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Physiological responses of Houbara bustards to high ambient temperatures

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Summary

Desert birds often experience a scarcity of drinking water and food and must survive episodes of high ambient temperature (T_a). The physiological mechanisms that promote survival during extended periods of high T_a have received little attention. We investigated the physiological responses of wild-caught and captive-reared Houbara bustards, *Chlamydotis macqueenii*, to T_a values ranging from below 0 °C to 55 °C, well above those in most previous studies of birds. Captive-reared Houbara bustards (mass 1245±242 g, N=7, mean ± S.D.) in summer have a resting metabolic rate (RMR) of 261.4 kJ day^{-1}, 26 % below allometric predictions, and a total evaporative water loss (TEWL) at 25 °C of 25.8 g day^{-1}, 31 % below predictions. When T_a exceeded body temperature (T_b), the dry heat transfer coefficient decreased, a finding supporting the prediction that birds should minimize dry heat gain from the environment at high T_a values. Houbara bustards withstand high T_a values without becoming hyperthermic; at 45 °C, T_b was on average 0.9 °C higher than at 25 °C. RMR and TEWL of captive-bred Houbara bustards were 23 % and 46 % higher in winter than in summer, respectively. Captive-reared Houbara bustards had a 17 % lower RMR and a 28 % lower TEWL than wild-born birds with similar genetic backgrounds. Differences in body composition between wild-caught and captive-reared birds were correlated with differences in physiological performance.

Key words: Houbara bustard, *Chlamydotis macqueenii*, resting metabolic rate, total evaporative water loss, thermoregulation, desert bird.

Introduction

Birds that occupy arid regions often experience a scarcity of drinking water and limited food supplies and must survive episodes of high ambient temperature (T_a); shade temperatures can exceed 50 °C in some deserts. Physiological adjustments that reduce water loss and energy expenditure in free-living desert birds include low rates of total evaporative water loss (TEWL) (Williams, 1996) and basal metabolism (BMR) (Dawson, 1984; Tieleman and Williams, 2000; Williams and Tieleman, 2001). Although anecdotal evidence suggests that extremes of heat can be a major source of mortality in some populations (Serventy, 1971), physiological mechanisms that promote survival during extended periods of high T_a have received little attention.

When exposed to high T_a, most birds elevate their TEWL, sometimes by two orders of magnitude, to maintain body temperature (T_b) below lethal limits (Calder and King, 1974; Dawson, 1984). Without replenishment of lost body water, defense of T_b by evaporative cooling cannot be sustained for long periods because of the associated changes in physiological function with dehydration. Presumably to reduce dependency on evaporative cooling, the T_b of many birds is elevated by

2–4 °C when they are exposed to a high T_a; this is termed hyperthermia (Calder and King, 1974; Weathers, 1981; Dawson, 1984; Tieleman and Williams, 1999). Using water as a currency, Tieleman and Williams (1999) modeled the costs and benefits of hyperthermia, and showed that small birds reduced TEWL when hyperthermic, but that larger species lost more water if they became hyperthermic during chronic heat stress (5 h) than if they maintained normothermic T_b. This latter finding was attributable primarily to an increased minute volume and a higher saturation vapor density in the lungs at higher T_b.

At high T_a values, birds should minimize heat gain from their environment, a parameter quantified as $h(T_b–T_a)$, where $T_b–T_a$ is the temperature gradient between the bird and the environment and h is the dry heat transfer coefficient (Dawson and Schmidt-Nielsen, 1966; Hinds and Calder, 1973; Weathers and Caccamise, 1975; Tieleman and Williams, 1999). Influenced by characteristics of feather insulation, skin vasodilation and surface-to-volume ratios, h is a complex variable that combines heat transfer coefficients for conduction, convection and radiation (Calder and King, 1974).

Minimal below the thermal neutral zone, h should increase to a maximum when T_a approaches T_b, whereas at T_a values above T_b, where heat flow is reversed, h should return to lower values (Dawson and Schmidt-Nielsen, 1966; Hinds and Calder, 1973; Frumkin et al., 1986; Tieleman and Williams, 1999). A review of studies on 22 species failed to support this prediction, but the conclusions were tentative because previous workers had not measured T_b continuously and, therefore, had not accounted for heat gain in body tissues in their calculations, and few studies have examined thermoregulation at T_a values exceeding 45 °C (Tieleman and Williams, 1999).

To minimize the need for evaporative cooling at high T_a values, birds could also reduce their heat production. One could predict that birds from hot deserts would benefit especially from a low BMR during summer, when T_a values are high. Seasonal variation in BMR has been observed in several temperate-zone birds: some species elevate BMR in winter compared with summer (Pohl and West, 1973; Cooper and Swanson, 1994), and others show the opposite pattern (Kendeigh, 1969; Barnett, 1970) or no seasonal differences (O'Connor, 1995).

Houbara bustards (*Chlamydotis undulata* Jacquin) inhabit semi-arid and arid areas from Asia through the Middle East westward across North Africa (Cramp, 1988). Although traditionally three subspecies have been recognized, Gaucher et al. (1996) proposed that the subspecies *C. u. macqueenii*, which occurs in the Arabian peninsula and northwards into Mongolia, should be regarded as a distinct species, *C. macqueenii*. In Arabia, *C. macqueenii* have declined in numbers over the past decades as a result of overhunting and habitat degradation (Seddon et al., 1995). A captive breeding program, sponsored by the National Commission for Wildlife Conservation and Development, Saudi Arabia, now exists for the purpose of reintroducing this species into its former habitat. To achieve this goal, attention has been devoted to the genetic composition of released birds to ensure that genotypes resemble wild stocks (Seddon et al., 1995). However, genetic similarity of reintroduced individuals does not ensure that released birds bear the same phenotype as wild-born birds because of the potential for accrual of ontogenetic differences during the captive-rearing process. Because birds in Arabia are often exposed to T_a values that exceed 50 °C, it is possible that an alteration in phenotype as a result of captive-rearing could carry survival costs, especially if the physiological function of captive-reared individuals is compromised compared with wild birds.

