmidt-Nielsen 1964; Serventy 1971; Dawson 1984). Since then, some studies on desert birds, typically on a single species, have reported low basal metabolic rate (BMR; Dawson and Bennett 1973; Weathers 1979; Arad and Marder 1982; Withers and Williams 1990), field metabolic rate (FMR; Nagy 1987), and water flux (Nagy and Peterson 1988). Still, apparently due to the lack of general comparisons, the idea that desert birds do not possess unique physiological adaptations to their environment has persisted (Maclean 1996).

Dawson and Bartholomew (1968), who originally suggested a lack of physiological adaptations among desert birds, cautioned that most early work was based on birds from North American deserts, regions that are relatively young on an evolutionary time scale (Axelrod 1983; Mead 1987), and suggested that adding species from Old World deserts might alter our concepts about physiological adjustments of birds to desert environments. During the past 2 decades, studies of birds in the deserts of Africa, the Middle East, and Australia have substantially increased the number of species for which data on energy and water balance are available. A first step toward understanding the physiological adaptations that enable birds to exist in arid environments, might come from a comparison of laboratory traits like BMR and total evaporative water loss (TEWL) between desert and nondesert species. Laboratory measurements gain evolutionary significance if one finds consistent patterns in data collected in the field, where natural selection operates on a combination of physiology and behavior. Since the advent of the doubly labeled water technique (Lifson and McClintock 1966; Nagy 1975; Speakman 1997), there are now sufficient field data on energy expenditure and water flux of birds to determine whether the results from laboratory measurements can be extended to field situations. In addition, the introduction of statistical methods that take into account phylogeny (Felsenstein 1985; Harvey and Pagel 1991; Garland et al. 1992) justifies a reevaluation of BMR, FMR, and water flux in desert birds compared with their nondesert counterparts.

A review based on 102 species showed that TEWL is lower

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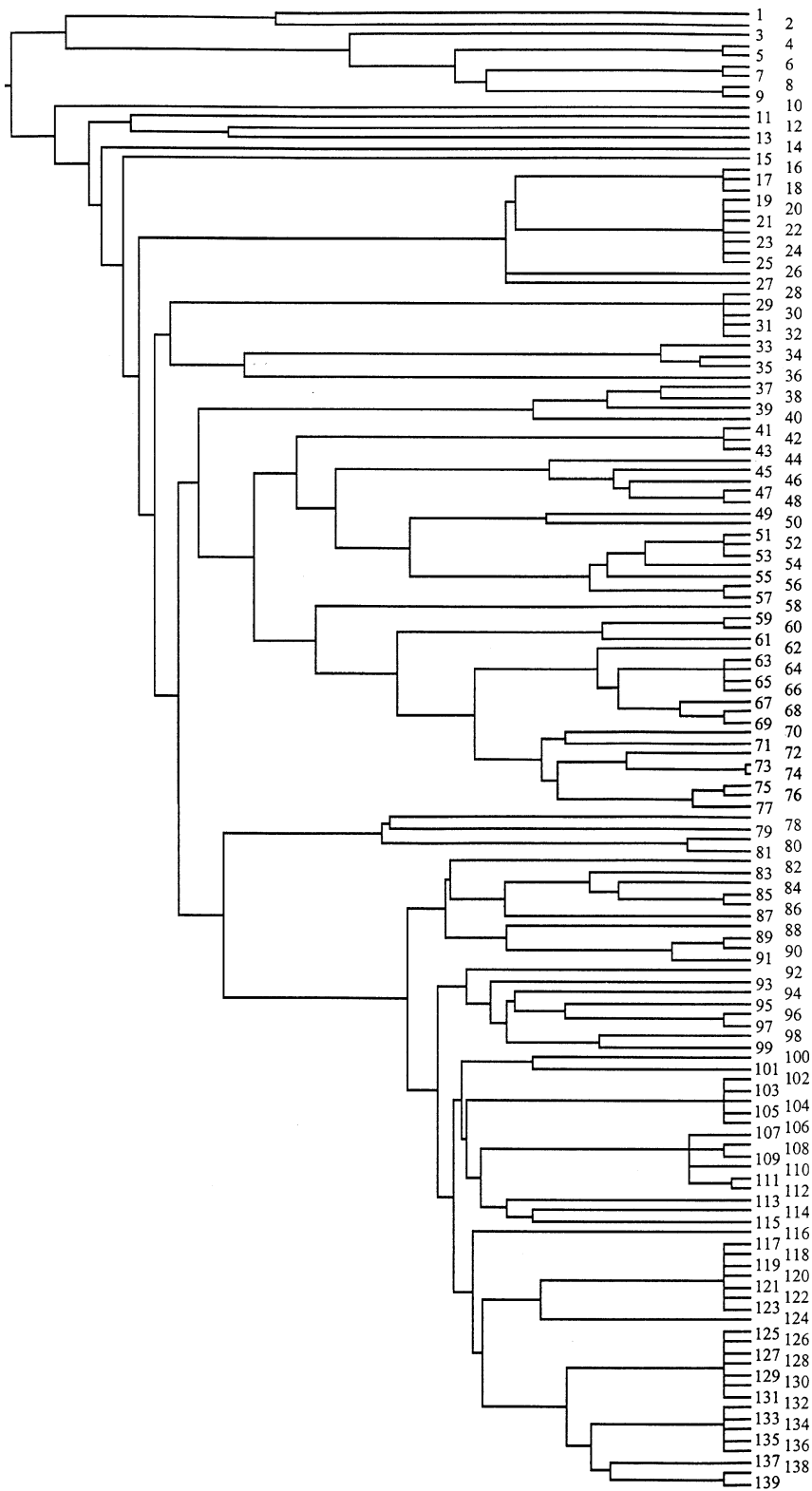


Figure 1. Hypothesized phylogenetic relationship of nonpasserine (1–77) and passerine (78–139) birds. Branch lengths are  $\Delta T_{50}H$  values based on DNA-DNA hybridization (Sibley and Ahlquist 1990). Total  $\Delta T_{50}H$  units = 28.0. Numbers refer to the species in Table 1.

Table 1: Body mass, basal metabolic rate (BMR), field metabolic rate (FMR), and water flux (WF) of birds from arid and mesic environments

