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Physiological and behavioural correlates of life-history variation: a comparison between tropical and temperate zone House Wrens

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Summary

1. We studied physiological, behavioural and demographic traits of House Wrens (*Troglodytes aedon*) in tropical Panama and temperate zone Ohio to explore the hypothesis that tropical birds with higher adult survival rates invest less in annual reproduction than their temperate zone counterparts.

2. Compared with wrens from Ohio, Panamanian wrens invested fewer resources in a given reproductive episode, as quantified by lower parental field metabolic rate (FMR) and water influx rate (WIR), a smaller number of feeding trips to the nest, and fewer chicks per brood.

3. Whole organism FMR and WIR were only 13–15% lower in tropical wrens, but because of their larger body size, mass-specific values were reduced by 34–37%. We propose that selection acts indirectly on whole-organism energy expenditure in the tropical wrens by specifically reducing mass-specific levels of metabolic rate, thereby postponing deleterious effects of aging and thus decreasing intrinsic mortality.

4. Declines in parental FMR and fledgling survival probability in the course of the season suggest that reproduction is more time-constrained in the temperate zone, compressed by the shorter breeding season, and as a result more energetically costly for the parents. In contrast, tropical wrens do not show temporal variation in FMR and nesting success and therefore are less constrained to breeding during a short season.

Key-words: Bird, energy expenditure, feeding frequency, reproductive effort, water influx rate

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Introduction

A central tenet of life-history theory is that the balance between parental investment and self-maintenance reflects the relative contributions of current and future breeding attempts to reproductive value (Williams 1966; Cody 1971; Stearns 1992). A prediction stemming from this tenet is that parental investment in current offspring should be high when adult survival rate is low, but when survival is high, investment in each reproductive event should be low. Temperate zone birds tend to have larger clutches but lower survival rates than do tropical species and, as such, comparisons of reproductive strategies between temperate and tropical birds can provide important tests of life-history theory (Moreau 1944; Skutch 1976; Martin *et al.* 2000; Ferretti, Llambias & Martin 2005). Tropical environments are considered to be more thermally stable and offer more reliable food resources throughout the year and, as a result, tropical species are thought to have lower mortality (Fry 1980; Ricklefs 1997; Ghalambor & Martin 2001), whereas temperate zone birds live in an environment characterized by larger seasonal variation. Some temperate zone species endure less favourable environmental conditions during winter, whereas others migrate long distances to

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more southerly areas, both strategies associated with high energy costs and increased mortality (Sillett & Holmes 2002; Nelson *et al*. 2002).

To understand how phenotypes are adapted to the environment and how physiological and behavioural mechanisms could constrain demographic patterns, we need to simultaneously analyse physiological, behavioural and demographic processes of birds living in different ecological contexts. Especially during the breeding season, trade-offs between processes that enhance survival with those that increase current reproductive output should be apparent. Adult survival could be enhanced, and simultaneously current reproduction compromised, by low metabolic rates, which reduces starvation risk and perhaps oxidative damage to tissues (Speakman 2005), and by low activity levels, which not only decrease energy expenditure but may also reduce the risk of predation (Martin 2004). Assuming that intrinsic (e.g. ageing) and extrinsic (e.g. predation) causes of mortality are correlated (Cichon 1997), increased survival of tropical birds compared with temperate zone equivalents should result from a combination of physiological and ecological factors. Field metabolic rate (FMR) integrates energy expenditure for all activities throughout the daily cycle and thus provides an important assessment of ecological and behavioural components of the life history (Drent & Daan 1980). FMR may also indicate the level of potential metabolic damage incurred by reactive oxygen species, i.e. ageing (Pearl 1928; Speakman 2005). However, if ageing is related not to whole-organism but to mass-specific levels of metabolic rate (Speakman 2005), then one might expect animals to have lower mass-specific metabolic rates in tropical areas than in temperate regions.

Species with large geographical distributions are uniquely suited for investigations of life-history diversification, because adaptations to environmental conditions can be studied without the potentially confounding effects of phylogeny. An ideal species to provide insights into the physiological and behavioural underpinnings of demographic variation in an environmental context is the House Wren (*Troglodytes aedon* spp.), an inhabitant of the New World with a distribution ranging from Canada to southern South America (Johnson 1998). Temperate zone House Wrens (subspecies group *aedon*) have low annual survival, large investments in reproduction and fast development of young, whereas tropical complements (subspecies group *musculus*) show relatively high survival, small clutch sizes and slow nestling growth (Table 1). Thus, this species provides a model system to study the interplay between physiological and behavioural processes involved in life-history variation relative to environmental variation.

We studied energy expenditure, both basal and field metabolic rate, water influx and food provisioning behaviour of adult House Wrens in a tropical (Panama) and a temperate (Ohio) region during the time that parents reared offspring. We explored the hypothesis that tropical wrens with higher adult survival rates invest less in annual reproduction, as reflected in fewer feeding trips to provision their young, and have lower basal and field metabolic rates related to an expected reduction in intrinsic mortality. In addition, we investigated if the relatively large environmental variation during a breeding season in temperate regions has consequences for the amount of energy and time required to produce offspring, compared with the relatively constant environmental conditions in the tropics.