We investigated the physiological responses of wild-caught and captive-reared Houbara bustards to T_a values ranging from below 0 °C to 55 °C, the highest value being well above those used in most previous studies of birds (Marder and Arieli, 1988). In addition to documenting seasonal changes in physiological function, we tested the predictions that Houbara bustards minimize dry heat transfer at T_a values exceeding T_b, and that birds weighing more than 1 kg do not use hyperthermia as a strategy to reduce evaporative water loss during chronic exposure to high T_a values (Tieleman and Williams, 1999). We provide evidence that captive rearing, as it is now practiced, alters the physiological phenotype of Houbara bustards. We explored whether differences in body composition of wild-caught and captive-reared Houbara bustards could account for the observed differences in physiological performance between the two groups.

Materials and methods
Animals

For metabolism trials during summer, we used captive-reared Houbara bustards *Chlamydotis macqueenii* Jacquin from the National Wildlife Research Center, Taif, Saudi Arabia. The founders of the captive breeding program originated from Pakistan and are genetically indistinguishable from current populations in Saudi Arabia (Seddon et al., 1995). The birds were housed separately in outdoor cages (4 m×4 m×2 m) and provided daily with water *ad libitum*, mealworms, crickets, fresh alfalfa and commercially prepared pellets. Their body mass averaged 1462±113 g (mean ± S.D.) for seven males and 1013±40 g for eight females, values that differed significantly (t=11.1, P<0.001). We measured six or seven birds at each T_a, equally divided between males and females. Measurements made on separate groups of birds during the day and night were performed during September 1997 after the birds had molted.

During the winter of 1999, we obtained eight wild-caught Houbara bustards from Afghanistan. Birds were transported to the National Wildlife Research Center, housed in outdoor cages and provided with the same food as captive-reared birds. We allowed 6 weeks for wild birds to acclimate to their environment before measurements were made. The body mass of eight captive-reared birds averaged 1248±206 g and that of eight wild-born individuals 1323±257 g (means ± S.D.).

Measurements of TEWL and oxygen consumption

A 113 l metabolic chamber was constructed from steel plate with a flat black interior (Porter, 1969) and was surrounded with an insulated water jacket. A rubber gasket rendered the Plexiglas lid air-tight when bolted shut. We covered the lid during measurements so that the inside of the chamber was dark. Birds were placed in the chamber on wire mesh above mineral oil that trapped excrement. A Neslab RTE-140 water bath controlled chamber T_a to within ±0.1 °C. To maintain T_a values below 5 °C, we placed the chamber in a freezer in addition to the Neslab cooler.

Rates of TEWL and oxygen consumption ($\dot{V}_{O_2}$) were determined for birds that had been without food for 3 h prior to measurement. An air compressor pushed air through two drying columns filled with Drierite, through a mass-flow controller (Brooks model 5851E) calibrated with a 5 l bubblemeter (Levy, 1964) and then into the metabolic chamber. We varied the flow rate between 5.3 and 10.4 l min^{-1}, depending on T_a, to maintain relative humidity in the metabolic chamber below 22 %. Subsamples of excurrent air passed through a dewpoint hygrometer (General Eastern, model

Hygro M4) and through columns of silica gel, Ascarite and silica gel, before passing through an Applied Electrochemistry model S-3AII O_2 analyzer calibrated using dry CO_2-free air. We monitored the dewpoint (°C) and O_2 concentration (%) of the excurrent air continuously with a Campbell CR10 data logger and PC208W software.

Visual inspection of our results allowed us to determine when steady-state conditions had been achieved. Birds remained in the chamber for 3 h; we averaged dewpoint and O_2 concentration of the excurrent airstream over a 20 min period. The water vapor density of the incurrent and excurrent air and TEWL were calculated following Williams and Tieleman (2000). We calculated $\dot{V}_{O_2}$ using equation 4 of Hill (1972). In summer (September), we performed metabolic trials during the day at T_a values ranging from 0 to 55 °C, and during the night at 0, 25 and 45 °C on captive-reared birds. In winter (December), we measured captive-reared and wild-born birds at 35 and 50 °C during the day. Body mass was determined, to ±1 g, before and after metabolic trials using a Philips top-loading balance (model HR 2385/A).

Body temperature

We recorded T_b of birds continuously with a 36 gauge thermocouple surrounded by a protective cotton swab inserted 5–8 cm into the cloaca. We affixed the thermocouple wire to the tail feathers with a plastic tie to ensure that it remained in place. The thermocouple was calibrated against a standard mercury in glass thermometer (Taylor) with a certificate of calibration traceable to the National Institute of Standards and Technology.