Species	Environment	Mass (g)	BMR (kJ d <sup>-1</sup> )	FMR (kJ d <sup>-1</sup> )	WF (mL d <sup>-1</sup> )	Reference
Struthioniformes:						
Struthionidae:						
Ostrich <i>Struthio camelus</i> (1)	Arid	95,400, 88,250, 88,250	5,195.2	18,040.0	3,129	Withers 1983; Williams et al. 1993
Casuariidae:						
Emu <i>Dromaius novaehollandiae</i> (2)	Arid	40,700	3,240.8	...	...	Maloney and Dawson 1993
Galliformes:						
Phasianidae:						
Gambel's quail <i>Callipepla gambelii</i> (3)	Arid	145	57.0	90.8	17.7	Goldstein and Nagy 1985
Blue grouse <i>Dendragapus obscurus</i> (4)	Mesic	1,131	428.3	656.7	...	Pekins et al. 1992, 1994
White-tailed ptarmigan <i>Lagopus leucurus</i> (5)	Mesic	326, 368.3, ...	205.6	326.0	...	Johnson 1968; Thomas et al. 1994
King quail <i>Coturnix chinensis</i> (6)	Mesic	44.9	31.8	...	...	Roberts and Baudinette 1986
Stubble quail <i>Coturnix pectoralis</i> (7)	Arid	95.8	54.9	...	...	Roberts and Baudinette 1986
Chukar <i>Alectoris chukar</i> (8)	Arid	..., 426.3, 446.2	...	269.7	66.8	Alkon et al. 1982, 1985; Degen et al. 1983; Kam et al. 1987
Sand partridge <i>Ammoperdix heyi</i> (9)	Arid	..., 187.7, 184.9	...	160.3	20.5	Degen et al. 1983; Kam et al. 1987
Piciformes:						
Picidae:						
Acorn woodpecker <i>Melanerpes formicivorus</i> (10)	Mesic	73.1, 82.3, 82.3	63.8	195.0	29.3	Weathers et al. 1990
Upupiformes:						
Phoeniculidae:						
Green woodhoopoe <i>Phoeniculus purpureus</i> (11)	Mesic	75.9	58.0	...	...	Williams et al. 1991a
Coraciiformes:						
Cerylidae:						
Pied kingfisher <i>Ceryle rudis</i> (12)	Mesic	76	...	210.0	...	Reyer and Westerterp 1985
Meropidae:						
Blue-throated bee-eater <i>Merops viridis</i> (13)	Mesic	33.8	25.7	77.4	...	Bryant et al. 1984
Coliiformes:						
Coliidae:						
Speckled mousebird <i>Colius striatus</i> (14)	Mesic	50	25.3	...	...	Bartholomew and Trost 1970
Cuculiformes:						
Neomorphidae:						
Roadrunner <i>Geococcyx californianus</i> (15)	Arid	284.7	126.2	...	...	Calder and Schmidt-Nielsen 1967
Psittaciformes:						
Psittacidae:						
Sulfur-crested cockatoo <i>Cacatua galerita</i> (16)	Mesic	776.1	295.3	...	...	Williams et al. 1991b
Galah <i>Cacatua roseicapilla</i> (17)	Arid	268.7, 307.0, 307.0	107.9	349.0	44.1	Williams et al. 1991b
Long-billed corella <i>Cacatua aenuirostris</i> (18)	Mesic	549.9	273.7	...	...	Williams et al. 1991b
Port Lincoln parrot <i>Barnardius zonarius</i> (19)	Arid	131.8, 145.0, 145.0	68.4	189.0	25.1	Williams et al. 1991
Barred parakeet <i>Bolborhynchus lineola</i> (20)	Mesic	55.7	37.8	...	...	Bucher 1981
Budgerigar <i>Melopsittacus undulatus</i> (21)	Arid	33.7, 27.9, 27.9	31.8	59.1	11	Weathers and Schoenbaechler 1976; Williams et al. 1991b
Elegant parrot <i>Neophema elegans</i> (22)	Mesic	48.9	54.2	...	...	Lindgren 1973
Rock parrot <i>Neophema petrophila</i> (23)	Mesic	48.4, 62.8, 62.8	54.8	106.1	11.1	Williams et al. 1991b
Red-tailed black cockatoo <i>Calyptorhynchus magnificus</i> (24)	Arid	535.3	256.4	...	...	Williams et al. 1991b

Table 1 (Continued)

Species	Environment	Mass (g)	BMR (kJ d <sup>-1</sup> )	FMR (kJ d <sup>-1</sup> )	WF (mL d <sup>-1</sup> )	Reference
Rainbow lorikeet <i>Trichoglossus haematodus</i> (25)	Mesic	137.1	103.1	...	...	Williams et al. 1991b
Monk parakeet <i>Myiopsitta monachus</i> (26)	Mesic	81.7	52.7	...	...	Weathers and Caccamise 1975, 1978
Green-cheeked amazon <i>Amazona viridigenalis</i> (27)	Mesic	337.8	128.5	...	...	Bucher 1985
Trochiliformes:						
Trochilidae:						
Black-chinned hummingbird <i>Archilochus alexandri</i> (28)	Mesic	3.7	...	29.1	6.3	Powers and Conley 1994
Anna's hummingbird <i>Calypte anna</i> (29)	Mesic	4.5	...	31.8	7.35	Powers and Nagy 1988
Bronze-tailed plumbeateer <i>Chalybura urochrysis</i> (30)	Mesic	7.2	...	58.1	14.47	Weathers and Stiles 1989
Blue-throated hummingbird <i>Lampornis clemenciae</i> (31)	Mesic	8.8	...	81.7	15.2	Powers and Conley 1994
Crowned woodnymphs <i>Thalurania colombica</i> (32)	Mesic	4.9	...	37.9	11.72	Weathers and Stiles 1989
Strigiformes:						
Strigidae:						
Spotted owl <i>Strix occidentalis</i> (33)	Mesic	571	231.1	...	...	Ganey et al. 1993
Snowy owl <i>Nyctea scandiaca</i> (34)	Mesic	2,024	384.7	...	...	Gessaman 1972
Great horned owl <i>Bubo virginianus</i> (35)	Mesic	1,000	284.3	...	...	Ganey et al. 1993
Eurostopoidea:						
Spotted-eared nightjar <i>Eurostopodus argus</i> (36)	Arid	88	35.2	...	...	Dawson and Fisher 1969
Columbiformes:						
Columbidae:						
Spinifex pigeon <i>Geophaps plumifera</i> (37)	Arid	89, 86.9, 86.9	36.5	73.5	18.4	Withers and Williams 1990; Williams et al. 1995
White-tipped dove <i>Leptotila verreauxi</i> (38)	Mesic	131	77.0	...	...	Vleck and Vleck 1979
Pigeon <i>Columba livia</i> (39)	Mesic	314.6	150.1	...	...	Calder and Schmidt-Nielsen 1966, 1967
Inca dove <i>Columbina inca</i> (40)	Mesic	40.4	23.2	...	...	MacMillen and Trost 1967; Lasiewski and Seymour 1972
Ciconiiformes:						
Pteroclididae:						
Pin-tailed sandgrouse <i>Pterocles alchata</i> (41)	Arid	242.9	84.8	...	...	Hinsley et al. 1993
Double-banded sandgrouse <i>Pterocles bicinctus</i> (42)	Arid	195	...	...	17.4	J. Williams and R. Little, unpublished data
Black-bellied sandgrouse <i>Pterocles orientalis</i> (43)	Arid	386.4	168.3	...	...	Hinsley et al. 1993
Scolopacidae:						
American woodcock <i>Scolopax minor</i> (44)	Mesic	156.7	92.1	...	...	Vander Haegen et al. 1994
Common redshank <i>Tringa totanus</i> (45)	Mesic	149	134.8	...	...	Speakman 1984
Ruddy turnstone <i>Arenaria interpres</i> (46)	Mesic	114	85.5	...	...	Kersten and Piersma 1987
Sanderling <i>Calidris alba</i> (47)	Mesic	54.6	...	141.0	...	Castro et al. 1992
Red knot <i>Calidris canutus</i> (48)	Mesic	130	76	...	...	Piersma et al. 1995
Charadriidae:						
Grey plover <i>Pluvialis squatarola</i> (49)	Mesic	226	153.8	...	...	Kersten and Piersma 1987
Oystercatcher <i>Haematopus ostralegus</i> (50)	Mesic	554	251.4	...	...	Kersten and Piersma 1987

Table 1 (Continued)