Materials and methods

STUDY AREAS: OHIO AND PANAMA

We worked during May–August 2003 in central Ohio on and around the Brown Environmental Center, operated by Kenyon College, Gambier, Ohio (40 N 82 W). We placed nestboxes in appropriate edge habitat in late March 2003. The breeding season of House Wrens in Ohio starts at the end of April and lasts about 3 months, during which time most pairs produce two clutches (Johnson 1998).

In the tropics, we conducted our study during March–July 2004 in park-like and residential areas of Gamboa and Summit Botanical Gardens, Republic of Panama (9 N 79 W). The area is characterized by humid lowland tropical forest with constant average annual temperatures of about 25 C and a rainy season from late April until December. We put up 65 House Wren boxes in early March, and searched for natural nests in addition. House Wrens breed year-round in Panama, but the major breeding activity occurs between April and October, the rainy season, during which time a pair on average breeds 1·35 times, but may produce up to three successful broods (Freed 1987).

TIMELINE OF MEASUREMENTS

We monitored nests daily towards the end of the incubation period to determine hatch date (day 0). Because the nestling period in Panama (19 days; Freed 1987) is longer than in Ohio (16–18 days; Johnson 1998), we shifted the timeline in Panama by one day to make measurements in the two areas more comparable with respect to stage of nestling development. We counted feeding rates of the parents when nestlings were of ages day 3, 6 and 10 in Ohio, and day 4, 7 and 11 in Panama. On day 5 (Ohio) and 6 (Panama) we captured both parents with nestbox traps or mist nets, injected them with doubly labelled water (see below) and banded them with colour bands for individual recognition. Ohio wrens also received an aluminium band supplied by the United States Fish and Wildlife Service. We measured tarsus length (mm), wing chord (mm), tail length (mm) and mass (g). We recaptured parents on day 7 (Ohio) and day 8 (Panama) to take a final blood sample for the doubly labelled water measurement. Finally, in Panama, parents were recaptured on day 12, and transported to the laboratory for body mass rate

Table 1. Demographic life-history attributes of House Wrens from tropical and temperate regions

Life-history variable	Tropics (Central America)	Temperate (Midwest US)	Reference
Annual survival	48%	29–30·7%	Freed (1987); Kendeigh & Baldwin (1937); Drilling & Thompson (1988)
Average no. eggs/clutch	3·5–3·6	6·0–7·5	Young (1994a); Johnson (1998)
No. clutch/year	1·35 (max. 3)	2	Freed (1987); Johnson (1998)
Migratory status	Resident	Migratory	Johnson (1998)
Incubation period (day)	14	12·5	Freed (1987); Johnson (1998)
Nestling period (day)	19	16–18	Freed (1987); Johnson (1998)
Post-fledging care period (day)	20–33	13	Freed (1987); Johnson (1998)

(BMR) measurements the same night. When we captured birds more than 3 h before the start of BMR measurements, we fed them mealworms. In addition, we fed the nestlings with mealworms or crickets after we caught the parents to compensate for the absence of parental feeding. We released the parents at their nest site after completing BMR measurements, usually between 01.00 and 03.00 h; all wrens resumed feeding their nestlings the following morning.

BEHAVIOURAL OBSERVATIONS AT THE NEST

Parents visiting the nest were observed with binoculars or a telescope from a distance of at least 25 m for 1 h between 06.00 and 10.00 (Ohio) and for 4–6 h between 06.00 and 12.00 h (Panama). Since adults were not colour banded until day 5 or 6, determination of sex of visiting adults was possible only on subsequent days. We compared feeding frequency between areas and between sexes.

DOUBLY LABELLED WATER MEASUREMENTS

Field metabolic rate (FMR) and water influx rate (WIR) were measured using the doubly labelled water (DLW) technique, in which the rate of decline of ^{2}H in the body water pool provides a measure of WIR (Nagy & Costa 1980), and the loss rates of both ^{2}H and ^{18}O yield an estimate of CO_2 production (Lifson & McClintock 1966; Nagy 1980; Speakman 1997). We caught birds and injected them with a 1:2 mixture of 99·9 atom percentage ^{2}H and 95·5 atom percentage ^{18}O using a 100- 1 Hamilton syringe (Hamilton Co, Reno, NV); the injection volume equalled 7 l per gram mass. We weighed birds with a Pesola spring balance. We kept females for a 1-h equilibration period (Williams & Nagy 1984), took a 80–100 l sample of blood (initial) from the brachial vein, and then banded and released them. Males were released immediately after injection and banding; estimates of CO_2 production were obtained for them using the single sample method (Ricklefs & Williams 1984; Speakman 1997). Our DLW procedures did not appear to disturb the subsequent behaviour of the wrens; birds generally returned to feed nestlings within 1–4 h of release. Usually after about 48 h (Ohio: 47·5 ± 00·43 hours, $n = 15$, range 45·3–50·6 h, and 24·1 h, $n = 1$; Panama: 47·0 ± 00·86 hours, $n = 16$, range 45·3–47·9 h, and 22·9 ± 00·80 hours, $n = 2$) we recaptured birds, took a second blood sample (final), measured body mass and released them. In each area, we took blood samples of four uninjected individuals to determine background levels of isotopes.

Validation studies on adult birds have shown that estimates of WIR using isotopes of hydrogen are usually within ± 10% of values obtained by standard laboratory methods (Nagy & Costa 1980), and average estimates of CO_2 production are within 8–10% while individual measurements of the latter can deviate up to 22% in small birds (Nagy 1980; Williams & Nagy 1984; Speakman 1997). Three validation studies on growing chicks suggest that the errors in the estimates of CO_2 production are in the same range as those for adult birds (Klaassen *et al.* 1989; Visser & Schekkerman 1999; Visser, Boon & Meijer 2000a). In Panama, we measured FMR and WIR of 7–10-day-old nestlings after their growth had slowed.