If there was a change in T_b during a measurement, we calculated the rate of heat storage (in $J\,h^{-1}$) as CdT_b/dt, where C is the specific heat of the bird ($J\,°C^{-1}$) and dT_b/dt is the change in T_b over time ($°C\,h^{-1}$). We calculated C from body mass and the specific heat of tissue ($3.35\,J\,g^{-1}\,°C^{-1}$) (Calder and King, 1974; Schmidt-Nielsen, 1984) and dT_b/dt from the slope of a regression line through data for T_b for the final 60 min of the 3 h trial.

Dry heat transfer coefficient

We calculated the dry heat transfer coefficient (h) as $(M–E–CdT_b/dt)/(T_b–T_a)$ (Birkebak, 1966; Porter and Gates, 1969), where M is metabolic heat production (in $J\,h^{-1}$) and E is evaporative heat loss (in $J\,h^{-1}$). At T_a values near T_b, calculations of h are problematic because small errors in measurements of variables can translate into large errors in h. Therefore, we used l'Hôpital's rule to calculate h at $T_a=T_b$ (Tieleman and Williams, 1999). For each bird, we fitted lines through metabolic rate, TEWL, T_b and CdT_b/dt as functions of T_a to calculate h at $T_a=T_b$ (Tieleman and Williams, 1999).

Organ size

After measurement of their metabolic rate in winter, we killed six captive-bred and six wild Houbara bustards and dissected out their brain, proventriculus, stomach, heart, intestine, liver, kidney, left pectoral muscle (including the supracoracoidus), thyroid glands, spleen and gonads. The organs were dried for 3 days at 75 °C before we measured dry mass, to 1 mg, with an electronic balance (Sauter RE 164).

Statistical analyses

Although we used individuals from the same group of 16 birds for the measurements during the summer, we did not obtain measurements for each individual at each T_a and therefore could not use a repeated-measures model in our analyses. Some individuals lost more than 100 g in mass even though we only handled them every third day, and we deemed it prudent not to cause additional stress in these birds. Hence, we treated each data point as independent and performed analyses of covariance (ANCOVAs) with body mass as a covariate. We tested for significant interactions of the main factors with the covariate in all cases, but report only those that were significant.

To analyze the differences between summer and winter data for captive-reared Houbara bustards, and between captive-reared and wild-born birds during winter, we performed separate ANCOVAs with body mass as the covariate and group as the fixed factor for T_a values of 35 and 50 °C. When group had a significant effect, we used contrast analyses of the type 'repeated' as *post-hoc* tests.

Proportions were arcsine-square-root-transformed before applying parametric statistics (Zar, 1996). In making simultaneous multiple comparisons, we used a sequential Bonferroni correction to avoid an increase in the probability of a Type I error (Rice, 1989). All statistical analyses were performed using SPSS (1999). Values are presented as means ±1 S.D., unless noted otherwise.

Results
Captive-reared Houbara bustards in summer

The metabolic rate (MR, $kJ\,day^{-1}$) of captive-reared Houbara bustards during summer can be described as MR=682.3–14.76T_a (r^2=0.80, $F_{1,22}$=85.1, $P<0.001$) at T_a values (in °C) below the thermoneutral zone (Fig. 1A). From 29 to 56 °C, resting metabolic rate (RMR) remained constant, averaging 261.4±36.8 $kJ\,day^{-1}$ (N=32). The intersection between the above equation and RMR provided an estimate of the lower critical temperature (T_{lc}), 28.5 °C. Metabolic rate at 25 and 45 °C did not differ between day and night or between the two T_a values (day–night, $F_{1,21}$=1.97, P=0.18; T_a, $F_{1,21}$=1.28, P=0.27).