Species	Environment	Mass (g)	BMR (kJ d <sup>-1</sup> )	FMR (kJ d <sup>-1</sup> )	WF (mL d <sup>-1</sup> )	Reference
Laridae:						
Dovekie <i>Alle alle</i> (51)	Mesic	163.7	...	696.1	136.6	Gabrielsen et al. 1991
Common murre <i>Uria aalge</i> (52)	Mesic	940	...	1,789.0	...	Cairns et al. 1990
Thick-billed murre <i>Uria lomvia</i> (53)	Mesic	834	...	1,475.0	...	Roby and Ricklefs 1986
Black guillemot <i>Cephus grylle</i> (54)	Mesic	..., 400, 380	...	750.0	210.52	Roby and Ricklefs 1986; Mehlum et al. 1993
Least auklet <i>Aethia pusilla</i> (55)	Mesic	83.5	...	357.9	71.1	Roby and Ricklefs 1986
Black-legged kittiwake <i>Rissa tridactyla</i> (56)	Mesic	391.6	...	995.0	206	Gabrielsen et al. 1987
Sooty tern <i>Sterna fuscata</i> (57)	Mesic	184	...	340.4	...	Flint and Nagy 1984
Falconidae:						
Common kestrel <i>Falco tinnunculus</i> (58)	Mesic	196.2	...	331.3	...	Masman et al. 1988
Sulidae:						
Northern gannet <i>Morus bassanus</i> (59)	Mesic	3,030, 3,210, ...	701	4,865.0	...	Birt-Friesen et al. 1989
Cape gannet <i>Morus capensis</i> (60)	Mesic	2,620	731	4,670.0	336	Adams et al. 1991
Red-footed booby <i>Sula sula</i> (61)	Mesic	1,069.9	...	1,224.3	...	Ballance 1995
Spheniscidae:						
King penguin <i>Aptenodytes patagonicus</i> (62)	Mesic	13,000	...	11,232.0	...	Kooyman et al. 1992
Macaroni penguin <i>Eudyptes chrysolophus</i> (63)	Mesic	..., 4,233.3, 3,900	...	4,492.8	803	Davis et al. 1989
Adelie penguin <i>Pygoscelis adeliae</i> (64)	Mesic	3,985	...	5,603.0	...	Nagy and Obst 1992
Chinstrap penguin <i>Pygoscelis antarctica</i> (65)	Mesic	3,806	...	5,597.0	1,419.6	Moreno and Sanz 1996
Gentoo penguin <i>Pygoscelis papua</i> (66)	Mesic	..., 6,000, 6,100	...	8,294.4	615.5	Davis et al. 1989
Little penguin <i>Eudyptula minor</i> (67)	Mesic	1,043.8	...	1,758.4	389.3	Gales and Green 1990
Jack-ass penguin <i>Spheniscus demersus</i> (68)	Mesic	3,170	...	2,414.3	418.4	Nagy et al. 1984
Humboldt penguin <i>Spheniscus humboldti</i> (69)	Mesic	3,870	820.65	...	...	Drent and Stonehouse 1971
Procellariidae:						
Wilson's storm-petrel <i>Oceanites oceanicus</i> (70)	Mesic	42.2	...	157.0	25.3	Obst et al. 1987
Leach's storm-petrel <i>Oceanodroma leucorhoa</i> (71)	Mesic	47.5, 45.1, 47.7	46.2	131.8	25.1	Ricklefs et al. 1986; Montevicchi et al. 1992
Northern fulmar <i>Fulmarus glacialis</i> (72)	Mesic	755.4	...	1,444.5	...	Furness and Bryant 1996
South Georgia diving-petrel <i>Pelecanoides georgicus</i> (73)	Mesic	119.2	...	463.5	104.5	Roby and Ricklefs 1986
Common diving-petrel <i>Pelecanoides urinatrix</i> (74)	Mesic	132.3	...	556.6	123.5	Roby and Ricklefs 1986
Grey-headed albatross <i>Diomedea chrysostoma</i> (75)	Mesic	3,706.5	...	2,401.9	1,010	Costa and Prince 1987
Wandering albatross <i>Diomedea exulans</i> (76)	Mesic	8,417	...	3,354.0	1,430	Adams et al. 1986
Laysan albatross <i>Diomedea immutabilis</i> (77)	Mesic	3,064	...	2,072.0	525	Pettit et al. 1988
Passeriformes:						
Furnariidae:						
Buff-throated woodcreeper <i>Xiphorhynchus guttatus</i> (78)	Mesic	45.2	38.7	...	...	Vleck and Vleck 1979
Thamnophilidae:						
Slaty antshrike <i>Thamnophilus punctatus</i> (79)	Mesic	21	29.6	...	...	Vleck and Vleck 1979
Tyrannidae:						
Red-capped manakin <i>Pipra mentalis</i> (80)	Mesic	14.5	25.7	...	...	Vleck and Vleck 1979
Golden-collared manakin <i>Manacus vitellinus</i> (81)	Mesic	15.6	24.1	...	...	Vleck and Vleck 1979
Maluridae:						
Superb fairywren <i>Malurus cyaneus</i> (82)	Mesic	8.2	...	34.0	5.4	Weathers and Stiles 1989

Table 1 (Continued)

Species	Environment	Mass (g)	BMR (kJ d <sup>-1</sup> )	FMR (kJ d <sup>-1</sup> )	WF (mL d <sup>-1</sup> )	Reference
Meliphagidae:						
Eastern spinebill <i>Acanthorhynchus tenuirostris</i> (83)	Mesic	9.7	21.5	52.9	8.7	Weathers et al. 1996
White-fronted chat <i>Ephthianura albifrons</i> (84)	Arid	12.4	...	...	7.7	Rooke et al. 1983
New Holland honeyeater <i>Phylidonyris novaehollandiae</i> (85)	Mesic	17.3	27.4	77.6	10.7	Weathers et al. 1996
Crescent honeyeater <i>Phylidonyris pyrrhoptera</i> (86)	Mesic	14.6	27.8	75.9	12.5	Weathers et al. 1996
Pardalotidae:						
White-browed scrubwren <i>Sericornis frontalis</i> (87)	Arid	11.4	...	...	9.4	Rooke et al. 1983
Laniidae:						
Northern shrike <i>Lanius excubitor</i> (88)	Arid	61.8	48.1	112.1	12.3	Degen et al. 1992
Corvidae:						
Yellow-billed magpie <i>Pica nuttalli</i> (89)	Mesic	151.9	126.9	...	...	Hayworth and Weathers 1984
Black-billed magpie <i>Pica pica</i> (90)	Mesic	158.9	103.2	...	...	Hayworth and Weathers 1984
Grey jay <i>Perisoreus canadensis</i> (91)	Mesic	71.2	59.1	...	...	Veghte 1964
Phainopepla <i>Phainopepla nitens</i> (92)	Arid	22.7	...	79.1	...	Weathers and Nagy 1980
Cinclidae:						
Dipper <i>Cinclus cinclus</i> (93)	Mesic	64.2	...	251.9	...	Bryant and Tatner 1988
Muscicapidae:						
Western bluebird <i>Sialia mexicana</i> (94)	Mesic	27.5	36.5	95.0	...	Mock 1991
European pied flycatcher <i>Ficedula hypoleuca</i> (95)	Mesic	15, 12.4, ...	21.1	69.8	...	Moreno and Carlson 1989; Moreno et al. 1995
Northern wheatear <i>Oenanthe oenanthe</i> (96)	Mesic	22.5, 24.3, 24.3	35.4	91.4	20.4	Moreno 1989; Tatner 1990 ; Moreno and Hillstrom 1992
European robin <i>Erithacus rubecula</i> (97)	Mesic	18.6	...	64.8	...	Tatner and Bryant 1986
Sturnidae:						
Northern mockingbird <i>Mimus polyglottos</i> (98)	Mesic	46.9	...	121.0	42.1	Utter 1971
Common starling <i>Sturnus vulgaris</i> (99)	Mesic	75.5	...	299.5	...	Ricklefs and Williams 1984
Certhiidae:						
Verdin <i>Auriparus flaviceps</i> (100)	Arid	6.6	13.4	30.0	3.1	Webster and Weathers 1988
House wren <i>Troglodytes aedon</i> (101)	Mesic	10.5	...	60.8	9.66	Dykstra and Karasov 1993
Paridae:						
Coal tit <i>Parus ater</i> (102)	Mesic	9.5	...	47.4	3.6	Moreno et al. 1988
Siberian tit <i>Parus cinctus</i> (103)	Mesic	12.8	...	51.4	...	Carlson et al. 1993
Crested tit <i>Parus cristatus</i> (104)	Mesic	11.1	...	40.6	4.5	Moreno et al. 1988
Great tit <i>Parus major</i> (105)	Mesic	18	...	101.0	...	Daan et al. 1990
Willow tit <i>Parus montanus</i> (106)	Mesic	..., 11.4, 11.3	...	44.2	4.9	Moreno et al. 1988; Carlson et al. 1993
Hirundinidae:						
Northern house martin <i>Delichon urbica</i> (107)	Mesic	18.1	...	87.2	...	Hails and Bryant 1979; Bryant and Westerterp 1980; Westerterp and Bryant 1984

