

The Role of the Nasal Passages in the Water Economy of Crested Larks and Desert Larks

B. Irene Tieleman^{1,*}

Joseph B. Williams²

Gilead Michaeli³

Berry Pinshow³

¹Zoological Laboratory, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands; ²Department of Zoology, Ohio State University, 1735 Neil Avenue, Columbus, Ohio 43210; ³Mitrani Center for Desert Ecology, Blaustein Institute for Desert Research and Department of Life Sciences, Ben-Gurion University, Midreshet Ben-Gurion 84990, Israel

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ABSTRACT

Condensation of water vapor in the exhaled air stream as it passes over previously cooled membranes of the nasopharynx is thought to be a mechanism that reduces respiratory water loss in mammals and birds. Such a mechanism could be important in the overall water economy of these vertebrates, especially those species occupying desert habitats. However, this hypothesis was originally based on measurements of the temperature of exhaled air (T_{ex}), which provides an estimate of water recovered from exhaled air as a proportion of water added on inhalation but does not yield a quantitative measure of the reduction in total evaporative water loss (TEWL). In this study, we experimentally occluded the nares of crested larks (*Galerida cristata*), a cosmopolitan species, and desert larks (*Ammomanes deserti*), a species restricted to arid habitats, to test the hypothesis that countercurrent heat exchange in the nasal passages reduces TEWL. T_{ex} of crested larks increased linearly with air temperature, (T_a): $T_{\text{ex}} = 8.93 + 0.793 \times T_a$. Following Schmidt-Nielsen and based on measurements of T_{ex} , we predicted that crested larks would recover 69%, 49%, 23%, and -5% of the water added to the inhaled air at T_a 's of 15°, 25°, 35°, and 45°C, respectively. However, with the nares occluded, crested larks increased TEWL by only 27%, 10%, and 6% at

T_a 's of 15°, 25°, and 35°C, respectively. At $T_a = 45^\circ\text{C}$, TEWL of the crested lark was not affected by blocking the nares. In contrast to our expectation, occluding the nares of desert larks did not affect their TEWL at any T_a .

Introduction

In deserts, places characterized by high ambient temperatures (T_a) and scarcity of drinking water (Louw and Seely 1982), natural selection may have favored species that minimize evaporative water loss, leading to a frugal water economy. Williams (1996) collated data from 102 species and found that total evaporative water loss (TEWL), the sum of respiratory and cutaneous water losses, was lower in desert birds compared with nondesert species at the thermally unstressful T_a of 25°C. This finding supported the hypothesis that natural selection has equipped desert birds with specific adaptations that reduce their TEWL, but the mechanisms that produce this result remain unclear.

Several processes have been suggested to contribute to decreasing evaporative water loss in birds, especially in desert species: hyperthermia (Calder and King 1974; Weathers 1981; Dawson 1984; Withers and Williams 1990), an increase in the lipid content of the skin (Menon et al. 1989), and a reduction in basal metabolic rates (Dawson 1984). A fourth mechanism, temporal countercurrent heat exchange in the nasal passages of some species, can ostensibly recover significant quantities of water from the exhaled air stream, thus lowering respiratory evaporative water loss (REWL; Jackson and Schmidt-Nielsen 1964; Schmidt-Nielsen et al. 1970; Berger et al. 1971; Murrish 1973).

Temporal countercurrent heat exchange in the nasal passages affects the temperature of the exhaled air (T_{ex}), which determines the water-vapor density, assuming that exhaled air is saturated with water vapor. When air is inhaled, its temperature rises to that of T_b , and the air is saturated with water vapor from the respiratory passages and lungs. Convective heat exchange and evaporation of water in the nasal passages during inhalation presumably cool the associated membranes, and on exhalation, the air is cooled by these nasal surfaces, with the result that water condenses on them. Measurements of T_{ex} and

*To whom correspondence should be addressed; e-mail: tieleman@biol.rug.nl.

T_a allow estimates of the amount of water that is recovered from the exhaled air stream based on the amount of water that is added to the air on inhalation. Influenced by variation in T_b , T_a , and evaporative processes throughout the entire respiratory system, measurement of T_{ex} does not directly assess the effect of the nasal passages on reducing the water content of exhaled air.