Isotope ratios of $^{2}H:^{1}H$ and $^{18}O:^{16}O$ were determined in duplicate (initial) or triplicate (final) for each sample at the Center for Isotope Research, University of Groningen (Visser & Schekkerman 1999). We calculated water influx with equation 3 of Nagy & Costa (1980), and corrected for isotope fractionation effects assuming an evaporative water loss of 25% and a fractionation factor of 0·941 (equation 7·6; Speakman 1997; Visser *et al.* 2000b). Total body water (TBW) was estimated from isotope dilution. For single sample measurements we estimated the initial isotope concentrations based on mass, injectate enrichment and injection volume. Rates of CO_2 production were calculated with equation 7·17 of Speakman (1997).

CO_2 production can be converted to energy expenditure when the diet is known; for an insectivorous diet, this conversion factor is 24·39 kJ l^{-1} CO_2 (Gessaman & Nagy 1988; Weathers & Sullivan 1989).

BASAL METABOLIC RATE OF ADULTS

We measured rates of oxygen consumption for post-absorptive birds during their nocturnal phase by standard flow-through respirometry methods (Williams 1999; Tieleman *et al.* 2002). Birds were placed in 2·1-litre stainless steel metabolism chambers that had a Lexan lid, rendered airtight with a rubber gasket. Birds perched

Table 2. Body mass (average ± SD), field metabolic rate (FMR, average ± SD) and water influx rate (WIR, average ± SD) of male and female House Wrens from tropical (Panama) and temperate zones (Ohio)

Location	Sex	Mass (g)	FMR (kJ day^{-1})	WIR (g day^{-1})	*n*
Tropics	Female	13·7 ± 0·78	38·6 ± 5·37	8·5 ± 1·68	9
	Male	14·1 ± 0·92	42·2 ± 5·91	9·6 ± 1·69	9
	Female and male	13·9 ± 0·84	40·4 ± 5·79	9·0 ± 1·73	18
Temperate	Female	10·5 ± 0·53	46·8 ± 5·54	10·4 ± 1·43	9
	Male	10·5 ± 0·35	46·1 ± 5·51	11·0 ± 1·42	7
	Female and male	10·5 ± 0·45	46·5 ± 5·35	10·7 ± 1·41	16

on a wire-mesh platform over a layer of mineral oil that trapped faeces. The chambers sat in a large cool-box fitted with a Peltier (Pelt-4, Sable Systems, Las Vegas, NV) to control ambient temperature (T_a) ±0·1 C. We measured oxygen consumption of birds at T_a of 31–32 C, a temperature within the thermoneutral zone of wrens (J. B. Williams, unpublished data). Compressed air coursed through columns of Drierite (W.A. Hammond Drierite Company, Xenia, Ohio, USA) to remove water, through previously calibrated (Levy 1964) mass flow controllers (2 SLPM; model FC-2900; Mykrolis, Billerica, MA) set at 518 ml min^{-1} (standard temperature and pressure, STP), and then into the chamber. Exiting air passed through an dew point hygrometer (Dewprime II, EdgeTech, Marlborough, MA) that had been recalibrated by the factory August 2003. In addition, we checked the calibration of the dew point hygrometer before experiments using a dew point generator and found <2% difference. A subsample of air was then routed through silica gel, Ascarite (Thomas Scientific, Swedesboro, NJ, USA), and silica gel to remove water and CO_2 before measuring the fractional concentration of O_2 with an oxygen analyser (S3A-II, Applied Electrochemistry, Pittsburgh, PA). We calibrated the entire system for measuring O_2 consumption by infusing pure O_2 into our chamber using a syringe pump with a precisely determined flow rate while simultaneously pushing room air through another port into the chamber via our flow controller. Comparisons of known O_2 influx via the syringe pump with calculated influx showed a mean difference of ±2% for our ten trials.

After birds were in the chamber for 3 h, we recorded O_2 concentration and dew points of inlet and outlet air, the temperature of the dew point hygrometer, and T_a in the chamber, using a data logger (CR23X, Campbell Scientific, Utah, UT). When, during the fourth hour of measurements, the traces for O_2 consumption were stable for at least 10 min, we noted these times and used these data for calculations. After completing the metabolism measurements, we immediately measured the body temperature of birds with a digital thermometer (Model Batt-12, Physitemp, Clifton, NJ) and a 36 gauge copper–constantan thermocouple. The relative humidity of outlet air was always between 10 and 40% (Lasiewski, Acosta & Bernstein 1966). Oxygen consumption was calculated with eqn (4) of Hill (1972). We used 20·08 J ml^{-1} O_2 to convert oxygen consumption to heat production (Schmidt-Nielsen 1997).

STATISTICAL ANALYSIS

Averages are reported ± 1 SD, unless otherwise specified. We used SPSS 12·0 for all statistical tests and used $P = 0\cdot05$ as the probability level for significance. Two–way interaction terms were always included in the ANOVA models, and removed when they were not significant before further testing the effects of main factors and covariates.