Table 1 (Continued)

Species	Environment	Mass (g)	BMR (kJ d <sup>-1</sup> )	FMR (kJ d <sup>-1</sup> )	WF (mL d <sup>-1</sup> )	Reference
Barn swallow <i>Hirundo rustica</i> (108)	Mesic	19.1	...	109.6	...	Westerterp and Bryant 1984
Pacific swallow <i>Hirundo tahitica</i> (109)	Mesic	14.1	16.6	76.6	...	Bryant et al. 1984
Tree swallow <i>Tachycineta bicolor</i> (110)	Mesic	19.7	...	130.7	18.4	Williams 1988
Purple martin <i>Progne subis</i> (111)	Mesic	49	...	156.2	31.9	Utter 1971; Utter and LeFebvre 1973
Sand martin <i>Riparia riparia</i> (112)	Mesic	14.3	...	81.7	...	Westerterp and Bryant 1984
Zosteropidae:						
Silver-eye <i>Zosterops lateralis</i> (113)	Mesic	..., 9.9, 9.5	...	43.0	18.1	Rooke et al. 1983
Sylviidae:						
Spinifex-bird <i>Eremiornis carteri</i> (114)	Arid	11.7, 12, 12	16.4	44.2	7.8	Ambrose et al. 1996
Arabian babbler <i>Turdoides squamiceps</i> (115)	Arid	73.3	...	117.4	28.5	A. Anava and A. Degen, unpublished data
Alaudidae:						
Dune lark <i>Certhilauda erythrochlamys</i> (116)	Arid	27.3, 27.1, 27.1	35.6	93.0	5.6	Williams 2000
Passeridae:						
Cut-throat finch <i>Amadina fasciata</i> (117)	Mesic	17.2	18.5	...	...	Marschall and Prinzing 1991
Gouldian finch <i>Chloebia gouldiae</i> (118)	Mesic	15.5	18.7	...	...	Marschall and Prinzing 1991
Orange-cheeked waxbill <i>Estrilda melpoda</i> (119)	Mesic	7.5	11.3	...	...	Marschall and Prinzing 1991
Black-rumped waxbill <i>Estrilda troglodytes</i> (120)	Mesic	6.7	15.2	57.4	...	Weathers and Nagy 1984
Dusky munia <i>Lonchura fuscans</i> (121)	Mesic	9.5	8.6	...	...	Weathers 1977
Java sparrow <i>Padda oryzivora</i> (122)	Mesic	25.4	26.6	...	...	Marschall and Prinzing 1991
Zebra finch <i>Taeniopygia guttata</i> (123)	Arid	12.1	17.5	...	...	Calder 1964; Marschall and Prinzing 1991
Sociable weaver <i>Philetairus socius</i> (124)	Arid	25.5	...	48.7	4.6	Williams and DuPlessis 1996
Fringillidae:						
Common redpoll <i>Carduelis flammea</i> (125)	Mesic	14.5	27.9	...	...	Pohl and West 1973
Pine siskin <i>Carduelis pinus</i> (126)	Mesic	13.8	30.0	...	...	Dawson and Carey 1976
Cassin's finch <i>Carpodacus cassinii</i> (127)	Mesic	26.8	32.0	...	...	Weathers et al. 1980; Weathers 1981
House finch <i>Carpodacus mexicanus</i> (128)	Arid	20.4	26.8	...	...	Weathers 1981
Apapane <i>Himatione sanguinea</i> (129)	Mesic	13.5	25.8	...	...	Weathers et al. 1983
Palila <i>Loxioides bailleui</i> (130)	Mesic	36	40.0	...	...	Weathers and Van Riper 1982
American goldfinch <i>Carduelis tristis</i> (131)	Mesic	13.6	29.0	...	...	Dawson and Carey 1976
Dark-eyed junco <i>Junco hyemalis</i> (132)	Mesic	19.6	...	76.6	9.4	Weathers and Sullivan 1993
Yellow-eyed junco <i>Junco phaeonotus</i> (133)	Mesic	19.7, 19.5, 19.7	31.2	71.7	7.7	Weathers and Sullivan 1993
Black-throated sparrow <i>Amphispiza bilineata</i> (134)	Arid	11.6	17.3	...	...	Weathers 1981



Table 1 (Continued)

Species	Environment	Mass (g)	BMR (kJ d <sup>-1</sup> )	FMR (kJ d <sup>-1</sup> )	WF (mL d <sup>-1</sup> )	Reference
Song sparrow <i>Melospiza melodia</i> (135)	Mesic	20	...	...	11.1	Stephenson and Minnich 1974
Savannah sparrow <i>Passerculus sandwichensis</i> (136)	Mesic	17.7, 18.1, 19.1	26.2	77.8	15.5	Williams and Hansell 1981; Williams and Nagy 1985; Williams 1987
Red-winged blackbird <i>Agelaius phoeniceus</i> (137)	Mesic	46.3	41.7	...	...	Weathers 1981
Northern cardinal <i>Cardinalis cardinalis</i> (138)	Mesic	41.3	43.4	...	...	Hinds and Calder 1973
Pyrrhuloxia <i>Cardinalis sinuatus</i> (139)	Arid	32	34.2	...	...	Hinds and Calder 1973

Note. Multiple values for body mass (g) refer to BMR, FMR, and WF, respectively.

in desert birds compared with nondesert species, at least when measured in the laboratory at 25°C (Williams 1996). This finding suggests one or more physiological mechanisms that may reduce evaporative water loss (Tieleman and Williams 1999; Tieleman et al. 1999), and that may affect field water fluxes in desert birds. In a compilation of field water fluxes, Nagy and Peterson (1988) found that desert birds ( $n = 5$ ) had lower water fluxes than nondesert birds. However, their conventional least squares regression analysis included multiple data for the same species, an approach that inflates the degrees of freedom for statistical tests and that may bias estimates of the slope and intercept in regression analysis (Pagel and Harvey 1988).

Desert birds can potentially reduce TEWL and water flux if they reduce BMR and FMR, respectively, thereby producing less heat. Although several authors have suggested that desert birds have a reduced BMR compared with nondesert species (Dawson and Bennett 1973; Weathers 1979; Arad and Marder 1982; Withers and Williams 1990; Schleucher et al. 1991), a formal comparative analysis has not been performed. Recently, Nagy et al. (1999) have reported that FMR of desert species was 50% of FMR for nondesert birds, but their analysis did not take into account phylogenetic relatedness between species.