It has been argued that countercurrent heat exchange in the nasal passages plays an important role in water recovery in mammals (Jackson and Schmidt-Nielsen 1964; Getz 1968; Schmidt-Nielsen et al. 1970; Collins et al. 1971), reptiles (Murrish and Schmidt-Nielsen 1970), and birds (Schmidt-Nielsen et al. 1970; Berger et al. 1971; Murrish 1973). Schmidt-Nielsen (1981) proposed that countercurrent heat exchange in the nasal passages is an adaptation to arid environments and that desert animals should have more complex nasal turbinates that allow cooling of T_{ex} to temperatures below those of nondesert species, resulting in a larger reduction in REWL in desert animals. However, to date, no one has proffered data to support such an idea.

By measuring TEWL and assuming that cutaneous evaporative water loss (CEWL) was constant, Hillenius (1992) showed for five species of small mammals that complex nasal turbinates reduced REWL. When animals were forced to breathe orally, REWL was increased by 36% to 143% over that of control animals using nasopharyngeal breathing at a T_a of 15°C. On the basis of the finding that little difference exists in the cooling of expired air between desert and nondesert species, Hillenius suggested that complex turbinates did not evolve as an adaptation to desert conditions but, rather, as a water recovery mechanism important for all mammals.

Given the differences in anatomical design between the taxa (Bang 1971), it is not clear that studies on water recovery in the noses of mammals can be extrapolated to birds. For birds, a direct determination of the amount of water recovered by countercurrent heat exchange in the nasal passages has not been made. However, the presence of countercurrent heat exchange in combination with complex nasal turbinates, similar to those in mammals, has led to the notion that this process significantly reduces REWL in birds as well (Schmidt-Nielsen et al. 1970; Berger et al. 1971; Schmidt-Nielsen 1981; Hillenius 1992, 1994; Ruben 1996).

In this article, we tested the hypothesis that countercurrent heat exchange in the nasal passages reduces TEWL of crested larks (*Galerida cristata*) and desert larks (*Ammomanes deserti*) over a range of T_a 's. In addition, we compared direct measurements of recovery of REWL with predictions based on T_{ex} in crested larks. Crested larks occur over a wide range of both mesic and arid habitats, while desert larks are restricted to arid habitats, where drinking water is scarce (Shkedy and Safriel 1991, 1992). If water recovery in the nasal passages is an adaptation to environmental conditions, one might expect that

this mechanism is quantitatively more important in reducing the TEWL of desert larks than of crested larks.

Material and Methods

Animals

We captured crested larks in the kibbutz Sde Boqer, and desert larks near a permanent pool of water (En Avdat), both located in the Negev desert highlands, Israel, where both species are resident (Cramp 1988). The birds were transported to the Mirani Center for Desert Ecology, Midreshet Ben-Gurion, and housed in outdoor cages. They were provided with water and food ad lib., the latter consisting of mealworms, hard-boiled eggs, and millet. Mean body mass was 33 ± 1.3 g (\pm SD) for the crested larks ($n = 6$), and 19 ± 1.5 g (\pm SD) for the desert larks ($n = 6$). Birds were collected under permit of the Israel Nature Reserves Authority.

Temperature of Exhaled Air

In order to estimate the amount of water that is recovered from the exhaled air stream, as previous researchers have done, we measured T_{ex} in three crested larks, at T_a 's from 15° to 40°C. Birds were placed in a dark environmental chamber that maintained $T_a \pm 0.1^\circ\text{C}$. We situated the birds in a plastic holding device that had been fashioned from a plastic tube cut in half lengthwise, and covered them with plastic screening to restrict movement but to allow some freedom for plumage adjustments. We inserted a 48-gauge copper constantan thermocouple 2 mm into the nasal opening, using a rack and pinion device. After verifying with a magnifying glass that the thermocouple did not touch the nasal membranes, we taped the thermocouple wire to the bill. When a regular breathing pattern was achieved, we monitored the temperature cycle of inspired and expired air (20 readings s^{-1}) during at least 3 min with an A/D board and computer software (Strawberry Tree-Workbench PC for Windows 2.60). The time constant of the thermocouple was 0.2 s. T_{ex} typically plateaued, indicating that equilibrium was reached. For a measurement of T_{ex} , we averaged values of 10 consecutive plateaus. To measure T_{ex} with the nares occluded, we inserted a small piece of cotton in the nasal opening, through which we inserted the thermocouple. After taping the thermocouple to the bill, we occluded the nares with plastic dental resin (see below).