Results

PARENTAL EFFORT: BROOD SIZE AND WORK LOAD

Brood size was 40% smaller in Panama (3·6 ± 0·73 eggs, $n = 9$) than in Ohio (6·0 ± 0·93 eggs, $n = 8$), a significant difference ($t = 6\cdot1$, df = 15, $P < 0\cdot0001$).

Body mass of House Wrens was 32% larger in Panama than in Ohio (Table 2). With ANOVA we found a significant difference in body mass between locations ($F_{1,31} = 204\cdot7$, $P < 0\cdot0001$), but no significant difference between sexes ($F_{1,31} = 0\cdot49$, $P = 0\cdot49$).

Whole organism FMR of wrens was 13% lower in Panama than in Ohio (Table 2), a significant difference between locations ($F_{1,31} = 10\cdot1$, $P = 0\cdot003$), but differences between sexes were not significant ($F_{1,31} = 0\cdot71$, $P = 0\cdot41$). When we included body mass as covariate, location and mass had a significant effect on FMR but sex did not (location $F_{1,30} = 23\cdot6$, $P < 0\cdot0001$; mass $F_{1,30} = 13\cdot9$, $P = 0\cdot001$; sex $F_{1,30} = 0\cdot28$, $P = 0\cdot60$; Fig. 1). Mass-specific FMR, calculated as FMR divided by body mass, was 34% lower in Panama than in Ohio.

Field water influx rate of wrens was significantly lower in Panama than in Ohio, by 15% ($F_{1,31} = 9\cdot7$, $P = 0\cdot004$, Table 2), but differences between sexes were not significant ($F_{1,31} = 2\cdot67$, $P = 0\cdot11$). When we included body mass as covariate, only location had a significant effect on WIR, while mass and sex did not (location $F_{1,30} = 5\cdot9$, $P = 0\cdot021$; mass $F_{1,30} = 1\cdot9$, $P = 0\cdot18$; sex $F_{1,30} = 2\cdot2$, $P = 0\cdot15$; Fig. 1). When we calculated mass-specific WIR by dividing WIR by body mass, average values were 37% lower in Panama than in Ohio.

Parents in Ohio made more feeding trips per hour to the nest than birds in Panama (Fig. 2). Location and age of chicks significantly contributed to a stepwise multiple regression model explaining variation in feeding frequency ($r^2 = 0\cdot28$, df = 49, $F_{2,47} = 9\cdot09$, $P < 0\cdot0001$;

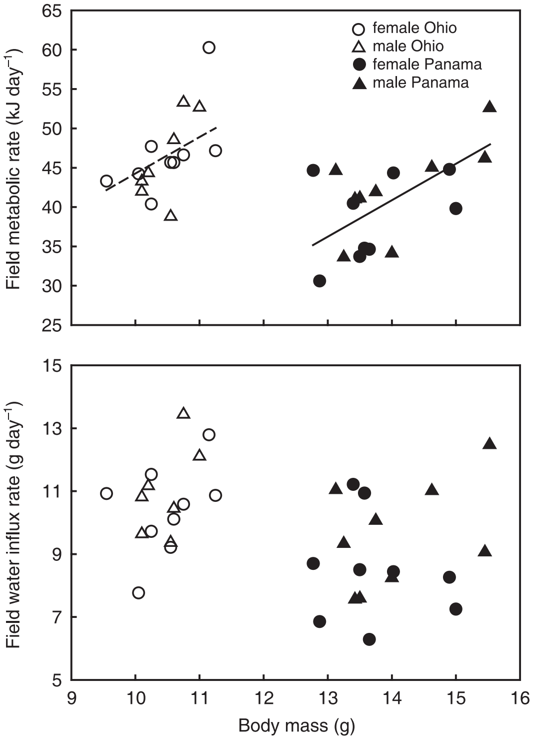

Fig. 1. Field metabolic rate (a) and field water influx rate (b) of adult wrens feeding nestlings as a function of body mass for male and female House Wrens in the tropics (Panama) and temperate zone (Ohio).

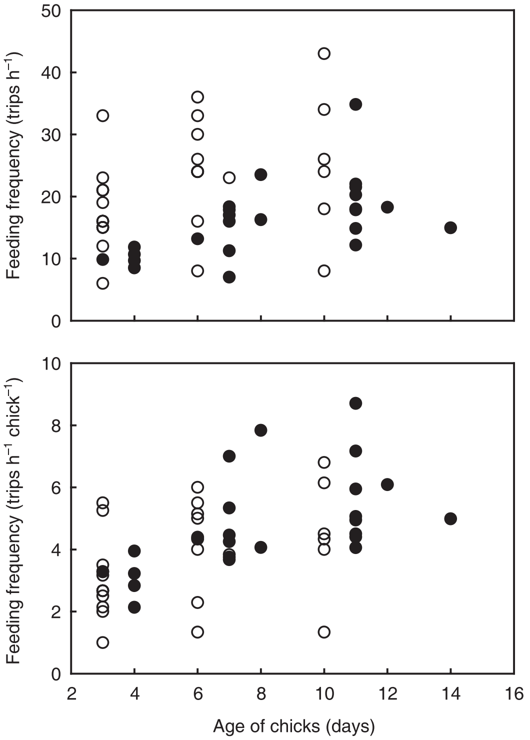

Fig. 2. Feeding frequency per nest (a) and per chick (b) as a function of nestling age in the tropics (Panama, black symbols) and temperate zone (Ohio, open symbols).