In this article, we examine the relationships between BMR, FMR, water flux, and body mass in birds and investigate whether these traits are reduced in desert birds compared with birds from mesic environments. First, we use conventional least squares regression, a technique that assumes an evolutionary model where all species have radiated from a common ancestor and have evolved at equal rates (Purvis and Garland 1993). Second, we use Felsenstein's (1985) method of phylogenetically independent contrasts to attempt to control for relatedness between species in an evolutionary model where species are placed in a branching hierarchical phylogeny. The specific questions that we address are: (1) Do birds from desert environments have a lower BMR than birds from mesic habitats? (2) Do birds from desert regions have a reduced FMR compared with birds from mesic areas? (3) Do birds from desert envi-

ronments have a low water flux in comparison with birds from nondesert areas?

## Material and Methods

Basal metabolic rate is measured under a specified set of experimental conditions that renders it an important basis of comparison among species (King 1974). We assembled data for BMR that were obtained on postabsorptive, inactive birds in darkened metabolic chambers during the rest phase of their circadian cycle at thermally neutral  $T_a$ 's. Some species show seasonal variation in BMR, whereas others do not (Weathers 1980; Piersma et al. 1995; Dawson and O'Connor 1996). We included species in our analysis regardless of the time of year measurements were made. We excluded studies that did not adequately describe experimental conditions (e.g., Kendeigh et al. 1977), studies that reported resting metabolic rate (sensu Bennett and Harvey 1987) instead of BMR, and studies that did not establish a thermoneutral zone (e.g., Yarbrough 1971).

FMR and water flux have been determined in a wide variety of field situations, often during the nestling phase of the breeding season. We included data from studies that used the doubly labeled water (DLW) technique on free-living birds without regard to time of the year but excluded data on incubating birds. This excluded eight species, all from mesic areas, and excluded data on several penguins that fast for extensive periods during incubation. In cases where studies reported several values (e.g., per season) for one species, or in cases where a number of independent studies reported values for the same species, we averaged the data to obtain one value per species. We excluded data for water flux of species that were not in water balance during the study (Weathers and Nagy 1980, 1984).

The classification of species as desert or nondesert is problematic because desert conditions are the result of a variety of factors, such as solar radiation, rainfall,  $T_a$ , and wind, which taken together form a continuum. We followed the judgment

Table 2: Allometric equations based on conventional least squares regression analyses

Equation	<i>Y</i>	<i>a</i>	<i>b</i>	<i>n</i>	<i>r</i> <sup>2</sup>	SE <sub>intercept</sub>	SE <sub>slope</sub>	<i>P</i>
1. All birds .....	BMR	.575	.638	82	.96	.030	.014	<.001
2. Desert .....	BMR	.505	.644	21	...	.036	.014	<.001
3. Nondesert .....	BMR	.584	.644	61	...	.028	.014	<.001
7. All birds .....	FMR	.983	.703	81	.93	.046	.021	<.001
8. Desert .....	FMR	.741	.704	15	...	.050	.017	<.001
9. Nondesert .....	FMR	1.035	.704	66	...	.037	.017	<.001
13. All birds .....	WF	.159	.719	58	.87	.079	.037	<.001
14. Desert .....	WF	-.126	.724	17	...	.075	.028	<.001
15. Nondesert .....	WF	.263	.724	41	...	.062	.028	<.001

Note. Equations are presented as  $\log Y = a + b \log M$ , where *Y* can be basal metabolic rate (BMR; kJ d<sup>-1</sup>), field metabolic rate (FMR; kJ d<sup>-1</sup>), or water flux (WF; mL d<sup>-1</sup>), and *M* = mass (g).

of the original authors in placing a species in the desert or nondesert category.

We used the topology of Sibley and Ahlquist (1990), based on DNA-DNA hybridization, to construct a phylogeny of the 139 bird species in our analysis (Fig. 1). Species that were not included in Sibley and Ahlquist (1990) were placed close to sister species, either with the advice from specialists or based on the classification scheme of Sibley and Monroe (1990). Branch lengths were based on  $\Delta T_{50}H$  values, unless the species were part of an unresolved polytomy, in which case we assigned an arbitrary branch length of one (Williams 1996). Common and taxonomic species names follow Sibley and Monroe (1990). For each analysis (BMR, FMR, water flux), we used the appropriate subset (Table 1) of the phylogenetic tree (Fig. 1).

We used the PDTREE module of the Phylogenetic Diversity Analysis Program (Garland et al. 1993, 1999) to compute Felsenstein's (1985) standardized independent contrasts for log-transformed values of body mass (g), BMR (kJ d<sup>-1</sup>), FMR (kJ d<sup>-1</sup>), and water flux (mL d<sup>-1</sup>). To test whether the contrasts were adequately standardized, we regressed the absolute values of the standardized contrasts against the standard deviations and verified that none of the variables (log BMR, log FMR, log water flux, log body mass) showed a linear trend (Garland et al. 1992). When a variable showed a linear trend, we performed a square root transformation of the branch lengths and obtained proper standardization (Díaz-Uriarte and Garland 1998).

Regression analyses of the standardized independent contrasts for log BMR, log FMR, and log water flux against those for log body mass, forced through the origin (Garland et al. 1992; Garland and Janis 1993), yielded estimates of the slopes of these relationships without the effects of genealogical history. To determine the intercepts, we solved the equation  $Y = a + bX$ , where *X* and *Y* are the root-node contrast values for log BMR (or log FMR or log water flux) and log body mass, respectively (Garland et al. 1999). The degrees of freedom were

calculated as the number of independent contrasts minus the number of unresolved branches (Purvis and Garland 1993).

To determine whether desert birds differed from those from mesic environments with respect to BMR, FMR, and water flux, we calculated independent contrasts for environment scored as zero for desert and one for nondesert (Williams 1996). Plots of the standardized independent contrasts of environment and their standard deviations revealed whether standardization had been adequate. If standardization was inadequate, we performed square root transformations of the branch lengths that successfully eliminated the linear trends. Using stepwise multiple regression through the origin, we tested for the influence of environment on BMR, FMR, and water flux in birds with the standardized contrasts of these log-transformed variables as the dependent variable and the standardized contrasts of environment and log body mass as independent variables (Williams 1996). The entry criterion for selection of variables in the equation was  $P = 0.05$ .

Statistical tests were carried out with the PDTREE module in the Phylogenetic Diversity Analysis Program (Garland et al. 1993, 1999) or with SPSS (1999). Means are presented  $\pm 1$  SD.

## Results

### Basal Metabolic Rate

Based on conventional analysis, log BMR varied positively with log body mass among all birds with a slope of 0.638 (Table 2, Eq. [1]). ANCOVA for equations for desert and nondesert species (Table 2) revealed that the slopes of these two equations did not differ significantly ( $F_{1,78} = 0.247$ ,  $P = 0.62$ ). Assuming a common slope, the intercept was significantly lower for the equation for desert birds (Table 2, Eq. [2]) than for nondesert species (Table 2, Eq. [3];  $F_{1,79} = 9.534$ ,  $P = 0.003$ ).

Using phylogenetically independent contrasts, log BMR varied positively with log body mass among all birds with a slope of 0.677 (Table 3, Eq. [4]). A stepwise multiple regression

through the origin of standardized contrasts for log BMR as dependent variable and standardized contrasts of log body mass, environment, and the interaction between log body mass and environment as independent variables disclosed that the latter interaction had an insignificant effect ( $t = 0.28, P = 0.78$ ), while environment had a significant effect in the equation ( $t = 2.82, P < 0.01$ ). We then separated the data on BMR based on the environment, generated a phylogenetic tree for each subset of data (based on Fig. 1), and calculated an equation for desert and nondesert birds (Table 3, Eq. [5], [6]). Hence, desert birds had a reduced BMR using both methods of analysis (Fig. 2).