Experimental Treatment to Prevent Air Flow through the Nares

To determine the role of the nasal passages in the water economy of the larks, we measured evaporative water loss both when the external nares were open and normal nasopharyngeal breathing was possible, and when the external nares were experimentally closed, forcing the bird to breathe orally. Air flow

through the nasal passages was prevented by occluding the nares with plastic dental resin (Kerr Heavy Bodied Permlastic) that was applied as a mixture of base and catalyst. This viscous paste would flow around the opening of the nares and within 5 min would harden, forming an airtight seal. The resin could easily be removed after a measurement, without damage to the bird. We assumed that CEWL was not affected by the treatment, and measured TEWL, the phenotypic trait that could affect survivorship. In contrast with measurements of REWL, TEWL could be assessed without restraining the animals.

Measurements of TEWL and Oxygen Consumption

We constructed two metabolic chambers, one from a 5-L metal can (crested larks), the other from a 3-L metal can (desert larks). The inner surface of each chamber was coated with flat black paint to reduce the reflectance of long-wave radiation (Porter 1969). Each day before measurements, we checked the lids of the chambers for leaks with soap solution. The birds were placed in the chamber on wire mesh, above a layer of mineral oil that trapped excrement. We placed the metabolic chamber in an environmental cabinet that had the capability of controlling T_a to within $\pm 0.1^\circ\text{C}$.

Rates of TEWL and oxygen consumption (\dot{V}_{O_2}) were determined for birds that had been without food during at least 3 h before the measurements. Dry, CO_2 -free outside air was pulled through the metabolic chamber with a Gast pump at a constant rate, regulated using a mass-flow controller (Brooks model 5810) that was calibrated with a bubble meter (Levy 1964). We varied the flow rate between 1180 and 1840 mL min^{-1} , depending on species and T_a , to maintain relative humidity in the metabolic chamber below 15%. Excurrent air was passed through a dew-point hygrometer (General Eastern model Hygro M4) and then routed through a column of drierite to remove water vapor. The dry air flowed through the mass-flow controller before passage through columns of drierite, ascarite, drierite, and an O_2 analyzer (Taylor Servomex model 1400B). Before each measurement, we calibrated the O_2 analyzer with dry CO_2 -free outside air. We recorded dew point and O_2 concentration of the excurrent air continuously with a Campbell 21X data logger and PC208W software, and graphed the results in real time. Visual inspection of our results allowed us to determine when steady state conditions were achieved. The birds were usually quiet in the metabolism chamber and often were asleep when we opened the lid. Typically, equilibration took about 90 min, after which we averaged dew point and O_2 concentration of the excurrent air stream over a minimum of 10 min for our measurements. Water-vapor densities of the incurrent and excurrent air were calculated from measurements of dew point using equations in the General Eastern's *Humidity Handbook* (1993). \dot{V}_{O_2} was calculated with equation 4b of Withers (1977).

The initial metabolic trials consisted of three consecutive

measurements, 90 min each, on the same individual, either with the nares open, closed, and then open or with the nares closed, open, and then closed. The initial treatment (nares open or closed) was alternated. When we were convinced that the first and last measurements gave statistically indistinguishable results, we reduced the metabolic trials to two runs, with the nares open and then closed or vice versa. Metabolic trials were performed during both day and night but, because our measurements were paired, the time when measurements were made should not affect our comparisons. Body mass was determined before and after the metabolic trial using an Ohaus top-loading balance (model CT1200-S). Mass changes during the trials at lower T_a 's were small, increasing to 2.9 ± 0.39 g ($n = 6$) for crested larks and 1.8 ± 0.32 g ($n = 3$) for desert larks at $T_a = 45^\circ\text{C}$.

Body Temperature

To determine whether oral breathing affected T_b before and immediately after each measurement, we assessed T_b with a 36-gauge thermocouple attached to an Omega thermometer (model 450 ATT). Our thermometer was calibrated against a standard mercury-in-glass thermometer (Taylor) with a certificate of calibration traceable to the National Institute for Standards and Technology. If there was a significant increase in T_b during a measurement, we calculated the rate of heat storage as $C(dT_b/dt)$ (J h^{-1}). Here, C is the specific heat of the bird in $\text{J }^\circ\text{C}^{-1}$, calculated as the product of body mass and the specific heat of tissue, $3.35 \text{ J g}^{-1} \text{ }^\circ\text{C}^{-1}$ (Calder and King 1974; Schmidt-Nielsen 1983), and dT_b/dt is the change in T_b with time ($^\circ\text{C h}^{-1}$).