location $t = -3·90$, $P < 0·0001$; age $t = 3·14$, $P = 0·003$). When we added number of nestlings as independent factor to the model, location no longer had a significant effect, while number of nestlings made a highly significant contribution to the model ($r^2 = 0·31$, df = 49, $F_{2,47} = 10·7$, $P < 0·0001$; number of nestlings $t = 4·27$, $P < 0·0001$; location $t = -0·95$, $P = 0·35$; age $t = 3·17$, $P = 0·003$). Hence, feeding frequency per nestling did not differ between Panama and Ohio (Fig. 2). To determine how male and female shared feeding duties, we calculated the fraction of feeds contributed by the male to the total number of feedings (for nests where we could assign 60% or more of the observations to either male or female). The fractional contribution of males was 0·53 ± 0·32 ($n = 14$) in Ohio and 0·52 ± 0·09 ($n = 17$) in Panama, an insignificant difference ($t = 0·13$, $P = 0·89$).

SEASONAL TRENDS IN PARENTAL WORK EFFORT: ENERGY, WATER AND BEHAVIOUR

As the breeding season progressed, mass-specific FMR declined for birds in Ohio, but not in Panama, whereas mass-specific WIR increased for birds in Panama (Fig. 3). To test for seasonal patterns, we performed ANOVA with mass-specific FMR as dependent variable, location as fixed factor and Julian day as covariate. We found a significant effect of the interaction between location and Julian day on mass-specific FMR ($F_{1,30} = 5·40$, $P = 0·027$). Regression analyses for Ohio and Panama revealed that mass-specific FMR decreased by 12% in the course of the season in Ohio but remained relatively constant in Panama (Ohio slope −0·013 ± 0·006 (SE), $r^2 = 0·27$, df = 15, $P = 0·038$; Panama slope 0·004 ± 0·005 (SE), $r^2 = 0·05$, df = 17, $P = 0·40$). Similar analyses for mass-specific WIR showed a significant effect of the interaction between location and Julian day on mass-specific WIR ($F_{1,30} = 9·89$, $P = 0·004$). In contrast to mass-specific FMR however, mass-specific WIR did not change significantly in the course of the breeding season in Ohio, whereas values increased by 52% in Panama (Ohio slope −0·003 ± 0·002 (SE), $r^2 = 0·15$, df = 15, $P = 0·14$; Panama slope 0·004 ± 0·001 (SE), $r^2 = 0·05$, df = 17, $P = 0·40$).

The ratio between WIR and FMR, known as the water economy index (WEI), may convey information about diet (Nagy & Peterson 1988). WEI remained constant throughout the season in Ohio (−0·000 ± 0·000 (SE), $r^2 = 0·00$, df = 15, $P = 0·97$), but significantly increased in Panama (0·001 ± 0·000 (SE), $r^2 = 0·28$, df = 17, $P = 0·024$). Because our first measurements coincided with the start of the rainy season, the increase in WEI in Panama may reflect an increasing wetness of food items in the course of the season and/or a change in the insect composition of the diet.

To test whether parental feeding effort, expressed as number of feedings per nestling per hour, varied in the course of the season and between locations, we included Julian day and nestling age as covariates in an ANOVA

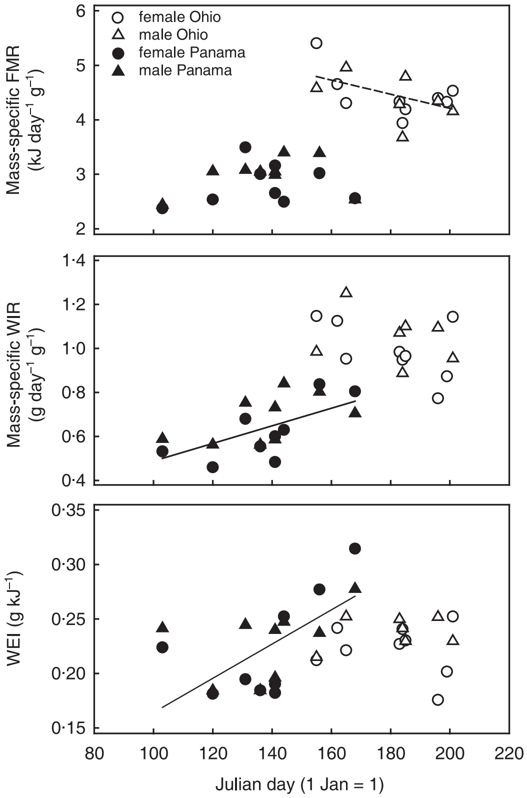

Fig. 3. Mass-specific field metabolic rate (a), water influx rate (b) and water economy index (c) of adult House Wrens feeding nestlings as a function of Julian day.

with location as fixed factor. Neither the interaction between location and Julian day ($F_{1,43} = 0{\cdot}09$, $P = 0{\cdot}77$), nor Julian day ($F_{1,46} = 1{\cdot}78$, $P = 0{\cdot}19$) significantly affected feeding frequency. Hence, changes in mass-specific FMR and WIR in the course of the season apparently were unrelated to parental feeding behaviour.

NESTLING FIELD METABOLIC RATE AND WATER INFLUX RATE

We compared FMR and WIR of House Wren nestlings from Panama with previously published data on nestlings from temperate zone Wisconsin (Dykstra & Karasov 1993a) (Table 3). Because Dykstra & Karasov (1993) calculated FMR differently from our method, we recalculated FMR and WIR using the same equations as theirs. We found that mass-specific FMR was 27% lower in tropical nestlings than in temperate zone chicks, while mass-specific WIR was on average 18% higher in the tropics.