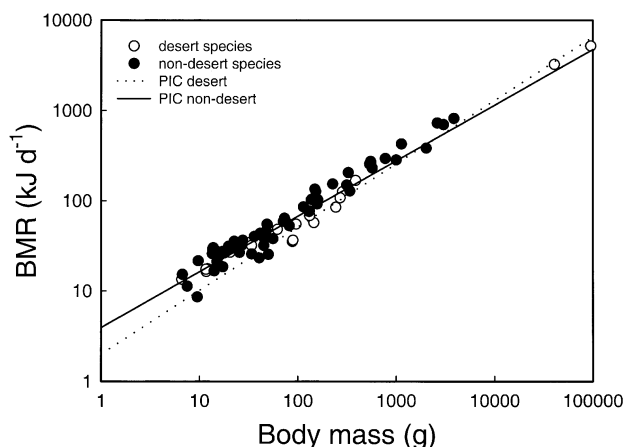


Figure 2. Logarithmic plot of basal metabolic rate (BMR) in desert birds (unfilled circles) and nondesert birds (filled circles) versus body mass. The allometric equations obtained by the method of phylogenetically independent contrasts are plotted for desert birds (dotted line) and nondesert species (solid line).

Field Metabolic Rate

Conventional analysis of log FMR versus log body mass for all birds yielded a slope of 0.703 (Table 2, Eq. [7]). We compared FMR between desert birds and nondesert species with ANCOVA and found that the slopes of equations were not significantly different ( $F_{1,77} = 1.7, P < 0.20$ ). Assuming a common slope, Equation (8) (Table 2), for desert birds, had a significantly lower intercept than did Equation (9) (Table 2), for nondesert species ( $F_{1,78} = 49.6, P < 0.001$ ).

The relationship between log FMR and log body mass among all birds, which resulted from a regression of independent contrast analysis, had a slope of 0.671 (Table 3, Eq. [10]). Stepwise multiple regression of standardized contrasts for log FMR as dependent variable and standardized contrasts of log body mass, environment, and the interaction between log body mass and environment as independent variables revealed that environment had a significant effect in the equation ( $t = 2.11, P < 0.04$ ), whereas the interaction had no significant influence ( $t = -1.57, P = 0.12$ ). We then separated the data on FMR based on environment, constructed a phylogenetic tree for each data set (based on Fig. 1), and calculated equations for each environmental category (Table 3, Eq. [11], [12]). Birds from deserts had significantly lower FMRs in both methods of analysis (Fig. 3A).

Field Water Flux

Based on conventional analysis of data for all birds, log water flux related to log body mass with a slope of 0.719 (Table 2, Eq. [13]). We tested for differences in water flux between desert and nondesert birds using ANCOVA and found that the slopes of the regression lines for desert and nondesert species did not differ significantly ( $F_{1,54} = 0.9, P = 0.34$ ; Fig. 3B). Assuming a common slope, Equation (14) (Table 2), for water flux in desert birds, had a significantly lower intercept than Equation (15) (Table 2), for nondesert species ( $F_{1,55} = 40.7, P < 0.001$ ).

The regression for log water flux and log body mass in all birds, based on phylogenetically independent contrasts, had a slope of 0.659 (Table 3, Eq. [16]). Stepwise multiple regression of standardized contrasts for log water flux as dependent variable and standardized contrasts of log body mass, environment, and the interaction between the latter two as independent variables revealed that neither the interaction term ( $t = -0.52, P = 0.60$ ) nor environment had a significant effect in the equa-

Table 3: Allometric equations based on phylogenetically independent contrast analyses

Equation	Y	a	b	df	r <sup>2</sup>	CI <sub>intercept</sub>	CI <sub>slope</sub>	F <sub>slope</sub>
4. All birds	BMR	.416	.677	52	.89	.204–.628	.623–.731	626.5
5. Desert	BMR	.304	.702	17	.96	.061–.547	.632–.772	442.2
6. Nondesert	BMR	.595	.616	41	.80	.326–.864	.535–.697	233.5
10. All birds	FMR	.907	.671	56	.85	.639–1.175	.606–.736	431.9
11. Desert	FMR	.719	.691	12	.96	.456–.982	.610–.772	351.6
12. Nondesert	FMR	.969	.676	44	.83	.892–1.046	.383–.969	316.2
16. All birds	WF	.150	.659	41	.64	-.356 to .656	.525–.793	98.7

Note. Equations are presented as  $\log Y = a + b \log M$ , where Y can be basal metabolic rate (BMR; kJ d<sup>-1</sup>), field metabolic rate (FMR; kJ d<sup>-1</sup>) or water flux (WF; mL d<sup>-1</sup>), and M = mass (g). CI is 95% confidence interval.

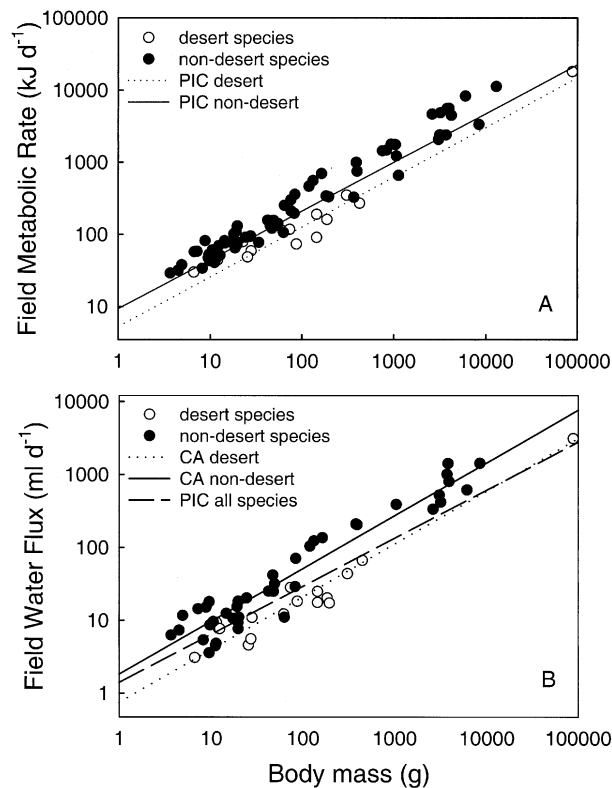


Figure 3. A, Logarithmic plot of field metabolic rate in desert birds (unfilled circles) and nondesert birds (filled circles) versus body mass. The allometric equations obtained by the method of phylogenetically independent contrasts are plotted for desert birds (dotted line) and nondesert species (solid line). B, Logarithmic plot of field water flux in birds from desert (unfilled circles) and nondesert (filled circles) habitats versus body mass. The allometric equations generated with conventional least squares regression analysis are plotted for desert (dotted line) and nondesert species (solid line). The equation for all birds obtained with the method of phylogenetically independent contrasts is represented by the dashed line.

tion ( $t = 0.68$ ,  $P = 0.50$ ). In contrast to our conventional analysis, the phylogenetic analysis did not reveal a significantly reduced water flux in desert birds compared with their nondesert counterparts.

#### Elimination of Seabirds from Analyses

Our initial analyses could be questioned because we included seabirds and terrestrial birds in our category of nondesert species. We repeated the comparison of BMR, FMR, and water flux between desert and nondesert birds with both comparative methods but eliminated seabirds (Laridae, Sulidae, Procellariidae, and Spheniscidae) from the data set. Results were consistent with our analyses that included all birds: BMR and FMR were reduced in desert birds compared with their mesic coun-

terparts, irrespective of the comparative method used. Water flux was significantly lower in desert birds based on conventional analysis but not based on independent contrasts.