Measurements of REWL

To measure the REWL of the crested larks, we constructed a plastic mask out of the barrel of a syringe, and held it to the bird's face with a velcro band behind its head. The bird was restrained as described previously before it was placed in our environmental chamber. The birds quieted quickly and appeared calm throughout the measurements. Air was pulled through the mask with a Gast pump at a flow rate of $351 \pm 1.2 \text{ mL min}^{-1}$. A rotameter (Brooks model R2 15D) that was calibrated with a bubble meter (Levy 1964) maintained a constant flow rate. Excurrent air passed through an EG&G Dew-point Hygrometer (model 660). Dew-point measurements were recorded every 10 s with our data acquisition software. Note that equilibration took less time (usually < 5 min) than for the TEWL measurements because the mask method does not require the washout of a large volume of air as does a metabolism chamber.

During a trial, dew-point measurements of the air in the environmental chamber determined the water-vapor density of the air flowing into the mask. These baseline measurements

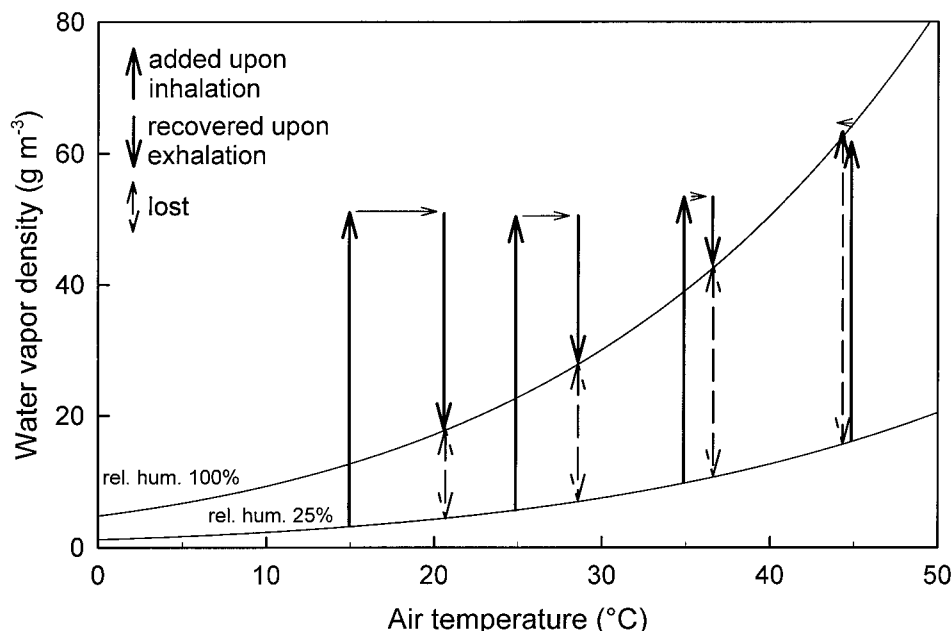


Figure 1. The amount of water vapor added to the air on inhalation (solid arrows pointing upward), the amount recovered on exhalation (solid arrows pointing downward), and the amount of water vapor lost on exhalation (dashed arrows). The temperature of the inhaled air is indicated by the location of the upward arrows and that of the corresponding exhaled air by the position of the downward arrows.

were alternated with dew-point measurements of the exhaled respiratory air. After an equilibration period of about 15 min, we averaged the data over a 5-min interval for a dew-point measurement. At T_a 's of 15°, 25°, and 35°C, a trial consisted of two consecutive measurements of the first treatment (either open or closed nares) followed by two measurements of the other treatment (either closed or open nares). At $T_a = 45^\circ\text{C}$, a trial consisted of one measurement of the first treatment (open or closed nares), followed by one measurement of the second treatment (closed or open nares). The maximal relative humidities in the environmental chamber during the measurements were 56% ($T_a = 15^\circ\text{C}$), 39% ($T_a = 25^\circ\text{C}$), 25% ($T_a = 35^\circ\text{C}$), and 18% ($T_a = 45^\circ\text{C}$).

Experimental Design and Statistical Analyses

Our experimental design was counterbalanced with repeated measurements on the same individuals (Stevens 1992). To determine the role of the nasal passages at the different T_a 's, we used a repeated-measures ANOVA with individual birds as the between factor, temperature as the within factor, and nares treatment nested within temperature (Stevens 1992). If missing values left the experimental design incomplete, we used the difference between closed and open nares as a dependent variable in a mixed-model ANOVA with temperature as a fixed effect and individual birds as a random effect (Zar 1984). When temperature significantly affected the difference between closed

and open nares, we calculated a priori contrasts of the type difference. Computations were performed with the procedures, general linear models–repeated (GLM–repeated) measures or GLM–general factorial, in SPSS 7.5 for Windows (SPSS, Chicago). Values are presented as mean \pm 1 SD.