Below 35 °C, TEWL varied little with T_a, while above 35 °C TEWL increased rapidly (Fig. 1B). At 25 °C, TEWL was 25.1±6.9 $g\,day^{-1}$ (N=6) during the day and 26.5±6.6 $g\,day^{-1}$ (N=6) at night, whereas at 45 °C, TEWL was 129.0±20.3 $g\,day^{-1}$ (N=6) during the day and 151.7±33.9 $g\,day^{-1}$ (N=7) at night. We detected no significant differences in TEWL between day and night ($F_{1,21}$=2.15, P=0.16), but found that TEWL was significantly higher at 45 than at 25 °C ($F_{1,21}$=229.9, $P<0.001$).
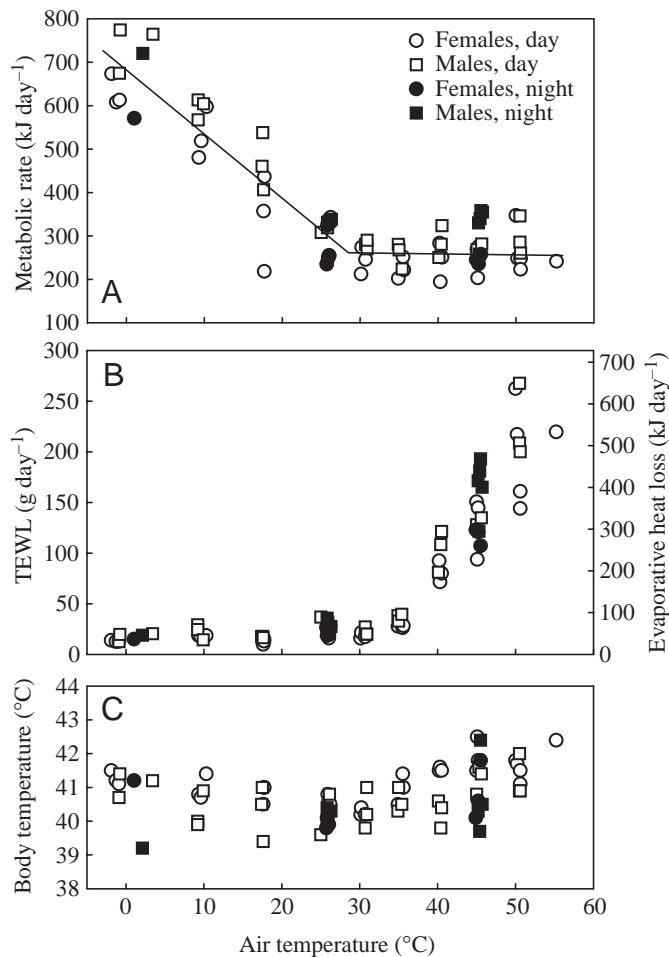
Fig. 1. Metabolic rate (A), total evaporative water loss (TEWL) (B) and body temperature (C) of captive-reared Houbara bustards during summer.
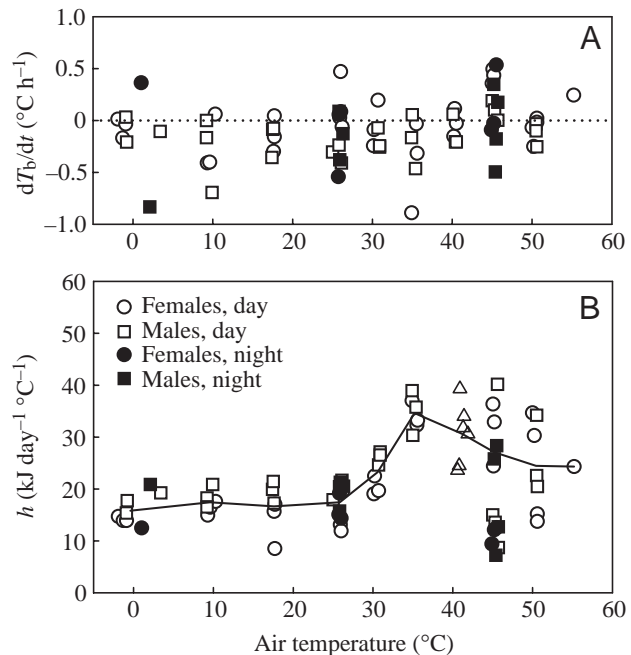

Fig. 2. (A) Change in body temperature (dT_b/dt) and (B) dry heat transfer coefficient h of captive-reared Houbara bustards during summer. The line in B connects the mean h at each air temperature.

Body temperatures varied between 39.2 and 42.5 °C at T_a values ranging from –1.9 to +55.2 °C (Fig. 1C). During the day, T_b was 40.4±0.5 °C (N=6) at T_a=25 °C and 41.6±0.6 °C (N=6) at T_a=45 °C; at night, T_b values were 40.1±0.2 °C (N=6) and 40.8±1.0 °C (N=7), respectively. When we tested for differences in T_b between day and night, and between T_a values of 25 and 45 °C, analyses revealed that T_b was 0.6±0.26 °C (mean ± S.E.M.) lower during the night ($F_{1,21}$=4.54, P=0.045) and that T_b was 0.9±0.27 °C (mean ± S.E.M.) lower at 25 °C ($F_{1,21}$=12.5, P=0.002).

At a given T_a, changes in T_b with time were generally less than 0.5 °C h^{-1}, even at high T_a values (Fig. 2A). The difference in dT_b/dt between day and night was not significant ($F_{1,21}$=2.57, P=0.12), but dT_b/dt was significantly higher at 45 °C than at 25 °C ($F_{1,21}$=5.16, P=0.034). Combining day and night measurements, dT_b/dt averaged 0.16±0.41 °C h^{-1} (N=13) at 45 °C and –0.04±0.32 °C h^{-1} (N=12) at 25 °C. Although these mean values of dT_b/dt differed from each other, neither was significantly different from zero (T_a=25 °C, t=–0.44, P=0.67; T_a=45 °C, t=1.4, P=0.18).

The mean dry heat transfer coefficient (h) had a minimal value of 16.8±3.2 kJ day^{-1} °C^{-1} or 1.60±0.26 W °C^{-1} m^{-2} (N=24) below the thermoneutral zone, increased gradually to a maximum of 34.6±3.2 kJ day^{-1} °C^{-1} (N=6) at 35 °C, and then decreased to 24.4±8.7 kJ day^{-1} °C^{-1} (N=7) at 50 °C (Fig. 2B). In a test for differences in h between 10, 35 and 50 °C, temperature had a significant effect ($F_{2,15}$=14.0, P<0.001). *Post-hoc* contrast analysis showed significant differences between h at 10 and 35 °C (contrast –17.4±3.3 kJ day^{-1} °C^{-1}, mean ± S.E.M., P<0.001), and between h at 35 °C and 50 °C (contrast 9.8±3.2 kJ day^{-1} °C^{-1}, mean ± S.E.M., P=0.008). Houbara bustards increased h significantly when T_a increased to 35 °C, and decreased h significantly when T_a exceeded T_b at 50 °C. When we tested whether h differed between day and night, and between T_a values of 25 and 45 °C, we found no significant difference between day and night ($F_{1,21}$=4.2, P=0.053), but a significant effect of T_a ($F_{1,21}$=7.0, P=0.015). When we confined our analysis to T_a=25 °C, we found no significant effect of time of day on h ($F_{1,9}$=0.80, P=0.39).