#### Discussion

We have shown that birds from desert habitats have a reduced BMR and FMR compared with species that live in mesic areas. The low energy expenditure of desert birds is accompanied by reduced rates of TEWL in the laboratory (Williams 1996). Water flux was reduced in desert birds when evaluated using conventional ANCOVA, but the analysis based on phylogenetically independent contrasts did not yield a significant reduction in water flux in desert birds. Usually, if data are phylogenetically diverse, as in this study, phylogenetic and conventional analysis arrive at similar conclusions (Weathers and Siegel 1995; Ricklefs and Starck 1996). The broad representation of taxa in our analyses (Table 1) and in the analysis of TEWL (Williams 1996) supported the hypotheses that reductions in the rates of energy expenditure and evaporative water loss of desert birds are adjustments to their environment, where primary productivity is low and surface water is scarce, and indicated that these conclusions were not solely based on a few taxonomic groups that have reduced rates of metabolism and water loss in general. The extent to which reduced rates of metabolism and water loss in desert birds are attributable to genetic differences, to acclimatization, or to a combination of both remains unresolved.

#### Basal Metabolic Rate

We used two comparative methods to determine the relationship between BMR and body mass for all birds. Although the slope and intercept of our conventional least squares regression equation fell within the 95% confidence intervals around the slope and intercept of the equation based on phylogenetically independent contrasts, the predictions made by the two lines differed considerably (Table 4). BMR of a 10-g bird as predicted by Equation (4) (Table 3) based on independent contrasts was 24% lower than when predicted by conventional analysis. Comparing our Equation (4) (Table 3) for BMR with another phylogenetically corrected equation for BMR in birds, based on a Monte Carlo simulation ( $\log \text{BMR} = 0.625 + 0.635 \log M$ ; Reynolds and Lee 1996), we found a steeper slope and a lower intercept. This resulted in lower predictions for BMR when the predictions were based on our phylogenetic analysis (Table 4). The allometric equation of Reynolds and Lee (1996) should be used with caution because there is no evidence that Monte Carlo simulations give unbiased estimates of slope and intercept. In addition to the Monte Carlo simulation, Reynolds and Lee (1996) analyzed their data using phylogenetically independent contrasts and found a slope of 0.722. Compared with the slope from our analysis using independent contrasts (0.677),

their slope is larger but still falls within our 95% confidence interval of 0.632–0.731.

The differences between our equations and the ones published by Reynolds and Lee (1996) may be partly the result of different criteria for BMR. Their analyses are based to a large degree on data from Bennett and Harvey (1987), who did not restrict their analysis to BMR but included data for resting birds that might include some costs of thermoregulation. Furthermore, Bennett and Harvey (1987) included data published by Kendeigh et al. (1977), who did not provide a detailed description of their methods. To test whether the nighttime measurements of BMR for 121 species, which were reported by Kendeigh et al. (1977) but had not been published in peer-reviewed journals, were consistent with data published in peer-reviewed journals, we compared these two data sets with conventional ANCOVA. The slopes of the regression lines through each data set did not differ significantly ( $F_{1,200} = 1.4$ ,  $P > 0.24$ ), but the intercept was significantly higher (by 10%) for the equation based on the data of Kendeigh et al. (1977;  $F_{1,201} = 15.2$ ,  $P < 0.001$ ). If allometric equations for BMR are to provide a reference for comparative work, data should be carefully selected before analyses.

Both comparative methods support the hypothesis that desert birds generally have a reduced BMR (Table 5). Based on conventional ANCOVA, we found a reduction of 17% in BMR from desert birds compared with their nondesert counterparts, independent of body mass. Based on the analysis that took into account the phylogeny of birds, the reduction in BMR varied from 38% in a 10-g bird to 7% in a 1,000-g bird. Despite the agreement of both methods that desert birds generally have a reduced BMR, problems arise when one attempts to compare predictions for mesic birds with those for desert birds. For example, predictions of BMR for desert birds using conventional analysis correspond more closely to predictions for nondesert species than to those for desert species based on independent contrasts (Table 5).

Reductions in BMR can result from a smaller amount of metabolically active tissue and/or metabolic tissue that is less active per unit mass. Less metabolically active tissue can be reflected in the size of a number of organs that have been shown to contribute substantially to BMR, for example, heart, kidneys, brain, and intestine (Daan et al. 1990; Konarzewski and Diamond 1995; Piersma et al. 1996; Kersten et al. 1998). Less active metabolic tissue can result from differences at the cellular level, such as reduced thyroxine secretion rates (Yousef and Johnson 1975; Scott et al. 1976; Merkt and Taylor 1994), fewer  $\text{Na}^+$ - $\text{K}^+$  pumps, fewer mitochondria per unit tissue, a decreased total mitochondrial inner membrane area, or lower protein turnover (Rolfe and Brown 1997).

#### *Field Metabolic Rate*

Using two comparative methods, we obtained allometric equations that relate FMR to body mass in all birds. The slope and

intercept of the conventional least squares regression were within the 95% confidence intervals of those for Equation (10) (Table 3) based on independent contrasts. The slopes and intercepts of earlier allometries for FMR, based on conventional least squares regression analyses (Nagy et al. 1999) and smaller sample sizes (Nagy 1987; Williams et al. 1993), also fell within the 95% confidence intervals for slope and intercept of Equation (10) (Table 3). Despite the general agreement between methods, the difference in predictions of FMR from conventional and phylogenetic analyses is a concern. Predictions based on independent contrasts (Table 3, Eq. [12]) are 22%–33% lower for birds over a body size range of 10–1,000 g than predictions based on conventional least squares regression (Table 2, Eq. [7]).

Desert birds had a significantly lower FMR than nondesert species, irrespective of the comparative method used for this analysis. Based on conventional ANCOVA, we found that FMR was reduced by 49% in desert birds compared with nondesert species, a confirmation of the conclusion by Nagy et al. (1999). In agreement with this result, the independent contrast comparison revealed a reduction of about 40% in desert birds. Despite general agreement about the reduced FMR of desert birds, predictions for FMR of desert and nondesert species based on either of the comparative methods may differ (Table 5).

Reductions in FMR can be brought about by physiological and/or behavioral adjustments. The corresponding finding of a 17% reduction in BMR in desert birds suggests that the reduction in FMR is only partially attributable to physiological differences. The relatively high  $T_a$ 's in many deserts might decrease the energetic costs for thermoregulation compared with some nondesert areas, thereby reducing FMR in desert birds. In addition, some desert species spend long periods at rest in the shade during the middle part of the day, a behavior that could reduce FMR.

Desert environments have three characteristics that might influence selection on FMR and BMR. First, the low primary productivity would favor individuals with low FMR. Low FMR would be accompanied by relatively low reproductive outputs and reflected in reduced BMR and small organs (Daan et al. 1990). Second, the relatively high  $T_a$ 's in deserts reduce thermoregulatory requirements and might result in a combined reduction of FMR and BMR. As food intake likely decreases in parallel to energy demand, organ systems involved in catabolism or elimination of wastes can decrease in size when food intake decreases, thereby reducing BMR (Williams 1999; Williams and Tieleman 2000a). Third, lack of drinking water may influence the energy balance of desert birds. In an environment where water is scarce, the need for evaporative cooling can be reduced by lowering endogenous heat production. Most likely, low primary productivity, high  $T_a$ 's, and lack of drinking water act in concert to select for a combination of reduced FMR and BMR in desert birds. The relative importance of the

Table 4: Comparison of predicted rates of basal metabolic rate (BMR) from Equation (1), based on conventional analysis (CA), Equation (4), based on phylogenetically independent contrasts (PIC), and the equation provided by Reynolds and Lee (1996)

Mass (g)	BMR (kJ d <sup>-1</sup> )		
	Equation (1) CA	Equation (4) PIC	Reynolds and Lee (1996)
10 .....	16.3	12.4	18.2
100 .....	71.0	58.9	78.6
1,000 .....	308.3	279.9	339.2

different selective pressures may vary with season and might be revealed by experimental manipulations of energy and water resources.