Results

Amount of Water Recovered by Cooling Exhaled Air

In the crested larks that were breathing normally, T_{ex} increased linearly with T_a : $T_{\text{ex}} = 8.93 + 0.793 \times T_a$ ($\text{SE}_{\text{slope}} = 0.045$, $n = 14$, $r^2 = 0.96$). With nares occluded, T_{ex} of the larks was 24.7°C at $T_a = 15^\circ\text{C}$, 30.8°C at $T_a = 25.3^\circ\text{C}$, and 37.7°C at $T_a = 35.7^\circ\text{C}$.

The estimated amount of water recovered by the cooling of exhaled air as a proportion of the water added on inhalation decreased with increasing T_a in the crested lark (Fig. 1). We emphasize that this predicted decrease in water recovery is the result of cooling processes in the complete respiratory system, which includes the upper respiratory tract and the nasal passages, and that it is not equivalent to the actual reduction in TEWL that results from countercurrent heat exchange in the nasal passages only. To facilitate comparison with the calculations for the cactus wren (*Campylorhynchus brunneicapillum*), we assumed that the relative humidity of the inhaled air was 25%, analogous to Schmidt-Nielsen et al. (1970). The solid arrows pointing upward in Figure 1, positioned at the corre-

sponding temperature of the inhaled air, indicate the amount of water added to the inhaled air as it is brought to saturation at T_b . The solid arrows pointing down, placed at the corresponding T_{ex} , indicate the amount of water recovered as a result of the cooling of the air. The predicted amount of water recovered decreased from 69% at $T_a = 15^\circ\text{C}$ to -5% at $T_a = 45^\circ\text{C}$.

The Effect of Breathing through the Nares on TEWL

Crested Larks. With their nares occluded, crested larks lost more water by evaporation than when they were breathing through open nares (Fig. 2A). The increase was 27%, 10%, and 6% at T_a 's of 15°, 25°, and 35°C, respectively (factor $F_{\text{temperature}}(15,3) = 368.1$, $P < 0.001$, $F_{\text{nares}}(5,1) = 0.14$, $P = 0.73$, $F_{\text{interaction}}(15,3) = 7.87$, $P = 0.002$). At $T_a = 45^\circ\text{C}$, blockage of the nares did not affect TEWL (contrast $t = 3.06$, $P = 0.03$). Note that, because the interaction term in this ANOVA was significant, we performed a contrast analysis to test at which T_a 's the difference in TEWL between closed and open nares treatments was significant. The latter P -value reported here signifies that TEWL was higher for the closed nares treatments at T_a 's of 15°, 25°, and 35°C but not at $T_a = 45^\circ\text{C}$. In addition, inspection of the standard deviations of our groups might lead one to conclude that no differences existed at any temperature. However, we point out that our statistical tests are based on paired comparisons rather than overall means.

The increase in TEWL could have been the effect of increased ventilation resulting from elevated metabolism if the birds were stressed by occluding the nares. When we compared the effect of the treatments on oxygen consumption (Table 1), it did not differ between treatments ($F_{\text{nares}}(5,1) = 0.08$, $P = 0.79$, $F_{\text{interaction}}(15,3) = 2.04$, $P = 0.15$). We concluded that blocking the nares did not cause increased ventilation rates compared with the control measurements with open nares.

Desert Larks. Blocking the nares did not significantly affect TEWL or \dot{V}_{O_2} in the desert larks (Fig. 2B; Table 1). The difference in TEWL and \dot{V}_{O_2} between birds with closed and open nares was not significant (TEWL: $F_{1,4,3} = 0.004$, $P = 0.95$; \dot{V}_{O_2} : $F_{1,4,1} = 0.08$, $P = 0.79$) and was not affected by temperature (TEWL: $F_{3,9} = 0.70$, $P = 0.58$; \dot{V}_{O_2} : $F_{3,9} = 0.41$, $P = 0.75$).

By looking at Figure 2, one might think that the increase in TEWL when the nares are occluded, expressed as proportion of TEWL, is equal for crested larks and desert larks. However, when expressed in this relative measure, crested larks increase their TEWL more than desert larks as a result of occluding the nares. At $T_a = 15^\circ\text{C}$, TEWL was increased by 27% for crested larks and by 10% for desert larks.