BASAL METABOLIC RATE OF ADULTS

Basal metabolic rate for 14 House Wren adults in Panama (body mass 13·2 ± 0·62 g), measured when feeding 12-day-old nestlings, was 18·2 ± 1·79 kJ day^{-1}. We calculated BMR for Ohio House Wrens from literature as the active phase standard metabolic rate (25·1 kJ day^{-1}; Kendeigh, Dolnik & Gavrilov 1977) divided by 1·24 (Aschoff & Pohl 1970), i.e. 22·1 kJ day^{-1} for a 9·7-g wren. Mass-specific BMR was 47% lower in Panama (1·38 kJ day^{-1} g^{-1}) than in Ohio (2·28 kJ day^{-1} g^{-1}), comparable with the difference found for FMR. The ratio FMR/BMR was 2·1 in Panama and 1·9 in Ohio.

Discussion

Compared with House Wrens from Ohio, Panamanian wrens invested fewer resources in a given reproductive episode, as quantified by lower parental FMR and WIR, a lower number of feeding trips to the nest, and fewer chicks per brood (Table 1). Whole organism FMR and WIR were only 13–15% lower in the tropical wrens, but owing to their larger body size, mass-specific FMR and WIR were reduced by 34–37% in the tropical birds. The larger body mass of Panamanian wrens is counter to the general pattern found in birds and described by Bergmann's rule, which states that within groups of closely related animals body size increases with latitude (Blackburn & Gaston 1996; Ashton 2002; Meiri & Dayan 2003). However, some other songbirds also show decreasing body mass with increasing latitude (e.g. Katti & Price 2003). Katti & Price (2003) explained this pattern in *Phylloscopus*-warblers by spatial patterns in food availability and prey size, with large individuals occurring in areas with higher food availability and larger prey size.

Some authors have invoked food limitation as the proximate factor explaining the small clutch sizes in tropical birds (e.g. Foster 1977; Martin 1987). However, in accordance with Katti & Price (2003), we suggest that food availability is not reduced for tropical House Wrens compared with Ohio wrens, because

Table 3. Body mass (average ± SD), field metabolic rate (FMR, average ± SD) and water influx rate (WIR, average ± SD) of House Wren nestlings from tropical (Panama) and temperate locations (Wisconsin; Dykstra and Karasov 1993a). To make data comparable, we recalculated values for the tropical nestlings using the same equations as Dykstra and Karasov (i.e. assuming no fractionation, conversion factor 25·7 kJ ml^{-1} CO_2)

Location	Age (day)	Mass (g)	FMR (kJ day^{-1})	WIR (g day^{-1})	*n*
Tropics with fractionation	7–11	11·9 ± 1·38	18·6 ± 5·97	7·2 ± 2·06	6
Tropics without fractionation	7–11	11·9 ± 1·38	25·2 ± 7·59	7·1 ± 2·03	6
Temperate without fractionation	10–13	9·6 ± 0·89	28·0 ± 6·66	4·9 ± 0·88[a]	17

[a] *n* = 16.

levels of whole-organism energy expenditure are similar in both areas and because body mass is larger in the tropical wrens. If food availability had been reduced in the tropics, one would have expected that evolution had selected for phenotypes with lower levels of energy expenditure, by decreasing either body size or mass-specific metabolic rate. Our suggestion is in accordance with a study on the timing of reproduction in House Wrens in Costa Rica, which showed that tropical House Wrens do not time their breeding to co-occur with peak food availability, indicating that sufficient food may be available throughout the year (Young 1994a,b). Levels of food availability therefore are unlikely to act as selective agent on overall levels of energy expenditure in tropical wrens. Instead, we propose that selection acts indirectly on whole-organism energy expenditure in the tropical wrens by specifically reducing mass-specific levels of metabolic rate, thereby postponing deleterious effects of ageing and thus decreasing intrinsic mortality (Speakman 2005). Reduced intrinsic mortality can be expected to have coevolved with the observed lower extrinsic mortality (Table 1; Cichon 1997), selecting for reduced reproductive rates in tropical wrens. The combination of lower metabolism and higher survival is in accordance with the inverse relationship between these variables predicted by the 'rate of living' theory (Pearl 1928; Speakman 2005). We estimated average life span as −1/[ln(annual survival)] to calculate lifetime energy expenditure: Lifetime energy expenditure for tropical and temperate zone wrens equalled 1447 kJ g^{-1} and 1337 kJ g^{-1} based on FMR (or +8% in the tropics), and 685 kJ g^{-1} and 691 kJ g^{-1} based on BMR (or −1%), respectively.

Interpretations of the evolutionary reasons for the reduced workload in tropical wrens, reflected in the combination of lower adult FMR, smaller clutch sizes and lower feeding frequency, are confounded by the simultaneous variation of these factors per location. The overall feeding frequency is lower in the tropical wrens, but the number of feedings per chick per daylight-hour is not different between the two locations. However, the number of daylight-hours per day is lower in the tropics than in the temperate zone during the breeding season. Therefore, on a 24-h basis, chicks are fed less often in the tropics and thus are expected to grow slower, a finding in accordance with the longer nestling period (Table 1). The shorter daylight period in the tropics also results in a larger contribution of the relatively low levels of metabolism during the night to adult FMR.