Effects of captive-rearing and seasonality

We compared the metabolic rate of captive-reared Houbara bustards between seasons and of captive-reared and wild-born individuals during winter at T_a values of 35 and 50 °C (Fig. 3A,B). At 35 °C, we found significant effects of group and body mass on metabolic rate (group, $F_{2,18}$=14.37, P<0.001; mass, $F_{1,18}$=18.73, P<0.001). *Post-hoc* analyses indicated significant differences between summer and winter in captive-reared Houbara bustards (contrast=–54.1±21.3 kJ day^{-1}, mean ± S.E.M., P=0.02) and between captive-reared and wild-born birds (contrast=–59.7±19.9 kJ day^{-1}, mean ± S.E.M., P=0.008). At
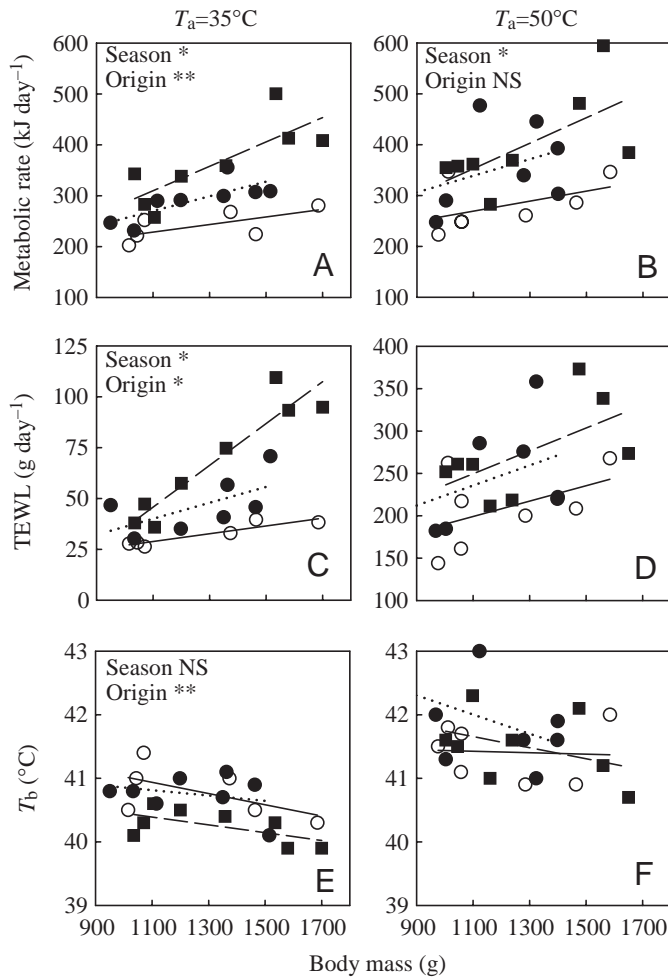
Fig. 3. Metabolic rate (A,B), total evaporative water loss (TEWL) (C,D) and body temperature (T_b) (E,F) of captive-reared Houbara bustards during summer (open circles, solid lines) and during winter (filled circles, dotted lines) and of wild birds during winter (filled squares, dashed lines) at 35 (A,C,E) and 50 °C (B,D,F). Significant differences among groups are indicated in the top left corner: NS, not significant; *P<0.05; **P<0.01.
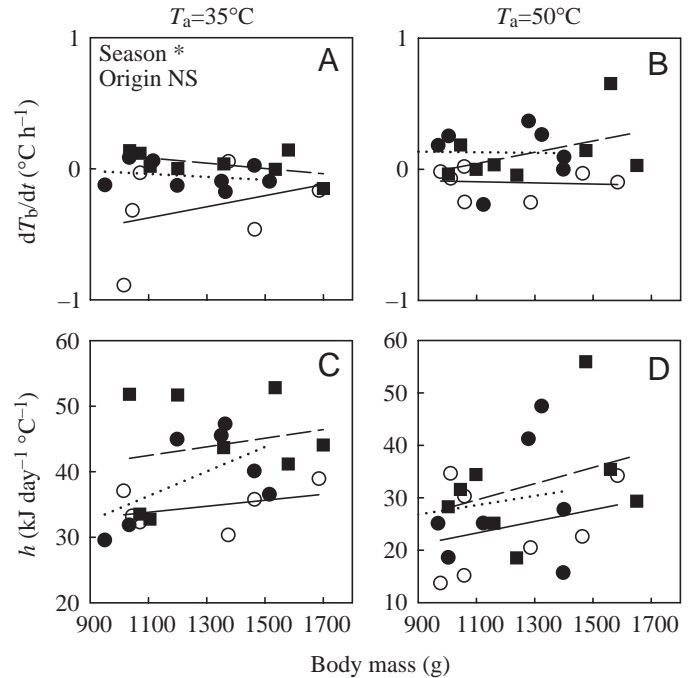

Fig. 4. (A,B) Changes in body temperature (dT_b/dt) and (B,D) dry heat transfer coefficient h of captive-reared Houbara bustards during summer (September 1997) (open circles, solid line) and during winter (December 1999) (filled circles, dotted line) and of wild birds during winter (December 1999) (filled squares, dashed line) at 35 (A,C) and 50 °C (B,D). Significant differences among groups are indicated in the top left corner: NS, not significant; *P<0.05.