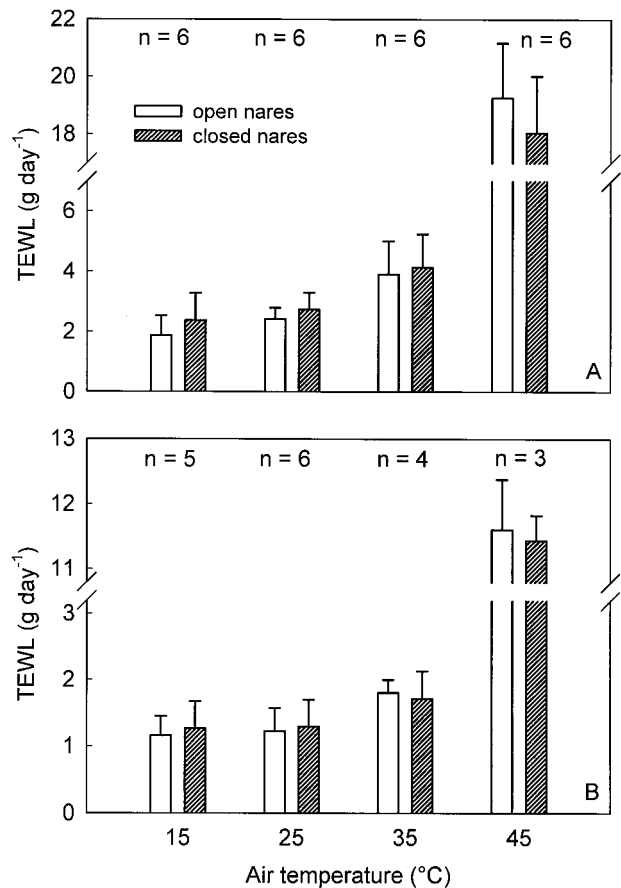


Figure 2. A, Total evaporative water loss (TEWL) of crested larks measured with open nares (unfilled bars) and with closed nares (filled bars) at various T_a 's. The error bars represent 1 SD. B, TEWL of desert larks measured with open nares (unfilled bars) and with closed nares (filled bars) at various T_a 's. The error bars represent 1 SD. Note the difference in scale on the Y-axes.

The Effect of Breathing through the Nares on REWL

Closing the nares to prevent countercurrent heat exchange in the nasal turbinates significantly increased REWL in the crested larks (Fig. 3). The difference in REWL between birds with closed and open nares was significant ($F_{1,5,3} = 26.01$, $P = 0.003$) and was not affected by temperature ($F_{3,14} = 0.38$, $P = 0.77$). When breathing through their open beaks, REWL of crested larks was greater than in control animals using nasopharyngeal breathing by 38%, 47%, 29%, and 2% at T_a 's of 15°, 25°, 35°, and 45°C, respectively (Fig. 3).

Respiratory versus CEWL

The contribution of REWL to TEWL in crested larks decreased with increasing T_a from 59% at $T_a = 15^\circ\text{C}$ to 35% at $T_a = 45^\circ\text{C}$. The crested larks relied increasingly on CEWL for evap-

Table 1: Oxygen consumption (mL min^{-1}) of crested larks and desert larks at various T_a 's

	15°C		25°C		35°C		45°C	
	Mean \pm SD	<i>n</i>	Mean \pm SD	<i>n</i>	Mean \pm SD	<i>n</i>	Mean \pm SD	<i>n</i>
Crested lark:								
Nares open	1.93 \pm .46	6	1.18 \pm .17	6	1.28 \pm .23	6	1.88 \pm .42	6
Nares closed	1.95 \pm .40	6	1.22 \pm .18	6	1.34 \pm .27	6	1.74 \pm .40	6
T_b	39.9 \pm .81	12	39.7 \pm .78	23	40.8 \pm .53	21	43.9 \pm .60	12
Desert lark:								
Nares open	1.46 \pm .09	5	.87 \pm .22	6	.69 \pm .05	4	1.05 \pm .42	3
Nares closed	1.46 \pm .26	5	.81 \pm .20	6	.65 \pm .10	4	1.10 \pm .42	3
T_b	39.8 \pm 1.59	10	38.9 \pm .92	11	41.1 \pm .70	8	44.2 \pm .54	8

orative cooling at higher T_a 's. REWL and TEWL were measured under different circumstances; therefore, the effects of closing the nares on REWL and TEWL are not statistically comparable. However, our estimate of the contribution of CEWL to TEWL is probably conservative because if restraint caused stress, REWL would have been higher in these birds.