Some insights into the effects of proximate factors such as temperature and day length on parental effort can be gained from studying seasonal trends within a location. In Ohio FMR of parents decreased in the course of the season, whereas their nestling feeding behaviour did not change. Three factors change or potentially change in the course of the season: day length, temperature and food availability. An increase in day length would have resulted in longer working hours and higher FMR in the course of the season. An increase in temperature would lower thermoregulatory costs and reduce FMR in wrens that breed later in the season. We predict that a change in food availability would be inversely related to a change in FMR. Food availability is usually thought to decrease in the course of a temperate zone breeding season, resulting in an expected increase in foraging costs. Our finding that FMR decreases in the course of the season in Ohio therefore suggests that temperature is the most important environmental factor influencing FMR: the increase in temperature during the breeding season lowers FMR of the parents while raising young, a result in agreement with an earlier study on temperate zone House Wrens that found a significant effect of overnight temperature on parental FMR (Dykstra & Karasov 1993b). Although from the perspective of minimizing parental FMR it may be advantageous to breed later in the season, this benefit apparently does not outweigh the three times higher survival probability for young that fledge early compared with those that fledge late in the season in the temperate zone (Drilling & Thompson 1988; Young 1994a). These seasonal trends in fledgling survival probability and parental FMR suggest that reproduction is more time-constrained in the temperate zone, compressed by the shorter breeding season, and as a result more energetically costly for the parents. In contrast, tropical wrens do not show temporal variation in FMR (Fig. 3) and nesting success (Young 1994b), and therefore are less constrained to breeding during a short season.

Comparisons between locations and studies of seasonal patterns in response to changes in environmental factors within an area remain correlative and do not point conclusively to the evolutionary causes for the life-history differences between tropical and temperate zone birds. An experimental approach, manipulating parental effort in tropical and temperate zone populations, could shed more light on the evolved trade-off between reproduction and self-maintenance in these areas. We predict that tropical wrens do not compromise investments in self-maintenance in response to experimentally increased costs of reproduction, whereas temperate zone wrens with a lower annual survival probability should be more willing to compromise their survival in order to maximize a current reproductive event.

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References

Aschoff, J. & Pohl, H. (1970) Rhythmic variations in energy metabolism. *Federation Proceedings* **29**, 1541–1552.

Ashton, K.G. (2002) Patterns of within-species body size variation of birds: strong evidence for Bergmann's rule. *Global Ecology and Biogeography* **11**, 505–523.

Blackburn, T.M. & Gaston, K.J. (1996) Spatial patterns in the body sizes of bird species in the New World. *Oikos* **77**, 436–446.

Cichon, M. (1997) Evolution of longevity through optimal resource allocation. *Proceedings of the Royal Society of London B* **264**, 1383–1388.

Cody, M.L. (1971) Ecological aspects of reproduction. *Avian Biology* (eds D.S. Farner, J.R. King & K.C. Parkes), pp. 461–512. Academic Press, New York.

Drent, R.H. & Daan, S. (1980) The prudent parent: energetic adjustments in avian breeding. *Ardea* **68**, 225–252.

Drilling, N.E. & Thompson, C.F. (1988) Natal and breeding dispersal in house wrens (*Troglodytes aedon*). *Auk* **105**, 480–491.

Dykstra, C.R. & Karasov, W.H. (1993a) Daily energy expenditure by nestling house wrens. *Condor* **95**, 1028–1030.

Dykstra, C.R. & Karasov, W.H. (1993b) Nesting energetics of house wrens (*Troglodytes aedon*) in relation to maximal rates of energy flow. *Auk* **110**, 481–491.

Ferretti, V., Llambias, P.E. & Martin, T.E. (2005) Life-history variation of a neotropical thrush challenges food limitation theory. *Proceedings of the Royal Society of London B* **272**, 769–773.

Foster, M.S. (1977) Ecological and nutritional effects of food scarcity on a tropical frugivorous bird and its fruit source. *Ecology* **58**, 73–85.

Freed, L.A. (1987) The long-term pair bond of tropical house wrens: advantage or constraint? *American Naturalist* **130**, 507–525.

Fry, C.H. (1980) Survival and longevity among tropical land birds. *Proceedings of the 4th Pan-African Ornithological Congress*, 333–343.

Gessaman, J.A. & Nagy, K.A. (1988) Energy metabolism: errors in gas-exchange conversion factors. *Physiological Zoology* **61**, 507–513.

Ghalambor, C.K. & Martin, T.E. (2001) Fecundity-survival trade-offs and parental risk-taking in bidrs. *Science* **292**, 494–497.

Hill, R.N. (1972) Determination of oxygen consumption by use of the paramagnetic oxygen analyzer. *Journal of Applied Physiology* **33**, 263.

Johnson, L.S. (1998) House wren. *The Birds of North America*. **380**, 1–30. St. Martin's Press, New York.

Katti, M. & Price, T.D. (2003) Latitudinal trends in body size among over-wintering leaf warblers (genus *Phylloscopus*). *Ecography* **26**, 69–79.

Kendeigh, S.C., Dolnik, V.R. & Gavrilov, V.M. (1977) Avian energetics. *Granivorous Birds in Ecosystems* (eds J. Pinowski & S.C. Kendeigh), pp. 127–204. Cambridge University Press, Cambridge.