50 °C, we found a significant effects of group and body mass on metabolic rate (group, $F_{2,19}=4.58$, $P=0.024$; mass, $F_{1,19}=7.15$, $P=0.015$). *Post-hoc* analyses revealed a significant difference in metabolic rate between summer and winter birds (contrast=-77.1 ± 35.7 kJ day^{-1}, mean ± S.E.M., $P=0.044$) but not between captive-reared and wild-born birds (contrast=-28.3 ± 35.1 kJ day^{-1}, mean ± S.E.M., $P=0.43$).

Total evaporative water loss varied with body mass and with T_a in all three groups (Fig. 3C,D). At 35 °C, a significant interaction between group and body mass indicated that the slopes differed among groups (Fig. 3C). The 95 % confidence intervals (CI) of the slopes (b) of the captive birds in summer ($b=0.019$, CI=-0.014–0.052) and winter ($b=0.039$, CI=0.0005–0.078) overlapped broadly, in contrast to the small overlap with the slope of wild birds in winter ($b=0.103$, CI=0.073–0.133). Therefore, we combined data for summer

and winter of the captive birds, recalculated the ANCOVA model, and calculated the increase in the error variance. The significant increase in error variance compared with the model that included all three groups indicated that the slope through the wild-bird data differed significantly from the slope of the captive birds ($F_{2,15}=4.12$, $P<0.05$). Houbara bustards of wild origin showed a larger increase in TEWL with body mass. Although the slopes of the relationship between TEWL and mass did not differ significantly between seasons in the captive-reared birds ($F_{1,9}=0.83$, $P=0.39$), the intercept was higher for birds in winter than in summer ($F_{1,10}=8.85$, $P=0.014$). At 50 °C, TEWL did not differ significantly among groups ($F_{2,19}=4.61$, $P=0.10$).

The body temperature of Houbara bustards at 35 °C was dependent on mass and group (mass, $F_{1,18}=5.68$, $P=0.028$; group, $F_{2,18}=6.67$, $P=0.007$; Fig. 3E). *Post-hoc* analysis revealed a significant difference in T_b between captive-reared and wild-born birds in the winter (contrast=0.45±0.15 °C, mean ± S.E.M., $P=0.007$), but no significant difference in captive birds between summer and winter (contrast= 0.05±0.16 °C, mean ± S.E.M., $P=0.75$). At 50 °C, T_b did not differ between groups ($F_{2,19}=1.30$, $P=0.30$).

Change in T_b with time, dT_b/dt, was independent of body mass in Houbara bustards (Fig. 4A,B) ($T_a=35$ °C, $F_{1,18}=0.03$, $P=0.88$; $T_a=50$ °C, $F_{1,19}=0.70$, $P=0.41$). At 35 °C, dT_b/dt was significantly different between groups ($F_{2,18}=5.05$, $P=0.018$),

Table 1. *Mean organ masses of wild-born and captive-bred Houbara bustards during winter*

Organ	Wet mass (% total mass)			Dry mass (g)			
	Wild	Captive	P	Wild	Captive	Change (%)	P
Brain	0.32±0.09	0.36±0.04	0.33	0.93±0.04	0.87±0.08	–6.5	0.035
Proventriculus	0.30±0.04	0.19±0.02	<0.001*	1.08±0.32	0.62±0.14	–43.6	0.001*
Stomach	1.51±0.14	1.05±0.10	<0.001*	7.30±0.16	4.52±1.02	–38.1	<0.001*
Heart	0.87±0.14	0.71±0.08	0.040	3.47±1.30	2.25±0.30	–35.2	0.028
Intestine	2.67±0.33	1.45±0.28	<0.001*	7.60±2.45	3.93±0.96	–48.3	0.003*
Liver	1.84±0.28	1.38±0.11	0.003*	8.34±3.50	4.82±0.89	–42.2	0.010*
Kidney	0.61±0.04	0.50±0.18	0.17	2.08±0.85	1.31±0.47	–37.0	0.035
Pectoral muscle[†]	9.38±0.48	8.77±0.39	0.038	42.32±9.31	29.68±4.39	–29.9	0.004*
Thyroid	0.014±0.004	0.008±0.003	0.008*	0.08±0.04	0.03±0.01	–62.5	0.023
Spleen	0.048±0.010	0.059±0.011	0.10	0.16±0.03	0.16±0.03	0	0.95

[†]Only includes the left pectoral muscle.

Values are means ± S.D. (N=6).

Wet mass is expressed as percentage of total body mass, and was arcsine-square-root-transformed before performing *t*-tests.

Dry masses (g) of wild and captive birds were compared with ANCOVA, using tarsus length as a covariate.

Significant *P* values after sequential Bonferroni correction are indicated by an asterisk.

and *post-hoc* analysis revealed that dT_b/dt of captive-reared birds differed between winter and summer (contrast= –0.25±0.11 °C h^{-1}, mean ± S.E.M., P=0.035), but that dT_b/dt did not differ between captive-reared and wild-born birds in winter (contrast=–0.09±0.10 °C h^{-1}, mean ± S.E.M., P=0.38). Neither captive rearing nor season affected the rate of heat storage at 50 °C ($F_{2,19}$=3.32, P=0.058).

The dry heat transfer coefficient of Houbara bustards did not vary with body mass (Fig. 4C,D) (T_a=35 °C, $F_{1,17}$=2.17, P=0.16; T_a=50 °C, $F_{1,19}$=1.57, P=0.23). We calculated *h* at 35 °C and 50 °C and found no significant differences between wild and captive birds or between summer and winter (35 °C, $F_{2,17}$=3.29, P=0.062; 50 °C, $F_{2,19}$=0.93, P=0.41).