Body Temperature

Treatment of the nares did not affect T_b in the crested larks (ANOVA $F_{1,8} = 0.1$, $P = 0.74$) and the desert larks (ANOVA $F_{1,6} = 3.7$, $P = 0.11$) at any T_a (crested lark: ANOVA $F_{3,32} = 0.3$, $P = 0.82$; desert lark: ANOVA $F_{3,9} = 3.0$, $P = 0.09$).

Crested Larks. Body temperature was relatively constant at T_a 's of 15° and 25°C and averaged $39.8^\circ \pm 0.79^\circ\text{C}$. T_b increased to 40.7°C at $T_a = 35^\circ\text{C}$ and to 43.9°C at $T_a = 45^\circ\text{C}$ (Table 1; ANOVA $F_{\text{temperature}}(3,59) = 111.1$, $P < 0.001$, contrast $P < 0.05$). At T_a 's of 15°, 25°, and 35°C, the birds maintained a stable T_b during the measurements, but at $T_a = 45^\circ\text{C}$, T_b increased significantly with time, at a rate of $0.53^\circ \pm 0.183^\circ\text{C h}^{-1}$ (ANOVA $F_{\text{temperature}}(3,32) = 9.3$, $P < 0.001$, contrast $P < 0.05$). This continuous increase in T_b corresponds to a rate of heat storage of $59 \pm 19.9 \text{ J h}^{-1}$.

Desert Larks. Desert larks maintained a constant T_b of $39.3^\circ \pm 1.32^\circ\text{C}$ at T_a 's of 15° and 25°C, and significantly increased their T_b to 41.1° at $T_a = 35^\circ\text{C}$ and to 44.2°C at $T_a = 45^\circ\text{C}$ (Table 1; ANOVA $F_{\text{temperature}}(3,28) = 41.5$, $P < 0.001$, contrast $P < 0.05$). Desert larks maintained a stable T_b during the measurements at all T_a 's (ANOVA $F_{\text{temperature}}(3,9) = 0.94$, $P = 0.46$).

Discussion

The Role of the Nasal Passages in Reducing TEWL of Crested Larks

Following the protocol of Schmidt-Nielsen et al. (1970) and measuring T_{ex} , we predicted that crested larks would recover

69% of the water that was added to the air on inhalation as a result of expiring air with a temperature of 21°C , at a T_a of 15°C . This estimate is close to the recovery of 74% of the water added on inhalation reported for the cactus wren (Schmidt-Nielsen et al. 1970). These calculations, however, do not reveal the relative importance of the nasal passages in reducing REWL or TEWL. A direct test of the hypothesis that the nasal passages reduce evaporative water loss in the crested lark showed that experimentally closing the nares increased TEWL by 27% and REWL by 38% at $T_a = 15^\circ\text{C}$. These comparisons demonstrate that direct measurement is the only way to ascertain the effect of nasal passages on the reduction of REWL and TEWL.

Further, the method of Schmidt-Nielsen et al. (1970) predicted that water recovery decreases with increasing T_a , a result of a smaller difference between T_{ex} and T_b at higher T_a 's (Fig. 1). Our experimental test in which we occluded the nares in crested larks supported this prediction: at $T_a = 15^\circ\text{C}$, TEWL was increased by 27% compared with the control measurements, and at a T_a of 45°C , the difference had declined to nil. At high T_a 's, one might expect that water recovery in the nasal passages would be minimized because T_{ex} is near T_b and because birds were panting.

TEWL at 25°C and 45°C

To test the hypothesis that the desert lark, a species that is restricted to drier habitats than the crested lark, has a lower TEWL, we compared the TEWL of both species with an allometric equation for the TEWL of desert birds at $T_a = 25^\circ\text{C}$ (Williams 1996). TEWL of the desert lark was 77% of that predicted for desert birds with a similar body mass, while TEWL of the crested lark was 104% of the value predicted for desert birds of the same size. To statistically compare TEWL between species, we divided TEWL by body mass^{0.75}, the exponent of the equation that relates TEWL to body mass in desert birds (Williams 1996). After adjusting for body mass, desert larks had a significantly lower TEWL than crested larks at a T_a of 25°C ($t = 2.29$, $df = 10$, $P < 0.05$).