Kendeigh, S.C. & Baldwin, S.P. (1937) Factors affecting yearly abundance of passerine birds. *Ecological Monographs* **7**, 93–123.

Klaassen, M., Bech, C., Masman, D. & Slagsvold, G. (1989) Growth and energetics of arctic tern chicks (*Sterna paradisaea*). *Auk* **106**, 240–248.

Lasiewski, R.C., Acosta, A.L. & Bernstein, M.H. (1966) Evaporative water loss in birds – I. Characteristics of the open flow method of determination, and their relation to estimates of thermoregulatory ability. *Comparative Biochemistry and Physiology* **19**, 445–457.

Levy, A. (1964) The accuracy of the bubble meter for gas flow measurements. *Journal of Scientific Instruments* **41**, 449–453.

Lifson, N. & McClintock, R. (1966) Theory of use of the turnover rates of body water for measuring energy and material balance. *Journal of Theoretical Biology* **12**, 46–74.

Martin, T.E. (1987) Food as a limit on breeding in birds: a life history perspective. *Annual Reviews in Ecology and Systematics* **18**, 453–487.

Martin, T.E. (2004) Avian life-history evolution has an eminent past: does it have a bright future? *Auk* **21**, 239–301.

Martin, T.E., Martin, P.R., Olson, C.R., Heidingen, B.J. & Fontaine, J.J. (2000) Parental care and clutch sizes in North and South American birds. *Science* **287**, 1482–1485.

Meiri, S. & Dayan, T. (2003) On the validity of Bergmann's rule. *Journal of Biogeography* **30**, 331–351.

Moreau, R.E. (1944) Clutch size: a comparative study, with reference to African birds. *Ibis* **86**, 286–347.

Nagy, K.A. (1980) CO_2 production in animals: analysis of potential errors in the doubly labeled water method. *American Journal of Physiology* **238**, R466–R473.

Nagy, K.A. & Costa, D.P. (1980) Water flux in animals: analysis of potential errors in the tritiated water method. *American Journal of Physiology* **238**, R454–R465.

Nagy, K.A. & Peterson, C.C. (1988). Scaling water flux rate in animals. University of California Publications in Zoology, Vol. 1, issue 20. University of California Press, Berkeley.

Nelson, R.J., Demas, G.E., Klein, S.L. & Kriegsfeld, L.J. (2002) *Seasonal Patterns of Stress, Immune Function, and Disease*. Cambridge University Press, Cambridge.

Pearl, R. (1928) *The Rate of Living: Being an Account of Some Experimental Studies on the Biology of Life Duration*. Alfred Knopf, New York.

Ricklefs, R.E. (1997) Comparative demography of new world populations of thrushes (*Turdus* spp.). *Ecology* **67**, 23–43.

Ricklefs, R.E. & Williams, J.B. (1984) Daily energy expenditure and water-turnover rate of adult European starlings (*Sturnus vulgaris*) during the nestling cycle. *Auk* **101**, 707–716.

Schmidt-Nielsen, K. (1997) Animal physiology: *Adaptation and Environment*. Cambridge University Press, Cambridge.

Sillett, T.S. & Holmes, R.T. (2002) Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology* **71**, 296–308.

Skutch, A.F. (1976) *Parent Birds and Their Young*. University of Texas Press, Austin, TX.

Speakman, J.R. (1997) *Doubly Labelled Water*. Chapman & Hall, London.

Speakman, J.R. (2005) Body size, energy metabolism and lifespan. *Journal of Experimental Biology* **208**, 1717–1730.

Stearns, S.C. (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford.

Tieleman, B.I., Williams, J.B., LaCroix, F. & Paillat, P. (2002) Physiological responses of Houbara bustards to high ambient temperatures. *Journal of Experimental Biology* **205**, 503–511.

Visser, G.H. & Schekkerman, H. (1999) Validation of the doubly labeled water method in growing precocial birds: the importance of assumptions concerning evaporative water loss. *Physiological and Biochemical Zoology* **72**, 740–749.

Visser, G.H., Boon, P.E. & Meijer, H.A.J. (2000a) Validation of the doubly labeled water method in Japanese quail *Coturnix c. japonica* chicks: is there an effect of growth rate? *Journal of Comparative Physiology B* **170**, 365–372.

Visser, G.H., Dekinga, A., Achterkamp, B. & Piersma, T. (2000b) Ingested water equilibrates isotopically with the body water pool of a shorebird with unrivaled water fluxes. *American Journal of Physiology* **279**, R1795–R1804.

Weathers, W.W. & Sullivan, K.A. (1989) Juvenile foraging proficiency, parental effort, and avian reproductive success. *Ecological Monographs* **59**, 223–246.

Williams, G.C. (1966) *Adaptation and Natural Selection*. Princeton University Press, Princeton, NJ.

Williams, J.B. (1999) Heat production and evaporative water loss of dune larks from the Namib desert. *Condor* **101**, 432–438.

Williams, J.B. & Nagy, K.A. (1984) Validation of the doubly labeled water technique for measuring energy metabolism in savannah sparrows. *Physiological Zoology* **57**, 325–328.

Young, B.E. (1994a) Geographic and seasonal patterns of clutch-size variation in house wrens. *Auk* **111**, 545–555.

Young, B.E. (1994b) The effects of food, nest predation and weather on the timing of breeding in tropical house wrens. *Condor* **96**, 341–353.

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