Organ masses of captive-reared and wild-born Houbara bustards in winter

The organ masses of captive-reared Houbara bustards differed from those of wild-born birds (Table 1), despite no significant differences in body mass (captive, 1196±198 g, N=6; wild, 1397±299 g, N=6, t=1.37, P=0.20) or structural size, as measured by tarsus length (captive, 97±6.6 mm; wild, 97±6.3 mm, t=0.04, P=0.97). The sum of the wet masses of brain, proventriculus, stomach, heart, intestine, liver, kidney, left pectoral muscle, thyroid and spleen was larger in wild birds (246±54 g, N=6) than in captive birds (173±27 g, N=6, t=2.9, P=0.015). When the size of each organ was expressed as a proportion of total body mass, the proventriculus, stomach, intestine, liver and thyroid were significantly larger in wild birds than in captive-reared animals (Table 1). Although the pectoral muscle, heart and kidney also tended to be larger in wild birds, the differences from those of captive-reared birds were not significant. We compared the dry masses of each organ between wild and captive birds using an ANCOVA with tarsus length as covariate, to control for the effect of body size.

In this analysis, we found a significantly larger proventriculus, stomach, intestine, liver and pectoral muscle in the birds of wild origin, but no significant differences in brain, heart, kidney, thyroid and spleen, although these latter organs also tended to be larger in wild birds (Table 1).

We calculated the relationships between BMR and body mass, and between each organ dry mass and body mass, for our entire data set (Table 2). The association between BMR and body mass (*M*) was given by the equation BMR=24.6+0.237*M* (N=12, r^2=0.67, P=0.001). All body components were closely associated with body mass as shown by the regressions and the large fractions of explained variance (r_1^2) in Table 2. For each bird, we calculated the residual BMR (measured BMR minus BMR predicted from the allometric equation) and the residual of each organ dry mass (measured organ mass minus organ mass predicted from the allometric equation). We calculated the correlations of residual BMR with those of each organ and found none that was significant (Table 2). We therefore concluded that larger birds had a higher BMR and larger organs, but that none of the organs contributed disproportionately to BMR.

Discussion
Captive-reared Houbara bustards in summer

During the past 10 years, captive-reared Houbara bustards in Saudi Arabia have been reintroduced into Mahazat as-Sayd, a reserve in the west-central Arabian Desert (22°N 41°E) and within the original distribution area of the species. Mahazat as-Sayd receives an average annual rainfall of 90±70 mm, and T_a ranges from an average maximum of 40.2 °C during June to an average minimum of 10.7 °C during January (National Wildlife Research Center, unpublished data). Daily extreme T_a values in summer regularly reach 50 °C. When Houbara bustards

Table 2. *Regressions of basal metabolic rate and dry organ masses* versus *wet body mass for 12 Houbara bustards*

y	$\log y$	r_1^2	P_1	r_2	P_2
BMR	24.6+0.237 mass	0.67	0.001		
Brain	0.647+0.00019 mass	0.53	0.007	0.04	0.90
Proventriculus	-0.558+0.00109 mass	0.72	0.001	0.23	0.47
Stomach	−2.384+0.00640 mass	0.76	<0.001	0.48	0.12
Heart	−1.293+0.00320 mass	0.59	0.004	0.21	0.52
Intestine	−4.525+0.00794 mass	0.64	0.002	0.15	0.64
Liver	−6.490+0.01008 mass	0.76	<0.001	0.27	0.41
Kidney	−1.707+0.00262 mass	0.82	<0.001	0.02	0.95
Pectoral muscle[†]	−6.324+0.03265 mass	0.81	<0.001	−0.12	0.72
Thyroid	−0.066+0.00009 mass	0.43	0.020	0.10	0.75
Spleen	−0.006+0.00013 mass	0.52	0.008	−0.02	0.95
Gonads	0.053+0.00002 mass	0.09	0.34	0.08	0.81

[†]Only includes the left pectoral muscle.

BMR, basal metabolic rate (kJ day^{-1}); masses were measured in grams.

r_1^2 is the fraction of variance explained by body mass, P_1 is the significance level of the regression line and r_2 is the coefficient of correlation between residuals of BMR and of organ mass (see text for details). P_2 is the significance level of this correlation.

incubate eggs during late spring, they are exposed to full sun and sit on a soil surface that reaches maximum temperatures exceeding 65 °C (B. I. Tieleman and J. B. Williams, unpublished data). There is no free-standing water available for drinking in Mahazat, except for short periods after rains. The relative humidity in the area varies between 20 and 40 % in summer and between 40 and 80 % in winter.

The physiological responses of Houbara bustards to temperature are consistent with expectations for birds adapted to hot and arid environments. The RMR of captive-reared birds in summer was 261.4 kJ day^{-1}, 26 % below allometric predictions of BMR for a 1245 g bird (Tieleman and Williams, 2000). We found no significant differences in RMR between day and night, supporting the idea that desert birds have minimal heat production during the day. Unlike most birds, Houbara bustards had an upper critical T_a that markedly exceeded T_b; they maintained a stable RMR for 3 h at 55 °C. Few other species extend their thermoneutral zone to T_a values exceeding 50 °C. Heat-acclimated rock pigeons (*Columba livia*) reared in environmental chambers have an upper critical T_a of at least 60 °C, although non-acclimated birds have an upper critical T_a of 40 °C (Marder and Arieli, 1988). Among wild-caught desert species, Withers and Williams (1990) recorded an upper critical T_a of at least 50 °C for the spinifex pigeon *Geophaps plumifera*.