At $T_a = 45^\circ\text{C}$, the TEWL of the desert lark was 69% of the

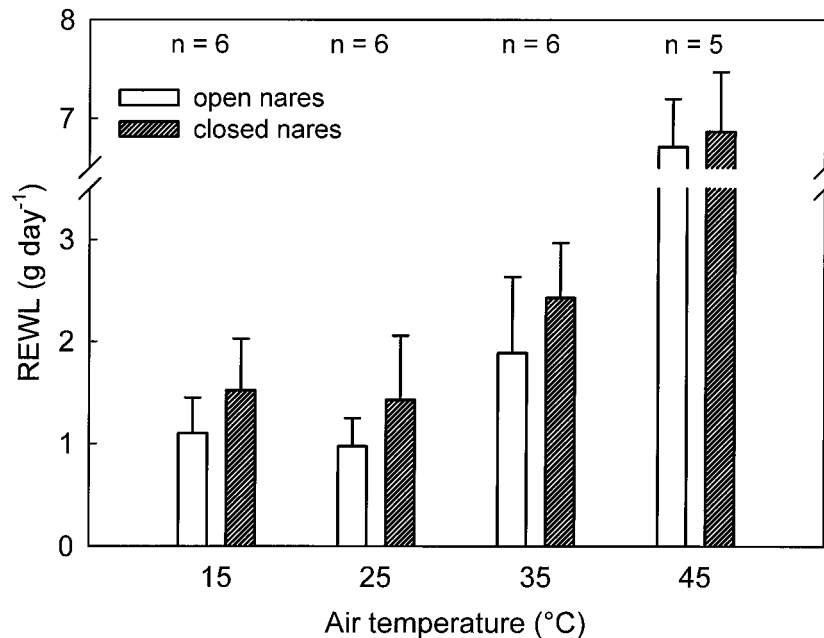


Figure 3. Respiratory evaporative water loss (REWL) of crested larks measured with open nares (*unfilled bars*) and with closed nares (*filled bars*) at various T_a 's. The error bars represent 1 SD.

predicted TEWL based on an allometric equation for TEWL at $T_a = 45^\circ\text{C}$ (Tieleman and Williams 1999). At this T_a , the TEWL of the crested lark was 87% of the value predicted for a similar-sized bird. After correcting for body mass by dividing TEWL by body mass^{0.56}, the exponent of the allometric equation found by Tieleman and Williams, desert larks had a significantly lower TEWL than crested larks at $T_a = 45^\circ\text{C}$ ($t = 2.68$, $df = 7$, $P = 0.03$).

Crested Larks and Desert Larks Compared

Desert larks had lower mass-specific rates of TEWL than crested larks, supporting the hypothesis that desert larks are better adapted to arid habitats than crested larks. If complex nasal turbinates are an adaptation to environmental conditions, as hypothesized by Schmidt-Nielsen (1981), one would expect that desert larks possess turbinates that are more complex than those of crested larks, with the result that desert larks might reduce their TEWL more. Contra this prediction, we were surprised to find that occluding the nares does not affect TEWL in desert larks, while it results in an increase in TEWL in crested larks, at least at the lower T_a 's. Therefore, this study does not support the hypothesis that water recovery in the nasal passages has evolved more extensively in desert species in response to environmental conditions.

Hillenius (1994) suggested that the shape of the bill deter-

mines the complexity of the nasal cavity and could affect the olfactory and cooling functions of the nasal turbinates in birds. We found a larger reduction in TEWL in crested larks, which have a significantly longer bill (18.4 ± 1.2 mm) than desert larks (15.1 ± 1.1 mm) ($t = 4.4$, $df = 8$, $P = 0.002$). A positive correlation between bill length and the cooling capacity of the nasal turbinates might explain the observed difference in reducing TEWL between the two species, a hypothesis in need of testing.

Temporal Countercurrent Heat Exchange in the Nasal Passages

Schmidt-Nielsen and his coworkers suggested that temporal countercurrent heat exchange in the nasal passages explains the low T_{ex} found in many animals (Jackson and Schmidt-Nielsen 1964; Getz 1968; Murrish and Schmidt-Nielsen 1970; Schmidt-Nielsen et al. 1970; Berger et al. 1971; Collins et al. 1971; Murrish 1973; Schmidt-Nielsen 1981). This hypothesis predicts that, when airflow through the nasal passages is prevented, the nasal membranes would not function as a heat exchanger and T_{ex} would be higher. Our measurements of T_{ex} made with the nares occluded give values only slightly higher than those determined when the nares were open. We suggest the alternative hypothesis that in birds T_{ex} is determined by the temperature of the un-insulated bill and surrounding tissue, which probably closely

follow T_a , instead of by countercurrent heat exchange as a result of evaporative processes at the nasal membranes.

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