*Field Water Flux*

We described the relationship between water flux and body mass in all birds with two allometric equations based on different statistical methods. The slope and intercept of our conventional least squares regression equation, and those from earlier studies (Nagy and Peterson 1988; Williams et al. 1993), fell within the 95% confidence intervals around the slope and intercept of our equation based on phylogenetic analysis. Despite this general agreement, the equation based on independent contrasts predicted lower rates of water flux than the equation based on conventional analysis.

Water fluxes of desert birds were 59% lower than those for nondesert species when the comparison was based on conventional ANCOVA (Table 5). In contrast, the stepwise multiple regression analysis using independent contrasts revealed no significant effect of environment on the water fluxes of birds. The conflicting results produced by the different comparative methods caught us by surprise after the seemingly striking difference between the data for desert and nondesert species (Fig. 3B). We have investigated the reasons for this disparity. The variance around the equation based on independent contrasts is considerably larger (Table 3;  $r^2 = 0.64$ ) than the variance around the equation based on conventional analysis (Table 2;  $r^2 = 0.87$ ). We explored whether differences could be attributed to a few outlying contrasts, but visual inspection of plots of contrasts did not reveal this to be a problem.

A reduced water flux of desert birds in the field would correspond to the low TEWL rates for desert birds measured in the laboratory (Williams 1996) and would suggest the presence of physiological and behavioral mechanisms that reduce water loss in desert birds. Tolerance of hyperthermia has been suggested to reduce evaporative water loss in birds (Calder and King 1974; Weathers 1981; Dawson 1984; Withers and Williams 1990), but no evidence is available to suggest that desert birds

elevate their body temperature more than nondesert species (Tieleman and Williams 1999). Second, some birds may reduce cutaneous water loss by altering the lipid composition of their skin (Webster and Bernstein 1987; Menon et al. 1989, 1996). Third, desert birds may have the ability to minimize water lost during expiration, either by exhaling unsaturated air (Withers et al. 1981) or by recovering water with the aid of counter-current heat exchange in the nasal passages (Schmidt-Nielsen et al. 1970). An experimental test of the latter hypothesis confirmed water recovery in one of two lark species but only at  $T_a$ 's up to 25°C (Tieleman et al. 1999). A fourth way to reduce evaporative water loss would be an improved potential for dry heat loss through an increased dry heat transfer coefficient ( $h$ ) when  $T_a$ 's are below body temperature and through a decreased  $h$  when  $T_a$ 's exceed body temperature. Fifth, desert birds may minimize excretory water loss, although currently there is no evidence that the concentrating ability of their kidneys is improved over nondesert species (Goldstein and Braun 1989; Williams and Tieleman 2000b). Sixth, reduced metabolic heat production would decrease the need for evaporative cooling in desert birds. Seventh, desert birds may increase their oxygen extraction efficiency to reduce ventilation and concurrent evaporative water loss. In addition to these physiological mechanisms, behavioral adjustments, including microclimate selection (Wolf and Walsberg 1995; Wolf et al. 1995; Williams et al. 1999) and reduced activity during the middle part of the day (Schleucher 1993; Hinsley 1994), probably play an important role in minimizing water loss in desert birds in the field.

An oft-applied measure to express the effectiveness of mech-

Table 5: Basal metabolic rate (BMR), field metabolic rate (FMR), and water flux as predicted for 10-, 100-, and 1,000-g birds using the allometric equations obtained by conventional ANCOVA and by the method of phylogenetically independent contrasts

Mass (g)	Conventional Analysis		Phylogenetic Analysis	
	Arid	Mesic	Arid	Mesic
BMR (kJ d <sup>-1</sup> ):				
10 .....	14.1	16.9	10.1	16.3
100 .....	62.1	74.5	51.1	67.1
1,000 .....	273.5	328.1	257.0	277.3
FMR (kJ d <sup>-1</sup> ):				
10 .....	27.9	54.8	25.7	44.2
100 .....	140.9	277.3	126.2	209.4
1,000 .....	712.9	1,402.8	619.4	993.1
Water flux (mL d <sup>-1</sup> ):				
10 .....	4.0	9.7	...	...
100 .....	21.0	51.4	...	...
1,000 .....	111.2	272.3	...	...

Note. Values are geometric means.

animals that conserve water is the water economy index (WEI; mL water  $\text{kJ}^{-1}$ ), calculated as the ratio of water flux and FMR (Nagy and Peterson 1988). Nagy and Peterson (1988) hypothesized that desert vertebrates conserve water more effectively than their nondesert relatives but found no statistical support when they tested this hypothesis in birds. After calculating the WEI, and verifying that the WEI was not related to body mass, we compared the WEI for desert and nondesert birds. The average WEI for desert species ( $0.16 \pm 0.061$ ,  $n = 14$ ) was significantly lower than for nondesert birds ( $0.20 \pm 0.089$ ,  $n = 40$ ;  $t = -1.65$ ,  $P = 0.05$ ).

Interpretations of the WEI are complex because water flux values do not necessarily reflect minimum water requirements, confounding inferences about water-conserving mechanisms based on WEI values. The WEI can be interpreted in light of the environmental context of a species only if one makes assumptions about drinking and about water and energy content of the diet. Assuming that water and energy intake reflect minimum requirements, one might expect a low WEI for animals in cold environments, where little or no evaporative cooling is required and a high metabolism is needed for thermoregulation. In contrast to this situation, many desert birds live in environments with high  $T_a$ 's where the need for evaporative cooling is potentially large. Given the low rates of metabolism of desert birds, one would not expect an unusually low WEI if water flux reflected these thermoregulatory needs. A reduced water flux can only be accomplished if either a large amount of water lost for evaporative cooling is compensated by a small loss of water through excretory pathways or if the potential for heat loss via nonevaporative pathways is increased, reducing the amount of water required for evaporative cooling. Therefore, under the assumption that water and energy intake reflect minimum requirements, the combination of a reduced FMR and a low WEI in desert birds suggests that water may dictate energy expenditure in desert environments.

#### *Different Results from Different Comparative Methods*

This article addresses the question whether birds in desert environments differ from nondesert species with respect to three potentially adaptive traits (BMR, FMR, and water flux) using multispecies comparisons that included species from the entire taxonomic spectrum of the modern-day avifauna. In light of the ongoing debate about the proper statistical analysis for multispecies allometries (Weathers and Siegel 1995; Westoby et al. 1995; Martins and Hansen 1996; Ricklefs and Starck 1996; Starck 1998), we used two comparative methods, namely, conventional ANCOVA and regression analysis based on phylogenetically independent contrasts (Felsenstein 1985; Garland et al. 1992). Although Ricklefs and Starck (1996) have found that the results of these two methods are usually in agreement, we found some striking differences in our results. Qualitatively, the two methods agreed that desert birds have reduced BMR

and FMR but disagreed about whether this was also the case for water flux. Quantitatively, predicting BMR, FMR, and water flux from the allometric equations obtained by the two comparative methods resulted in large differences.

The discussion about comparative methods has focused on finding the correct statistical approach, but considering the variety of goals for which comparative analyses are used, one can imagine that different purposes require different approaches. As long as the issue of how to correct for phylogeny is subject to debate (Miles and Dunham 1993; Weathers and Siegel 1995; Westoby et al. 1995; Martins and Hansen 1996; Ricklefs and Starck 1996; Björklund 1997; Starck 1998), it might be wise to combine broad multispecies comparisons with intrafamily or intraspecific comparisons to strengthen conclusions about adaptation.

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