At 25 °C, TEWL of Houbara bustards averaged 25.8 g day^{-1}, 31 % below the allometric prediction (Williams, 1996), whereas at 45 °C their TEWL was 140.3 g day^{-1}, 20 % below that predicted (Tieleman and Williams, 1999). Low rates of TEWL would be beneficial to birds in deserts, because of the lack of drinking water. However, mechanisms that reduce TEWL may compromise the capability for evaporative cooling and may be feasible only when alternative avenues for heat dissipation are well developed (Williams and Tieleman, 2001).

When T_a exceeded T_b, the dry heat transfer coefficient of Houbara bustards decreased, a finding supporting the prediction that birds should minimize heat gain by convection, conduction and radiation from the environment at high T_a (Hinds and Calder, 1973; Weathers and Schoenbaechler, 1976; Tieleman and Williams, 1999). At high T_a, Houbara bustards were apparently not able to decrease h to the minimal values achievable at T_a values below the thermoneutral zone. Because h is determined not only by ptiloerection but also by vasodilation in the dermal bed, h at high T_a may be a compromise between minimizing dry heat gain and maintaining cutaneous water loss ability that might represent an important avenue for evaporative cooling at these T_a values (Marder and Arieli, 1988; Menon et al., 1989, 1996).

The apparently efficient mechanisms for evaporative cooling and dry heat loss of Houbara bustards led to remarkably constant low T_b values when the birds were exposed to high T_a values. When Houbara bustards were exposed to 45 °C for 3 h, T_b was on average 0.9 °C higher than at 25 °C for the same time period. This finding lends support to the idea that larger birds may not save water when hyperthermic during chronic episodes of high T_a (Tieleman and Williams, 1999).

Seasonal variation in captive-bred birds

Among captive-bred Houbara bustards, RMR differed significantly between seasons. For a Houbara bustard of 1300 g at 35 °C, RMR averaged 243 kJ day^{-1} during summer and 299 kJ day^{-1} during winter, 33 % and 18 % below allometric predictions, respectively (Tieleman and Williams, 2000). RMR in winter was 23 % higher than in summer. TEWL at 35 °C averaged 32.7 g day^{-1} in summer and 47.9 g day^{-1} in winter, a significant increase of 46 %, but TEWL at 50 °C did not differ between seasons. Although the increase in TEWL may be partly due to increased ventilation rates associated with the higher RMR in winter compared with summer, the percentage increase is larger in TEWL than in RMR, and it is likely that other factors are involved. The

reduction of TEWL in summer may require structural changes in the skin that might involve the transport of lipids from intra- to extracellular spaces and *vice versa* (Menon et al., 1996) or may result from differences in neurological processes that might be involved in regulating vapor diffusion through bird skin (Arieli et al., 2000).

Captive-bred versus *wild-born Houbara bustards*

The physiological phenotypes of wild-caught and captive-reared Houbara bustards with similar genetic backgrounds (Seddon et al., 1995) differed with respect to RMR, TEWL and T_b at 35 °C, but revealed no difference in response to exposure to 50 °C. The RMR of a 1300 g bird from the captive breeding program was 17 % lower than the RMR from a wild-caught individual (Fig. 3). The latter had an estimated RMR of 358 kJ day^{-1}, only 2 % below allometric predictions (Tieleman and Williams, 2000). Similarly, TEWL at 35 °C was 28 % lower in captive-reared birds (47.9 g day^{-1}) than in birds from wild populations (66.3 g day^{-1}).

The identical physiological responses to exposure to 50 °C suggested that captive-reared and wild-born birds both have similar abilities to cope with high T_a values. However, the difference in RMR at 35 °C indicated that the physiology does differ between these groups of birds. Differences in metabolic rate could, at least in part, be accounted for by differences in size of the metabolically active organs of the digestive system (proventriculus, stomach, intestine and liver) and the pectoral muscles, which were larger in birds from wild populations (Table 1). Larger organs may have resulted in higher rates of metabolism. Because previous studies found a significant effect of kidney and heart mass on BMR (Daan et al., 1990), we explored whether any of the organs contributed disproportionately to RMR, but found no significant correlations in our analysis of residuals (Table 2). The low RMR of captive-bred birds could have consequences for their aerobic performance once these individuals are released into the wild. It is often suggested that a link exists between resting and maximum levels of oxygen consumption (Bennett and Ruben, 1979; Hayes and Garland, 1995; Chappell et al., 1999). This effect on the physiological performance of released animals could have consequences for their ability to escape from predators or to migrate when local conditions are poor.

The observed physiological differences between the wild-born and captive-reared phenotypes might be due to different conditions during development. In other studies, periods of a few days or weeks have been sufficient for acclimation to occur (Piersma and Lindström, 1997; Williams and Tieleman, 2000). In the present study, the primary difference between the captive-bred and wild-born birds is probably due to differences in their environment during chick growth. As chicks, captive-reared birds had access to food and water *ad libitum*, and locomotion was minimized as a result of living in outdoor aviaries. Houbara bustard chicks in the wild travel large distances as they follow the female parent in search of food and thereafter, as adults, rely far more on locomotion than do their captive-reared counterparts. However, to gain insight into the flexibility and reversibility of variables such as BMR, captive-bred birds must be studied before and after their release into the wild. Such a study could reveal whether captive-reared birds are able to adjust their physiology to the same metabolic rates as birds from wild populations.

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